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Relationships of Three Species of Bats Impacted by White-Nose Syndrome to Forest Condition and Management

Alexander Silvis, Roger W. Perry, and W. Mark Ford

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Authors:

Alexander Silvis, Research Assistant Professor, Department of Fish and Wildlife Conservation, 310 W. Campus Drive, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061; **Roger W. Perry**, Research Wildlife Biologist, U.S. Department of Agriculture, Forest Service, Southern Research Station, Hot Springs, AR 71902; and **W. Mark Ford**, Research Wildlife Biologist, U.S. Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit, Blacksburg, VA 24061.

Cover Photo

A female northern long-eared bat (*Myotis septentrionalis*) captured on the Fort Knox Military Reservation, Kentucky, USA. (Photo by Sean Langley, Apogee Environmental and Archaeological, Inc.)

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CONTENTS

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ABSTRACT

Forest management activities can have substantial effects on forest structure and community composition and response of wildlife therein. Bats can be highly influenced by these structural changes, and understanding how forest management affects day-roost and foraging ecology of bats is currently a paramount conservation issue. With populations of many cave-hibernating bat species in eastern North America declining as a result of white-nose syndrome (WNS), it is increasingly critical to understand relationships among bats and forest-management activities. Herein, we provide a comprehensive literature review and synthesis of: (1) responses of northern long-eared (*Myotis septentrionalis*) and tri-colored (*Perimyotis subflavus*) bats—two species affected by WNS that use forests during summer—to forest management, and (2) an update to a previous review on the ecology of the endangered Indiana bat (*Myotis sodalis*).

Keywords: Bat conservation, forest management, forestry, habitat relationships, Indiana bat (*Myotis sodalis*), North America, northern long-eared bat (*Myotis septentrionalis*), roost, tri-colored bat (*Perimyotis subflavus*), white-nose syndrome.

INTRODUCTION

Bats and Forests

Well-managed forests are those managed for long-term sustainability using a variety of management tools that include harvesting and thinning, burning, replanting, and other similar practices. These forests provide valuable solid wood, fiber and biomass products; ecosystem services; green space; and recreational opportunities such as hunting, fishing, bird-watching, biking, and hiking. Managed forests also provide habitat for a wide array of vertebrate and invertebrate species. However, not all forest management objectives are simultaneously compatible. Most individual forest stands in the private sector and many in the public sector are managed to meet specific objectives, which may include promoting recreational opportunities, reducing wildfire risk, producing wood products, restoring ecosystems, and providing habitat for endangered species. Managed forest landscapes often provide a mosaic of forest structural conditions that allow many competing objectives to be accomplished at larger landscape scales. Understanding the effects on wildlife of different forest management techniques that are used to accomplish any given objective is considered a keystone of good forest stewardship.

Although the public largely associates bats with cave environments, many species of bats in the Eastern United States and Canada use caves only during hibernation (approximately October–April, depending on latitude) (fig. 1), and spend the remainder of the year in forests.

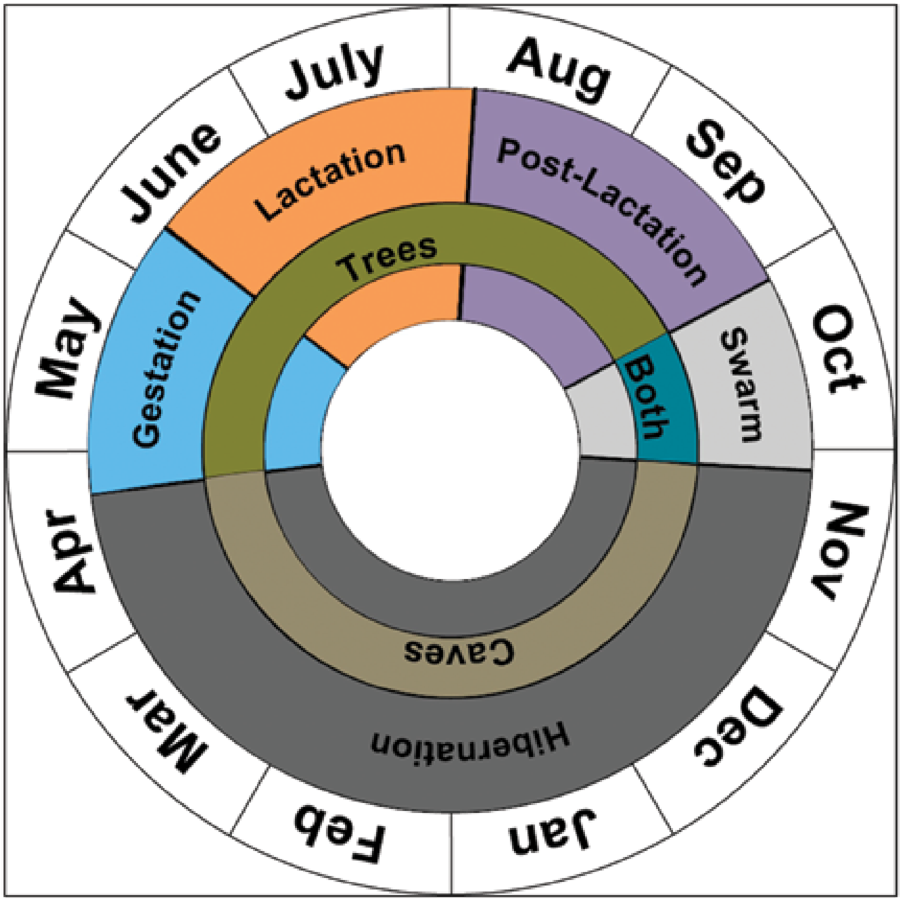

Figure 1—Generalized life cycle diagram of roosting for eastern North American cave bats. This diagram does not apply to gray bats (*Myotis grisescens*), Ozark big-eared bats (*Corynorhinus townsendii ingens*), or Virginia big-eared bats (*C. townsendii virginianus*) that occupy caves year round.

