Research Article

Indiana Bats in the Midwest: The Importance of Hydric Habitats

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Abstract

*The endangered Indiana bat (*Myotis sodalis*) requires very specific habitats to provide necessary day-roosting and foraging resources during the spring and summer months throughout its distribution in the eastern United States. Maternity colonies of Indiana bats are almost always found under the exfoliating bark of dead or dying trees. Furthermore, they switch frequently among multiple roosts within large but still somewhat local areas. Therefore, habitats with large numbers of snags or decadent trees are needed to support Indiana bat maternity colonies. These habitats arise naturally and anthropogenically in a variety of ways. However, these conditions often are rare relative to other forest conditions. In the Midwest, such as southern and central Illinois, USA, maternity colonies are more commonly associated with bottomland, riparian, wetland, or other hydric forest types. It is unclear if this occurs because areas with large numbers of snags are more common in these habitats, if maternity colonies prefer these habitats for their foraging resources, or if decades of intensive agriculture have restricted colonies to these habitats. Because many large maternity colonies have been observed in hydric habitats of the Midwest, I hypothesize that these are preferred maternity habitats. Moreover, very few large maternity colonies have been located using upland forest habitats within the region. Elsewhere, such as in the central and southern Appalachians, maternity colonies have been located in upland areas where bottomland habitats are less extensive. However, these colonies are usually characterized by small numbers of bats and ephemeral persistence. Future conservation efforts for the Indiana bat should focus on protecting and regenerating bottomland habitats along the major river systems of the midwestern United States. It is within these bottomland and riparian habitats that future large and long-term maternity colonies will be established.* (JOURNAL OF WILDLIFE MANAGEMENT 70(5):1185–1190; 2006)

Key words

bottomlands, habitat use, hydric habitats, Indiana bats, landscapes, Myotis sodalis*, riparian.*

Recent advances in radiotracking technology for wildlife applications have resulted in an increase in research and knowledge about the natural history of the endangered Indiana bat (*Myotis sodalis*). Since the late 1980s and early 1990s, when radiotransmitters became small enough to attach to small vespertilionid bats, the number of articles on this topic in peer-reviewed journals has increased dramatically. Additionally, increased use of ultrasonic acoustical detectors, such as the frequency-division Anabat II system (Titley Electronics, Ballina, Australia), has added to the increase in research, particularly with regard to foraging habitat relationships (Owen et al. 2004, Ford et al. 2005). Perhaps the greatest increase in knowledge of Indiana bat natural history in recent years has come in our understanding of summer ecology. While the increase in research has not led to a complete understanding of the ecology of the species, it has documented a few underlying trends that seem to transcend most research on this species.

Female Indiana bats leave hibernation sites throughout the Midwest and Northeast in spring and travel to summer maternity grounds (U.S. Fish and Wildlife Service 1999, Menzel et al. 2001, Britzke et al. 2006). These bats may travel long distances to suitable areas (Kurta and Murry 2002). At maternity grounds, females form large maternity colonies of up to 100 or more individuals in the core of their range, or smaller colonies of 40 or less in the eastern portion of the range (Menzel et al. 2001, Britzke et al. 2003, 2006). These colonies are most often found under the exfoliating bark of dead or dying trees (Menzel et al. 2001). While some trees may make better roosts than others, there is probably not a definitive list of usable tree species, as use changes with geography and habitat type (Carter and Feldhamer 2005*a*). It is likely that the physical characteristics of a tree are as, if not more, important than the actual species of tree (Callahan et al. 1997, Britzke et al. 2003). Some of the physical characteristics, common among studies of roost trees include the presence of exfoliating bark, large diameter, and high levels of solar exposure (Kurta 2005). Additionally, female Indiana bats switch roosts as often as every few days to a week, and a maternity colony uses many trees within a season (Menzel et al. 2001). These trees may be used multiple times and over multiple years, as long as they remain standing and retain suitable exfoliating bark (Menzel et al. 2001, Kurta and Murray 2002, Britzke et al. 2003, Whitaker et al. 2004).