Depending on the species, bats rely on forests for day and night roosting, either in foliage, in tree cavities, or under loose bark of live and dead (snag) trees. Similarly, bats in these landscapes rely on different-aged forests and riparian zones within forests for foraging. Individual bat species vary tremendously in their ecology, but it is apparent that forest condition at the stand to landscape scale affects bat community composition, distribution, resource selection, and individual behavior (Bobrowiec and Gribel 2010, Borkin and Parsons 2014, Chaverri and others 2007, Chaverri and Kunz 2010, Ford and others 2005, Johnson and others 2010a, Smith and Gehrt 2010, Titchenell and others 2011).

Forest structural characteristics, particularly vegetation density, stand volume, tree heights, and stratification, are important factors determining local bat community composition, and these factors directly influence patterns of activity (Adams and others 2009, Fukui and others 2011, Hodgkison and others 2004, Menzel and others 2005b, Smith and Gehrt 2010). Similarly, forest composition and structural characteristics influence composition, density, and availability of bat invertebrate prey, and consequently bat activity (Dodd and others 2012b). Specific structural components, such as snags, are required by many forest-roosting bats, and bats select roosts in part based on local and surrounding landscape features, both physical and biotic (Kunz and Lumsden 2003). Both landscape and local stand characteristics are important in roost selection (Miles and others 2006, Perry and others 2008), and availability of and proximity to water is an important criteria for many species. Stream corridors not only provide critical drinking areas, they also provide excellent foraging habitat for most bats, and these areas frequently have greater levels of activity than surrounding areas (Carter 2006, Ford and others 2006a, Johnson and others 2010a, Menzel and others 2005b, Ober and Hayes 2008).

White-Nose Syndrome

Since its discovery in the winter of 2006–2007 in New York State, white-nose syndrome (WNS) has led to the deaths of millions of bats across much of the Eastern United States and southeast Canada, resulting in local to regional extirpation of once common bat species (Frick and others 2010). Now known to be caused by the cold-adapted fungus *Pseudogynmoascus destructans* (Lorch and others 2011), WNS impacts physiology, water balance, and arousal patterns of hibernating bats in lethal ways (Cryan and others 2010, Reeder and others 2012, Willis and others 2011). To date, 11 species or subspecies in the Eastern United States have shown signs of *P. destructans* fungal growth (table 1). Although mortality rates for many of the species that display clinical signs of WNS are high (Frick and others 2015), persistence of impacted species in some infected caves appears to be related in part to group size and microclimate factors (Langwig and others 2012). Likewise, although the spread of WNS is correlated with distribution of caves and climate (Maher and others 2012), the risk of infection for individual caves and timing of mortality appears to be related to distance to nearest WNS-positive cave and colony size (Wilder and others 2011).

White-nose syndrome is now widespread across the Eastern United States, and the U.S. Fish and Wildlife Service (USFWS) has listed the once common northern long-eared bat (*M. septentrionalis*) as threatened under the Endangered Species Act (2015 Federal Register § 80(63): 17974-18033). Given significant declines in populations of tri-colored (*Perimyotis subflavus*) and little brown (*M. lucifugus)* bats, it is possible these species may also be listed. Ecological impacts of bat population declines on forests remain unclear. It is apparent WNS impacts reproductive activity and annual recruitment of surviving bats (Francl and others 2012), thereby rendering impacted species more vulnerable to additive mortality. Moreover, WNS has altered community composition and foraging habitat use of WNS-impacted and nonimpacted species (Jachowski and others 2014a).

As populations of northern long-eared bats and other WNS-impacted species continue to decline, managers increasingly will be tasked with managing forests for bats and/or considering them in forest management and development plans, particularly as Federal listings potentially increase scope and extent of regulatory constraints. Decreased population sizes may render traditional mist-net sampling largely ineffective in many WNS-impacted regions (Coleman and others 2014). Therefore, documenting and studying bat ecology and distribution to guide management will require increasing reliance on acoustical surveys and/or observations of

Table 1—White-nose syndrome bat species in the Eastern United States with population trend post-WNS[a]

Species	Pre-WNS status	WNS-related population trend	Extinction risk
Northern long-eared bat (*Myotis septentrionalis*)	Common	Extreme decline	High
Indiana bat (*Myotis sodalis*)	Endangered	Mild decline	Moderate
Tri-colored bat (*Perimyotis subflavis*)	Common	Extreme decline	Moderate
Eastern small-footed bat (*Myotis leibii*)	Uncommon, locally abundant	Unknown	Moderate
Big brown bat (*Eptesicus fuscus*)	Common	Slight decline	Low
Little brown bat (*Myotis lucifugus*)	Common	Extreme decline	Moderate
Gray bat (*Myotis grisescens*)	Endangered	Unknown/slight decline	Unknown
Southeastern bat (*Myotis austroriparius*)	Uncommon	Unknown	Unknown
Rafinesque's big-eared bat (*Corynorhinus rafinesquii*)	Uncommon, locally abundant	No apparent impact	Unknown
Ozark big-eared bat (*C. townsendii. ingens*)	Endangered	Unknown	Unknown
Virginia big-eared bat (*C. t. virginianus*)	Endangered	No apparent impact	Unknown

[a] Local extinction risks were calculated by Frick and others (2010, 2015).

past landscape- and stand-level habitat associations that were developed pre-WNS (Jachowski and others 2014a, Silvis and others 2014a). Efforts to continue refining our understanding of relationships between these species and forest disturbance/stand development are currently limited by lack of comprehensive syntheses and assessments that can be used as the basis for proactive management of day-roosting sites and foraging areas. Because information from acoustic surveys is limited with regard to understanding roost selection and other aspects of bat ecology (Hayes 2000, Miller and others 2003), it is also increasingly important that historical data be thoroughly examined and synthesized.

Purpose

Three species of bats are particularly susceptible to WNS; these bats hibernate in caves and abandoned mines during winter but spend the growing season roosting and foraging in forests. The tree-roosting northern long-eared and tri-colored bats are at risk of extinction or regional extirpation due to WNS. To facilitate conservation of these species, we provide a review and synthesis of the literature addressing relationships among forest management, disturbance and successional processes, and responses of these species. Additionally, we provide an update to a previous review (Menzel and others 2001) on the ecology of the endangered Indiana bat (*Myotis sodalis*).

NORTHERN LONG-EARED BAT
(*Myotis septentrionalis*)

Introduction

The northern long-eared bat is a small to medium-sized colonial species of forest-dwelling bat in the family Vespertilionidae. Considered a subspecies of Keen's myotis (*Myotis keenii*) until 1979 (van Zyll de Jong 1979), northern long-eared bats occupy a distinct, non-overlapping range in eastern North America and now are described as a monotypic species (Caceres and Barclay 2000). The northern long-eared bat is distributed from Manitoba to Newfoundland, south through the Midwest to Georgia and Louisiana (fig. 2). Northern long-eared bats are distinct among *Myotis* bats in eastern North America based on their long ears and long, pointed tragus. Body mass ranges from 5 to 9 grams, and total length may be as much as 95 mm, with forearms between 34 and 38 mm (Caceres and Barclay 2000). Sympatric species over much of the species' range include the Indiana bat, little brown bat, big brown bat (*Eptesicus fuscus*), and tri-colored bat.

Growing Season Roost Ecology

Northern long-eared bats are infrequent users of anthropogenic structures such as buildings and bat boxes (Burke 1999, Krynak 2010). The species is primarily considered a forest-dwelling bat because most recorded roosts are in live trees or snags (Broders and others 2006, Foster and Kurta 1999, Johnson and others 2012, Lacki and Schwierjohann 2001, Menzel and others 2002b, Morris and others 2010, Perry and Thill 2007a). During summer (May–July), females form maternity colonies within cavities of snags or declining live trees (fig. 3), under exfoliating bark of live trees and snags, or in crevices in trees (fig. 4) (Carter and Feldhamer 2005, Lacki and Schwierjohann 2001, Menzel and others 2002b, Silvis and others 2012). Colonies of approximately 100 individuals have been documented in both forest (Owen and others 2002) and anthropogenic settings such as buildings and bat houses (Burke 1999, Krynak 2010), but smaller colonies containing 10–30 individuals appear to be more typical (Badin 2014, Johnson and others 2012, Owen and others 2002, Patriquin and others 2013, Perry and Thill 2007a, Sasse and Pekins 1996, Silvis and others 2014a). Individual maternity colonies have been documented using up to 42 different roost trees in a single year (Silvis and others 2015a). Colony size may vary throughout the maternity season in conjunction with the reproductive condition of bats within a colony (Lacki and Schwierjohann 2001, Sasse and Pekins 1996).

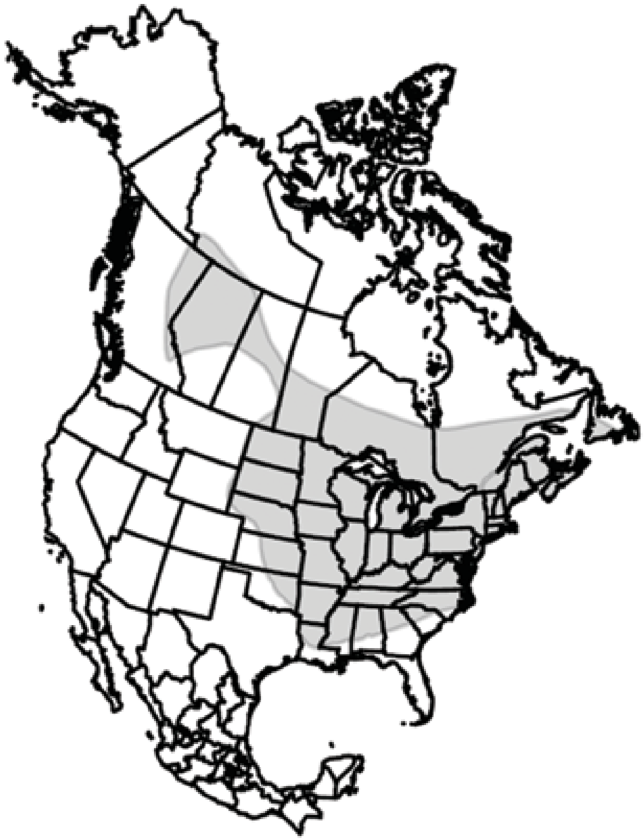

Figure 2—Approximate range of northern long-eared bats (*Myotis septentrionalis*). Range data modified from National Atlas of North American bat ranges (U.S. Geological Survey 2014).

Figure 3—A bottom-up view of a northern long-eared bat (*Myotis septentrionalis*) maternity roost snag and associated canopy gap in a mixed-mesophytic forest on the Fort Knox Military Reservation, Kentucky, USA. White arrow identifies roost tree. (Photo by Alexander Silvis, Virginia Polytechnic Institute and State University).

Maternity colonies of northern long-eared bats are socially structured, with bonds between individuals showing some temporal structuring (Garroway and Broders 2007). Adult females within maternity colonies appear to be related, but genetic relatedness is only weakly correlated with patterns of social relationships (Patriquin and others 2013). It is noteworthy that prior to WNS, northern long-eared bats had high genetic diversity and considerable gene flow across their range (Johnson and others 2013). Social structure of maternity colonies is defined by a fission-fusion dynamic in which individuals and small groups within the colony periodically "fuse" together into a single roosting group and then "diffuse" into smaller roosting groups (Garroway and Broders 2007, Johnson and others 2012, Silvis and others 2014a). Social bonds among females are manifested through roost switching movements wherein individuals with close associations share roosts more than expected by chance. Social connections among bats based on switching and sharing roosts are known as "roost networks" (Johnson and others 2012, Silvis and others 2014a).