Early authors suggested that riparian forests were the preferred habitat, but that habitat use varies across the range of the species (Humphrey et al. 1977). This variation has led to a debate regarding the habitat requirements of maternity colonies. Kurta (2005) argues that the idea that Indiana bats are riparian specialists is no longer valid. While I agree that Indiana bat maternity colonies use other habitats besides riparian habitats, I also believe riparian or other hydric-type habitats (e.g., floodplains, bottomland, and wetlands) are critical for larger, long-term maternity colonies such as those seen in the Midwest. These larger, more permanent midwestern colonies may use a variety of habitats to acquire

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Table 1. Literature references for data on the habitat-type associations of Indiana bat maternity colonies organized by state, and the hypothesis that I examined using reference data.

State(s)	Reference	Hypothesis[a]
Illinois	Carter et al. 2002	I
	Carter and Feldhamer 2005*a,b*	II, III
	Gardner et al. 1991*a,b*	II, III
	Menzel et al. 2005	III
	Kurta et al. 1993*b*	II
Indiana	Sparks et al. 2005	I, III
	Ulrey et al. 2005	I
Kentucky	Kiser and Elliott 1996	III
Michigan	Kurta et al. 1993*a*	II
	Murray and Kurta 2004	III
Missouri	Callahan et al. 1997	II
New York/Vermont	Britzke et al. 2006	II
North Carolina/ Tennessee	Britzke et al. 2003	II
Pennsylvania	Butchkoski 2005	III
Region wide	Gardner and Cook 2002	I
West Virginia	Beverly and Gumbert 2005	II

[a] Habitat use of Indiana bat maternity colonies is the result of Hypothesis I: anthropogenic factors; Hypothesis II: the availability of, or preference for roosting resources; or Hypothesis III: the availability of or preference for foraging resources.

the resources they need, but hydric habitats are a consistent feature documented in all large, stable maternity colonies.

A review of the literature clearly shows that in the core of the species' range in the midwestern United States, the vast majority of studied colonies are larger and have persisted over multiple years (or at least greater than the length of the study) and, in all cases, the colony makes extensive use of hydric habitats (Menzel et al. 2001, 2005, Carter and Feldhamer 2005*a*, Sparks et al. 2005). Most of the maternity colonies located exclusively in upland situations have occurred in the Appalachians (Britzke et al. 2003, Beverly and Gumbert 2005, Watrous et al. 2006, C. Sanders, Environmental Inc., personal communication, W. M. Ford, United States Forest Service, personal communication), but these are small colonies that often seem to persist in a local area for only a few seasons. Thus, I argue the data from large, long-term colonies appears to consistently support the idea that Indiana bats do best when hydric habitats are available.

I used a literature review to explore 3 hypotheses for why large, stable maternity colonies of Indiana bats use in large part hydric habitats. First, that anthropogenic factors have forced these colonies to use these habitats; second, that availability of, or preference for, roosting resources has caused Indiana bats to focus on hydric habitats; and third, that availability of or preference for foraging resources has caused Indiana bats to favor hydric habitats.

Methods

Range-wide, large-scale habitat-use studies are difficult to perform because of the large amounts of time and resources required. Therefore, I used data from a variety of existing published and grey-literature sources (Table 1) to address why large, stable maternity colonies of Indiana bats use, in large part, hydric habitats.

Table 2. Proportion of bottomland and other (upland) forest types around Indiana bat maternity sites and of available forest types in Illinois and across the core range of the species.

	Bottomland	Other forest types
Maternity sites (IL)[a]	38.0%	20.7%
Available habitat state wide (IL)[a]	1.0%	5.0%
Available habitat in core range[b]	4.2%[c]	37.0%

[a] From Carter et al. 2002.
[b] From Gardner and Cook 2002.
[c] Bottomland defined as Oak–gum–cypress, Elm–ash–cottonwood, Maple–beech–birch, and water.