Using roost network maps, both Silvis and others (2014a) and Johnson and others (2012) showed that, similar to Indiana bats (Silvis and others 2014b), northern long-eared bat maternity colonies used "primary" and "secondary" roosts; primary roosts are characterized by intense use relative to all other roosts, and secondary roosts by

Figure 4—Northern long-eared bat (*Myotis septentrionalis*) maternity colony (crevice near top of tree) in a 20-cm d.b.h. pine snag, located in a recently thinned and burned pine stand. (Photo by Roger W. Perry, U.S. Forest Service)

limited use. Number of bats using secondary roost trees on individual nights may be similar to the number that use primary trees (Johnson and others 2012). It has been suggested that the social structure of bats may be related to roost availability (Chaverri 2010), but this may not be the case for northern long-eared bats when a large number of potential roosts are available (Silvis and others 2014a). Most research suggests roost switching occurs every few days (table 2) (Badin 2014, Carter and Feldhamer 2005, Foster and Kurta 1999, Garroway and Broders 2007, O'Keefe 2009, Silvis and others 2014a).

Conversely, relatively little is known about roosting ecology of male northern long-eared bats. Males tend to roost alone (Broders and Forbes 2004, Perry and Thill 2007a) but have been found to occasionally share roosts with other males (Ford and others 2006b). It is likely that juvenile males use maternity roosts during the year of their birth, as has been documented for Indiana bats (Silvis and others 2014b). Arnold (2007) suggested that dispersal from maternity sites is male-biased. The number of individual roosts used by males appears to be relatively small over any given period of time (2.3 ± 0.4 SE, Ford and others 2006b) with roost switching every few days (1.2–3.1 days; O'Keefe 2009, Jung and others 2004) (table 2).

Stand and landscape condition—Distribution of northern long-eared bats covers a substantial proportion of the Eastern United States, including southeastern and southcentral Canada. Consequently, the species has been documented roosting in many different forest types outside of hibernation. Forest types include: boreal coniferous and mixed pine (Broders and Forbes 2004, Henderson and Broders 2008), Laurentian mixedwood (Jung and others 2004), northern hardwood (Broders and others 2006, Sasse and Pekins 1996), aspen-mixedwood (Crampton and Barclay 1998), mixed mesophytic-Allegheny hardwood (Ford and others 2006b, Menzel and others 2002b, Owen and others 2002), mixed mesophytic (Krynak 2010, Lacki and Schwierjohann 2001), western mixed-mesophytic (Silvis and others 2014a), upland hardwood (Badin 2014, Timpone and others 2010), bottomland hardwood (Carter and Feldhamer 2005, Timpone and others 2010), Appalachian upland oaks (*Quercus* spp.) (O'Keefe 2009), and mixed shortleaf pine (*Pinus echinata*)-hardwood (Perry and Thill 2007a). As expected with such a wide distribution, roosts have been found in a wide variety of forest stand and landscape conditions. Still, there appear to be some clear patterns in habitat use at the stand and landscape level.

Generally, studies have documented roosts in deciduous forest stands, but preference for deciduous forest over other forest types based on roosts reported in the literature is biased due to the majority of studies occurring in deciduous-forest landscapes. Within coniferous-dominated landscapes, roost-stand selection results differ between semi-boreal and austral locations. In Arkansas, northern long-eared bats (both sexes combined) preferred roosting in mature pine-dominated stands and mixed pine-hardwood forests (Perry and others 2007). In New Brunswick, Broders and Forbes (2004) reported selection for deciduous forest stands over coniferous stands by female northern long-eared bats.

Table 2—Studies characterizing roost switching by northern long-eared bats (*Myotis septentrionalis*)

					Roost switching frequency	
Study	Location	Number of bats studied	Number of roosts	Sex	Mean	SE
Badin (2014)	Indiana	23	71	♀	3.1 switches/5.3 days[a]	—
Carter and Feldhamer (2005)	Illinois	10	19	♀	2.5 switches/3.9 days[a]	—
Ford and others (2006b)	West Virginia	10	16	♂	2.3 roosts/3 days[c]	0.4 roosts/0.4 days
Foster and Kurta (1999)	Michigan	12	32	♀	2.8 switches/5.6 days[a]	—
Garroway and Broders (2007)	Nova Scotia	17	36	♀	1.6 days[b]	0.5 days
Johnson and others (2009) fire	West Virginia	25	30	♀	1.4 days[b]	0.2 days
Johnson and others (2009) no fire	West Virginia	44	40	♀	1.3 days[b]	0.1 days
Jung and others (2004)	Ontario	10	16	♂	3.1 days[b]	0.3 days
Lacki and others (2009)	Kentucky	18	54	♀	3.8 roosts/—	0.4 roosts/—
Menzel and others (2002b)	West Virginia	7	12	♀	5.3 days[b]	2.0 days
O'Keefe (2009)	North Carolina	18	52	♀	1.8 days[b]	0.3 days
O'Keefe (2009)	North Carolina	16	50	♂	1.2 days[b]	0.2 days
Owen and others (2002)	West Virginia	61	43	♀	3.0 days[b]	1.5 days
Patriquin and others (2010)	Nova Scotia	40	99	♀	1.4 days[b]	0.6 days
Sasse and Pekins (1996)	New Hampshire	32	47	♀	2.2 roosts/4.5 days[a]	—
Silvis and others (2014a)	Kentucky	54	108	♀	2.4 days[b]	0.3 days
Timpone and others (2010)	Missouri	13	39	—	3.1 roosts/4.9 days[a]	0.4 roosts/2.9 days

[a] Average number of times bat switched roosts/number of days tracked.
[b] Roost switching frequency (mean number of days bat spent in each roost).
[c] Mean number of roosts used/mean number of days tracked.
SE = Standard error; ♀ = female; ♂ = male; — = values not available.

Roost-stand selection appears to occur at multiple spatial scales, with small-scale selection (250 m) in pine-dominated landscapes indicating increased roosting probability in areas with abundant, thinned mature pine forest and group-selection cuts, but decreased amounts of immature pine (Perry and others 2008). Examination of large-scale selection (1 km) found increased probability of roosting in areas with abundant older (>100 years old) pine-hardwood stands and seed tree stands, and lower amounts of closed-canopy pine plantations; fewer but larger patches; more edge; and greater interspersion of patch types than random (Perry and others 2008). In northerly latitudes, male northern long-eared bats appear to either select for coniferous stands (Broders and Forbes 2004) or use coniferous stands in proportion to their abundance (Jung and others 2004). Despite selection preference for deciduous stands in some areas, occurrence records make it clear that northern long-eared bats will roost and reproduce in pine-dominated forest stands (Jung and others 2004, Lausen and others 2008, Morris and others 2010, Perry and Thill 2007a). However, young, closed-canopy pine plantations (prior to thinning) are rarely used for roosting (Perry and Thill 2007a, Perry and others 2008), likely because of their dense, cluttered conditions, small tree sizes, and relatively low abundance of snags/dying trees.

Forest stands where northern long-eared bats roost typically have continuous canopy (Badin 2014, Johnson and others 2012, Lacki and Schwierjohann 2001, Menzel and others 2002b, Perry and Thill 2007a, Sasse and Pekins 1996). Nonetheless, comparisons of roost stands and roosting areas with potential roost stands or random stands are variable, with some studies finding contrary results. For example, Carter and Feldhamer (2005), Menzel and others (2002b), and Perry and Thill (2007a) found that some stands used for tree roosting had relatively complex canopies with greater or lesser canopy closure. In contrast, Owen and others (2002) found no difference in forest complexity between roosts and potential roosts, and Sasse and Pekins (1996) found less canopy closure in roost stands than in available stands. It is likely that roost-stand selection is related to local landscape history, use, and configuration, as well as climate, elevation, and regional forest and ecosystem type. Despite differences in these factors, northern long-eared bats appear to be consistent throughout much of their distribution in preferring forest stands and points within stands with overstory trees generally larger than those at random points (Badin 2014, Johnson and others 2012, Lacki and Schwierjohann 2001, Menzel and others 2002b, Perry and Thill 2007a, Sasse and Pekins 1996). As a caveat, many studies comparing roost and random trees have included overstory, midstory, and understory trees in the random set. Therefore, preference for "largest trees on the landscape" may be biased by inclusion of nonoverstory trees in comparisons of tree diameter at breast height (d.b.h.) and tree height. Similarly, because random trees used for comparisons often are selected from within the same stand as roost trees, the scale of inference for many studies is limited to the roost stand.

Little information is available on basal area (BA) or stem density of stands used for roosting; therefore, it is difficult to determine thresholds to predict roosting. However, conditions used by northern long-eared bats for roosting range from forested pasture (Foster and Kurta 1999) to heavily thinned stands in industrial hardwood forests (Menzel and others 2002b, Owen and others 2002), to mature forest arising from old-field successional processes (Silvis and others 2012), which suggests that the species is tolerant of a wide range of basal area. In one well-studied population in Arkansas, the largest proportion of northern long-eared bat roosts were in stands with overstory BAs around 16 m^2/ha (70 square feet per acre) with little or no midstory (Perry and Thill 2007a). Overstory BA at roosts in that study ranged from 2.8 to 21.6 m^2/ha (12–94 square feet per acre), with stand BA ranging up to 32 m^2/ha (140 square feet per acre).[1] Use of industrial and otherwise harvested forests for roosting (Johnson and others 2009, Menzel and others 2002b, Owen and others 2002, Sasse and Pekins 1996) indicates tolerance both for disturbance and heterogeneous landscapes. Persistence in landscapes where forest distribution is highly fragmented also has been documented, as both Henderson and others (2008) and Kniowski and others (2012) captured northern long-eared bats in woodlots and forest stands within largely agricultural landscapes.

Although the species is capable of existing in fragmented landscapes, Henderson and others (2008) reported that probability of forest stand use was best predicted by amount of deciduous forest area within 2 km, with an increase in odds of 1.6 for every additional 100 ha of deciduous forest. Likewise, Carter and Feldhamer (2005) found that roosts were best distinguished from random trees by distance to forest, with roosts closer to contiguous forests. However, males and females may react to fragmentation differently, as Henderson and others (2008) found probability of use by males was better predicted by amount of deciduous forest within 2 km, and probability of use by females was predicted by amount of deciduous forest within a patch. Minimum forest patch sizes where bats have been captured vary among studies, with minimums of 17.1 and 15.9 ha for females and males, respectively, on Prince Edward Island (Henderson and others 2008) and 86 ha in northeastern Ohio (Krynak 2010).

Roost characteristics—Maternity colonies of northern long-eared bats are primarily found in snags and decaying or declining live trees, as are solitary males and females. Because maternity roosts have been the main focus of research, hereafter "roosts" will be used to mean maternity roost unless otherwise specified. Although roosting under loose bark and in crevices is common, use of tree cavities accounts for greater proportions of roosts used in hardwood forests (Badin 2014, Foster and Kurta 1999, O'Keefe 2009, Silvis and others 2015b). Decay stage of roost trees commonly ranges between 2 and 6 on the Cline and others (1980) scale, and decay stage generally is greater than that of other trees in forest stands (Badin 2014, Broders and Forbes 2004, Krynak 2010, Silvis and others 2015b). However, tree decay stage may not necessarily differ between snags used as roosts and potentially available snags (Menzel and others 2002b).