To examine the hypothesis that anthropogenic factors have driven Indiana bats to use hydric habitats, I used data from 2 sources. Carter et al. (2002) examined habitat use within Illinois. Habitats surrounding 78 maternity roosts were compared to the habitat characteristics around >5,000 random points from across the state. The second source (Gardner and Cook 2002) reported an analysis of the distribution of habitats occurring in counties with and without records of Indiana bat presence, from across the core range of the species. I also use anecdotal data from Sparks et al. (2005) and Ulrey et al. (2005), who examined foraging activity of Indiana bats within Indiana in a rural–urban interface.

To examine the hypothesis that roosting requirements have forced Indiana bats to use hydric habitats, I reviewed a variety of literature on roosting habits of Indiana bats (Table 1). Roost trees in all these studies were located using radiotelemetry, and the microhabitat and landscape characteristics were reported.

I used data from 7 sources to examine the third hypothesis that foraging habitat requirements have driven Indiana bats to use hydric habitats (Table 1). These studies examined foraging activity of Indiana bats directly (i.e., Carter and Feldhamer 2005*b*, Menzel et al. 2005, Sparks et al. 2005), while the other sources presented anecdotal information on foraging activity (e.g., Murry and Kurta 2004).

Results

Anthropogenic Forces

In my first hypothesis, I questioned whether anthropogenic changes in land use or land cover resulted in Indiana bats being forced into hydric habitats. Both the Carter et al. (2002) and Gardner and Cook (2002) studies clearly show that Indiana bats select areas with greater amounts of bottomland or hydric habitats than are available within Illinois or across the core range of the Indiana bat (Table 2). Recent work in Indiana has shown that the species appear to avoid areas of high human activity during foraging (Sparks et al. 2005). However, this does not explain why they do not use the large expanses of available upland forest habitats (Parker and Ruffner 2004). Throughout the species' range, other upland forest types make up a larger proportion of available forestland (Table 2), and yet Indiana bat maternity

Table 3. Proportions of used and available habitat for Indiana bats in Indiana, USA, at multiple scales from 2002. Habitats were placed in order of highest to lowest availability.[a]

Habitat	Total available[b]	95% home range[c]	Data points[d]
Agricultural land	0.309	0.501	0.378
Pasture	0.330	0.097	0.073
Urban[e]	0.196	0.067	0.057
Commercial	0.072	0.038	0.030
Parks	0.014	0.020	0.027
High-density residential	0.110	0.009	0.000
Woodlands	0.127	0.281	0.453
Low-density residential	0.030	0.045	0.035
Open water	0.009	0.009	0.005

[a] Table reproduced from Sparks et al. 2005.
[b] Total available habitat was determined by placing an 8.37-km buffer (farthest distance flown by any one bat) around each roost.
[c] Home ranges were determined by using 95% minimum convex polygons.
[d] Data points were estimated based on multi-azimuth triangulations.
[e] Urban habitats were segregated into subclasses for the coarse-scale analysis.

colonies are consistently found in bottomland and other hydric forest types. The influences of human-related activities cannot be significantly different between all bottomland and all upland-type habitats, therefore human influences cannot fully account for the disparities in habitat use.

Perhaps a low tolerance for human-related activities (e.g., lights, sound, buildings, cars) has caused Indiana bats to select bottomland habitats where human influences are less. However, there are many examples of Indiana bats using hydric habitats that are impacted by humans (e.g., Ulrey et al. 2005) and there are extensive upland forested areas, including wilderness areas on the Shawnee and Hoosier National Forests in southern Illinois and Indiana, USA, that are not heavily impacted by humans and where Indiana bat maternity colonies have not been documented.

Roosting Resources

In my second hypothesis, I examined the idea that there are more snags (i.e., roosting resources) in hydric habitats, resulting in the bats using these habitats because of limited roosting resources elsewhere throughout the range. While snags are often common in bottomland, riparian, and wetland-type habitats, upland forest habitats can have abundant or scarce snags depending on stand age, stand composition, and disturbance frequency (Mcgee et al. 1999, Moorman et al. 1999, Fan et al. 2003). Insects, fire, wind, and other factors can cause large amounts of dead or dying trees throughout eastern forests (McCullough et al. 1998, Ford et al. 1999, Negron et al. 2001, Mcnab et al. 2004, Conner and Saenz 2005). As with my first hypothesis, I expected to see habitat use of Indiana bats follow the availability of roosting resources. Yet this was not observed. In some cases, portions of colonies were found roosting in uplands (Gardner et al. 1991*a*, Callahan et al. 1997), but no large maternity colonies were reported exclusively using upland habitats. Therefore, availability of snags does not appear to be the force driving Indiana bats to select hydric habitats.