Roost tree height and d.b.h. are highly variable among and within studies (Badin 2014, Krynak 2010, Lacki and others 2009a, Silvis and others 2015b) (table 3). Based on consolidated data from across the range of the northern long-eared bat, roost trees were most commonly 15 to 55 cm in diameter, and some studies have found roost trees larger than random (Lacki and Schwierjohann 2001, Owen and others 2002, Sasse and Pekins 1996). The level of observed variability in these measures suggests that the species is not dependent upon trees of specific characteristics for roosting. Rather, because roost trees tend to be larger than nearby or random trees and occupy larger canopy gaps (Jung and others 2004, O'Keefe 2009,

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[1] Perry, R.W. [N.d.]. Unpublished data. On file with: R.W. Perry, U.S. Department of Agriculture, Forest Service, Southern Research Station, Hot Springs, AR 71902.

Table 3—Roost parameters from studies characterizing day-roosts used by northern long-eared bats (*Myotis septentrionalis*)

Study	Location	Number of bats	Number of roosts	Sex	Roost tree d.b.h. (cm)		Roost tree height (m)		Roost height (m)		Canopy openness (%)		Dominant location (%)	
					Mean	SE	Mean	SE	Mean	SE	Mean	SE	Bark	Cavity
Badin (2014)	Indiana	23	71	♀	—	—	—	—	8.4	—	—	—	26.8	64.7
Carter and Feldhamer (2005)	Illinois	10	19	♀	37.3	4.7	15.8	2.0	9.2	1.4	56.0	7.2	58.0	42.0
Cryan and others (2001)	South Dakota	9	21	♀	39.0	1.8	9.1	1.1	4.2	0.9	—	—	—	—
Ford and others (2006b)														
Snags	West Virginia	3	6	♂	16.6	1.5	—	—	10.3	1.2	—	—	—	—
Live trees	West Virginia	7	10	♂	53.4	6.3	—	—	31.5	1.7	—	—	—	—
Foster and Kurta (1999)	Michigan	11	32	♀	65.0	1.0	23.3	0.2	10.5	0.9	56.0	7.0	48.3	51.7
Garroway and Broders (2008)														
Pre/post-lactation	Nova Scotia	—	22	♀	41.0	3.2	13.4	1.4	8.0	0.9	26.0	6.8	—	—
Lactation	Nova Scotia	—	22	♀	43.0	3.6	22.1	1.0	16.4	0.7	48.0	7.9	—	—
Johnson and others (2009)														
Burned	West Virginia	36	25	♀	24.3	3.2	14.0	1.3	8.6	1.0	17.6	1.9	—	—
Unburned	West Virginia	36	44	♀	30.9	2.6	16.3	1.2	8.8	0.7	9.4	0.2	—	—
Jung and others (2004)	Ontario	10	16	♂	42.6	3.8	20.1	1.1	—	—	64.0	3.5	84.6	15.4
Krynak (2010)	Ohio	8	21	♀	55.8	4.7	—	—	19.5	1.2	21.0	2.7	81.0	19.0
Lacki and others (2009b)														
Pre-burn	Kentucky	18	16	♀	—	—	—	—	10.0	3.6	—	—	50.0	50.0
Post-burn	Kentucky	18	35	♀	—	—	—	—	9.1	1.4	—	—	21.7	78.3
Lacki and Schwierjohann (2001)														
Bark roosts	Kentucky	15	57	Mixed	32.0	2.9	—	—	6.5	0.7	16.6	0.3	100.0	0.0
Cavity roosts	Kentucky	15	57	Mixed	16.8	2.3	—	—	3.5	0.5	7.2	0.1	0.0	100.0
Menzel and others (2002b)	West Virginia	7	12	♀	29.2	1.6	18.7	1.5	10.8	1.0	—	—	8.3	91.7
O'Keefe (2009)														
Females	North Carolina	18	52	♀	45.6	4.3	18.4	1.8	—	—	—	—	—	—
Males	North Carolina	16	50	♂	31.9	4.5	15.7	1.6	—	—	—	—	—	—
Owen and others (2002)	West Virginia	61	43	♀	27.2	1.0	17.8	0.7	10.8	0.6	—	—	34.9	65.1
Perry and Thill (2007a)														
Males	Arkansas	17	43	♂	15.0	1.3	7.9	0.7	4.9	0.6	—	—	60.0	40.0
Females	Arkansas	23	49	♀	18.7	1.0	8.7	6.0	5.2	0.5	—	—	43.0	57.0
Sasse (1995)	New Hampshire	26	48	♀	30.9	2.8	14.8	1.0	—	—	83.0	1.4	—	—
Silvis and others (2015b)	Kentucky	121	215	♀	31.8	1.6	15.9	0.7	—	—	4.5	0.5	1.4	98.6
Timpone and others (2010)	Missouri	13	37	—	43.0	2.3	15.7	2.9	9.6	2.9	44.0	—	59.0	41.0

— = Values not available; d.b.h. = diameter at breast height; SE = standard error; ♀ = female; ♂ = male.

Owen and others 2002, Silvis and others 2015b), specific roost characteristics relative to other trees in the forest stand are important. However, roost trees are not always larger than neighboring trees (Menzel and others 2002b, O'Keefe 2009). Larger canopy gaps surrounding roost trees than gaps around random trees may be an artifact of using snags and senescing live trees as roosts. Conversely, these trees may be used to maximize solar exposure by females during the maternity period; female tree-roosting bats may select warmer roosts during parturition (Kerth and others 2001), which speeds development of young (Racey and Swift 1981, Zahn 1999). Additionally, variation in roost selection by North American bats may be related to regional climate (Fabianek and others 2015). Because no manipulative studies using northern long-eared bats have been conducted, it is difficult to determine whether selection of snags is for solar exposure or simply based on roost availability (i.e., cavities and loose bark). Roosts often are located on ridge tops and south-facing aspects (Johnson and others 2009, Jung and others 2004, Lacki and Schwierjohann 2001, Silvis and others 2012). Use of ridgetops and south-facing aspects may provide better solar exposure and therefore decrease costs of thermoregulation to reproductive females (Garroway and Broders 2008, Johnson and others 2009, Kunz and Lumsden 2003). However, ridgetops also have the highest natural disturbance frequency and severity (Lorimer and White 2003), and as suggested by Silvis and others (2012), may provide a greater number of potential roosts.

Little is known about characteristics of cavities used by northern long-eared bats. Measurements on the internal characteristics of a small number of cavities used by females in Kentucky suggest that cavities vary tremendously in length, volume, and diameter, but that cavity volume may be positively related to number of entrances (Silvis and others 2015c).

It is important to consider that bats likely do not select roosts based on a single roost characteristic, but rather on overall characteristics of potential trees, forest stands, and surrounding landscape. Studies on roost selection by northern long-eared bats make it clear that roosts are generally in overstory trees and in later stages of decay than neighboring or random trees, and are located in canopy gaps (Johnson and others 2009, Lacki and Schwierjohann 2001, Menzel and others 2002b, Perry and Thill 2007a). However, the process behind selection of individual roosts on any given occasion remains unclear. Gender, reproductive condition, weather and climate, and social bonds may all play a role in selection, with relative weight of each factor in roost selection varying. Garroway and Broders (2008) found that lactating females in Nova Scotia selected taller trees in more open forest conditions than non-lactating females, possibly to provide juvenile bats with easy practice for flying and foraging. Silvis and others (2012) also found that lactating bats selected sites with greater canopy openness, but in contrast to Garroway and Broders (2008), the model differentiating roosts used during this reproductive period was only weakly supported. In Arkansas, females selected significantly larger diameter trees than males and roosted at sites with significantly fewer midstory trees than males, likely because of different physiological and environmental requirements of reproductive females (gestation) versus males (increased torpor depth) (Perry and Thill 2007a). Geographic location, particularly latitude, also may affect roost selection, as bats at the extremes of the species' range will have different thermal stresses to overcome. Roost characteristics and likelihood of roost switching may be related to changing daily weather conditions (Patriquin and others, in press). Presence of non-random social groups and roost networks (Johnson and others 2012, Silvis and others 2014a) and temporally structured social bonds (Garroway and Broders 2007) would not be observed if social factors did not influence roost selection.

Tree species used/preferred—Species of trees used for roosting varies greatly (Garroway and Broders 2008, Johnson and others 2009, Lacki and Schwierjohann 2001, Perry and Thill 2007a), and a tremendous number of tree species have been documented as roosts (table 4).

Table 4—Tree species used for roosting by northern long-eared bats (*Myotis septentrionalis*)

Species	Preferred	Species	Preferred
American beech (*Fagus grandifolia*)		Pignut hickory (*Carya glabra*)	
American elm (*Ulmus americana*)		Pin oak (*Quercus palustris*)	
American sycamore (*Plaatus occidentalis*)		Ponderosa pine (*Pinus ponderosa*)	
American basswood (*Tilia americana*)		Red maple (*Acer rubrum*)	X
Big-tooth aspen (*Populus grandidentata*)		Red oak (*Quercus rubra*)	
Black cherry (*Prunus serotina*)		Red spruce (*Picea rubens*)	
Black gum (*Nyssa sylvatica*)		Sassafras (*Sassafras albidum*)	X
Black locust (*Robinia pseudoacacia*)	X	Scarlet oak (*Quercus coccinea*)	
Black oak (*Quercus velutina*)		Shagbark hickory (*Carya ovata*)	X
Black walnut (*Juglans nigra*)		Shortleaf pine (*Pinus echinata*)	X
Blue ash (*Fraxinus quadrangulata*)		Silver maple (*Acer saccharinum*)	X
Boxelder (*Acer negundo*)		Slippery elm (*Ulmus rubra*)	
Chestnut oak (*Quercus prinus*)		Sourwood (*Oxydendrum arboreum*)	X
Chinkapin oak (*Quercus muehlenbergii*)		Sugar maple (*Acer saccharum*)	X
Common persimmon (*Diospyros virginiana*)		Sweet gum (*Liquidambar styraciflua*)	
Eastern hemlock (*Tsuga canadensis*)		Tree of heaven (*Ailanthus altissima*)	
Eastern redbud (*Cercis canadensis*)		Trembling aspen (*Populus tremuloides*)	
Eastern redcedar (*Juniperus virginiana*)		White ash (*Fraxinus americana*)	
Flowering dogwood (*Cornus florida*)		White birch (*Betula papyrifera*)	
Green ash (*Fraxinus pennsylvanica*)		White oak (*Quercus alba*)	
Hackberry (*Celtis occidentalis*)		White pine (*Pinus strobus*)	X
Hawthorn (*Crataegus* spp.)		Winged elm (*Ulmus alata*)	
Loblolly pine (*Pinus taeda*)		Yellow birch (*Betula alleghaniensis*)	X
Mockernut hickory (*Carya tomentosa*)		Yellow-poplar (*Liriodendron tulipifera*)	
Northern red oak (*Quercus rubra*)			

X = Preference or intense use was observed.

Roost-tree species is clearly tied to the local tree-species assemblage, and conditions resulting from past disturbance regimes (e.g., insect and fungal outbreaks, ices storms, fire, etc.) that created structural characteristics suitable for roosting in a particular tree species. Preference for certain tree species often occurs (Ford and others 2006b, Lacki and Schwierjohann 2001, Perry and Thill 2007a, Silvis and others 2012), which may be related to past disturbance events. Nonetheless, the process of selection for individual species is poorly understood. Silvis and others (2012) and Ford and others (2006b) suggested that selection for tree species may be related to successional trajectories of individual forest stands; both studies observed selection for an early successional tree species that atypically occurred in the overstory in mature second-growth forests. In both cases, the early successional species largely were overtopped by larger trees and were in late stages of decay/decline. Despite noted selection preferences, the wide variety of tree species used indicates that this bat may be a generalist and is not dependent upon an individual species or genus for roosting. Likewise, selection for atypical species or circumstantial availability of species (Ford and others 2006b, Perry and Thill 2007a, Silvis and others 2012) indicates that the species is flexible enough to be considered opportunistic in selecting tree species. At a broad level, there appears to be few commonalities in characteristics of tree species used as roosts; used species range from shade tolerant to shade intolerant, and position from overstory to understory. In some cases, limited roost availability may drive northern long-eared bats to use anthropogenic structures (Henderson and Broders 2008).