Table 4. Percent habitat composition of the study area (Oakwood Bottoms and Bluff Lake combined) and of female Indiana bat home ranges tracked in southern Illinois, USA, during the summer of 2003.[a]

Habitat type	Average bat	SE	Study area
Agriculture, open, urban	13.3	4.3	33.4
Large roads, railroad, power lines	2.6	0.2	1.8
Small roads	0.8	0.2	0.3
Closed-canopy bottomland	36.9	3.2	20.7
Open-canopy bottomland	30.4	6.2	14.1
Upland	8.2	3.2	29.0
Water (swamp, river, ponds, ditches)	7.8	2.9	0.8

[a] Table reproduced from Carter and Feldhamer 2005*b*.

Indiana bats may simply prefer the snags in bottomland habitats to those in upland habitats. To address this idea we must understand the microclimate characteristics provided by roost trees. In my review of the literature, I found that female Indiana bats selected snags that were larger, had at least some exfoliating bark, had high levels of solar exposure, and were close to forest cover (Kurta et al. 1993*b*, Menzel et al. 2001, Britzke et al. 2003, 2006, Carter and Feldhamer 2005*b*). Snags with characteristics preferred by Indiana bats can be found in all forested habitats (Morrison and Raphael 1993, Moorman et al. 1999). The very fact that Indiana bats have been found in snags in upland habitats confirms that snags with these same key features can be found in all habitats (Gardner et al. 1991*b*, Kurta et al. 1993*a*, Callahan et al. 1997, Britzke et al. 2003, Beverly and Gumbert 2005, C. Sanders, personal communication).

Foraging Resources

In my third hypothesis, I questioned if hydric habitats were preferred habitats because of foraging resources. Few studies have examined foraging habitat used by maternity colonies of Indiana bats. In Indiana, Sparks et al. (2005) documented a preference of agricultural areas and woodlands, including riparian habitats at the scale of home range (Table 3). While agricultural areas were heavily used, the authors state, "Movements throughout this agricultural landscape centered on a riparian corridor" (Sparks et al. 2005:716). Also, the polygon nature of home-range estimators often underemphasizes the importance of linear-type habitats (Blundell et al. 2001). Additionally, the actual distribution of telemetry data points in each habitat type shows an even greater selection for woodland habitats (Table 3). Menzel et al. (2005) found that bats in Illinois foraged closer to nonriparian forest, roads, and riparian habitats than expected based on habitat availability. The authors discussed the importance of both forested and riparian habitats throughout the article. Carter and Feldhamer (2005*b*) also found foraging Indiana bats preferred bottomland-type habitats over other habitats (Table 4). In all 3 studies (Carter and Feldhamer 2005*b*, Menzel et al. 2005, Sparks et al. 2005), ample alternate habitats were available; never-

Table 5. Comparison of % and ranked cover availability and use by reproductively active radiotagged Indiana bats at Fishhook Creek study area, Adams and Pike counties, Illinois, USA, during 1987 and 1988.[a]

Cover type	% cover		Available[b] ranking	Used[c] ranking
	Available[b]	Used[c]		
Cropland (row crops)	43.0	49.0	1	6
Hayland/pasture	18.0	7.1	3	10
Old field	3.0	7.1	5	5
Other agriculture (including residential)	2.0	1.8	6	11
Upland forest				
Closed canopy	24.4	11.6	2	9
Intermediate canopy	5.2	5.4	4	8
Open canopy	0.9	0.4	8	7
Floodplain forest				
Closed canopy	1.7	14.8	7	1
Intermediate canopy	0.4	2.7	9	2
Open canopy	0.1	1.0	10	4
Impounded water (farm ponds)	0.1	0.07	10	3

[a] Table reproduced from Gardner et al. 1991*a*.
[b] 3,672-ha study area.
[c] Convex polygon (100%) composition of radiotagged bats.

theless, the majority of the home ranges were in bottomland habitats. Gardner et al. (1991*b*) summarized work done on Indiana bats in central Illinois and found that floodplain forests were ranked among the lowest in availability yet among the highest in use, while upland forests were more available, but among the lowest of the used habitats (Table 5). While Murray and Kurta (2004) did not specifically examine foraging habitat use, they did document the habitats in the major centers of activity of foraging activity for female Indiana bats. All but one of the foraging areas used by the colony included some hydric habitat (e.g., forested wetlands or riparian habitats). While Indiana bats have been documented foraging in other habitat types in the Appalachians (Kiser and Elliot 1996, Butchkoski 2005, Ford et al. 2005), hydric habitats are a common theme in all foraging studies (Gardner et al. 1991*a*, Murray and Kurta 2004, Carter and Feldhamer 2005*b*, Menzel et al. 2005, Sparks et al. 2005).

Discussion

Anthropogenic forces have altered the forest structure of the eastern United States since presettlement time (Carter et al. 2003). If Indiana bats were forced into hydric forested habitats by anthropogenic changes (e.g., conversion of natural land covers to agriculture), one would expect to see habitat use follow availability. Because this is not observed, it is unlikely that anthropogenic changes have physically forced Indiana bats into selectively using bottomland-type habitats. Since upland roosts comprise a small proportion of the documented Indiana bat roosts, I suggest that it must be the location of snags in relation to other landscape features that dictates suitability, not habitat type. The foraging studies suggest foraging preferences are a significant driving force for habitat selection shown by large maternity colonies. Additionally, most anecdotal data on foraging habitat imply the importance of these habitats (Menzel et al. 2001). The diversity of habitat used suggests that Indiana bats are plastic in their foraging habitat use; however, a bottomland, riparian, wetland, or some other hydric component may be a requirement.

Although hydric habitats may be critical foraging components that drive the location of Indiana bat maternity colonies at the landscape level, food resources are only one aspect of the species' life history. Sufficient roosting resources, in terms of quantity and quality, are also essential for a successful maternity colony (Menzel et al. 2001, Britzke et al. 2003, Kurta 2005). Therefore, not all hydric habitats can support Indiana bat maternity colonies. Only those habitats that also have readily accessible and suitable roosting resources are likely to support colonies. Additionally there is likely a temporal component that affects when these roosting resources are of sufficient number and structure, following large-scale disturbances (Carter 2003). Since the early 1900s, the lower Midwest (i.e., Illinois, Missouri, and Kentucky, USA) has seen a tremendous change in the hydrologic and disturbance regimes of bottomland habitats from navigational and flood-control activities (Parker and Ruffner 2004). The maternity colonies located in southern Illinois occupy a habitat created because of the 500+-year flood of 1993 that exceeded the capacity of the United States Army Corp's levee system (Carter 2003). While afforestation efforts in bottomland hardwood forests increase (Battaglia et al. 2002, Groninger 2005), flood control has led to lower disturbance rates for these bottomland forests, resulting in reduced availability of roosting resources for the Indiana bat.

Management Implications

I recommend that management efforts within quality foraging habitat focus on maintaining roosting resources at a rate that is sustainable over the long term. Within the eastern portions of the range, Indiana bat maternity colonies likely persist in a shifting mosaic of habitat. While management efforts for the Indiana bat within these areas will likely benefit the species, the ephemeral nature of these maternity colonies coupled with the relatively low numbers of animals (Clawson 2002) suggests that these areas are unlikely to contribute significantly to recovery of the species. In contrast, the larger and more stable maternity colonies of the Midwest are likely to be the engine that drives species' recovery.

I recommend that future conservation efforts focus on protecting and regenerating bottomland habitats along the major river systems of the Midwest. It is within these bottomland and riparian habitats that future large and long-term maternity colonies will be established.

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