Roosting area space use—Northern long-eared bats demonstrate some inter-annual fidelity to roost areas, with use of capture sites up to 5 years after initial capture (Perry 2011), but all individuals within maternity colonies may not return each year (Silvis and others 2015a). No reliable estimates for inter-annual survival rates, particularly post-WNS, are available, making it unclear if low inter-annual return rates observed by Silvis and others (2015a) were due to low survival post-WNS or dispersal. Stronger matrilineal relationships among individuals within maternity colonies than with individuals from neighboring maternity colonies (Patriquin and others 2013) suggest long-term site fidelity to areas, if not individual roosts, across generations. Intra-annual roost fidelity is apparent and related to social structure (Garroway and Broders 2007, Johnson and others 2012, Silvis and others 2014a). It is unclear how far northern long-eared bats move from summer maternity grounds to hibernacula, as well as vice versa.

Estimates of area used for roosting are complicated by different methods used to estimate area and variable sample sizes among studies, but roosting area of maternity colonies in contiguous forest have been reported between 1.3 and 58.3 ha (mean 38.05 ± 20 SD ha) by Silvis and others (2015a), with associated subgroups using 1.45–35.33 (mean 12.6 ± 9.9 SD ha) (Johnson and others 2012). In a fragmented agricultural landscape, Henderson and Broders (2008) found roosting areas of 0.3 ha and 4.13 ha for two separate colonies, with the larger area used by a colony in a more-forested landscape. Individual roosts may be considerable distances apart (e.g., 2.55 km) (Foster and Kurta 1999), but clustering of roosts appears to be common (Johnson and others 2009, Sasse and Pekins 1996, Silvis and others 2014a). Colonies also may use "core" areas that coincide with primary roosts and especially dense clusters of roosts (Silvis and others 2014a). Colony-level roosting areas appear to be distinct and non-overlapping (Silvis and others 2014a) and persist across years (Silvis and others 2015a).

Roosting areas used by individual females appear to be relatively small in most cases, with reported averages of 8.6 (± 9.2 SD) ha (Broders and others 2006) and 5.4 (± 1.1 SE) ha (Badin 2014). Perry and Thill (2007a) found individuals typically moved among roost trees in an area <5 ha. Few studies have reported habitat composition of home ranges, but roosting areas reported by Silvis and others (2015c) and Henderson and Broders (2008) consisted entirely or primarily of closed canopy forest. Roosting areas do not appear to be located closer to water or openings than random locations (Badin 2014), although Perry and others (2008) found roosts were more likely to be located near group-selection stands with numerous openings. Although use of interior forests seems to be the norm in landscapes fragmented by agriculture, some roosts may be located in close proximity to a variety of types of forest edges (Krynak 2010). In more-forested landscapes, use of interior forests, including those mechanically thinned, appears to be frequent (Johnson and others 2009, Menzel and others 2002b, Silvis and others 2015b).

Movement distances between summer roosts generally average <0.8 km (Badin 2014, Broders and others 2006, Foster and Kurta 1999, Gumbert and others 2002, O'Keefe 2009, Silvis and others 2015a), but maximum distances of up to 2 km have been recorded (Foster and Kurta 1999). Broders and others (2006) and O'Keefe (2009) reported longer distance movements by females than males, which may be due to stricter roost requirements for females (Broders and others 2006). Some evidence suggests that female reproductive condition also may impact movement distances (Silvis and others 2015a). Individual bats are believed to use a small number of roosts (~3) (Krynak 2010, O'Keefe 2009, Silvis and others 2014a), but as many as seven different roost trees have been used by an individual during a 2-week radio tracking period.[1] Jackson (2004) found the number of roost trees used by individual females averaged 8.6 (range 2–11). Silvis and others (2015a) found that tracking period was positively related to roost discovery rate, so estimates may be biased low by the reported tracking periods of only a few days. Reproductive condition does not appear to influence number of roosts used by individual bats (Silvis and others 2015a). For a colony, tracking 10 bats for 5 days will identify a substantial proportion of the roosts used (fig. 5).[2] Average distances to roosts from point of capture is <0.7 km (Broders and others, 2006, Ford and others 2006b, Henderson and Broders 2008, Johnson and others 2009, Krynak 2010, O'Keefe 2009, Sasse and Pekins 1996).[2] The maximum reported distance from capture site to roost location in the literature is 2,649 m (Badin 2014), but bats may go farther, as R.W. Perry (unpublished data) located roosts 9.8 km from the capture site in Arkansas.[1]

Acoustic Activity Patterns and Foraging Ecology

Using acoustic detectors to monitor bat activity is becoming increasingly common. Unfortunately, acoustic detectors are unable to distinguish between individuals or sexes, and often cannot separate species based on quantitative characteristics of their echolocation calls (Britzke and others 2011, Clement and others 2014, Hayes 2000). Nonetheless, acoustic detectors are useful for monitoring purposes and understanding bat ecology (e.g., Weller 2008). Acoustic detectors cannot differentiate specific bat behaviors (e.g., searching for a new roost vs. commuting or foraging), with the exception of "feeding buzzes." Because acoustic detectors cannot differentiate individuals, differences in number of calls recorded among areas do not necessarily indicate differences in bat numbers among those areas. Consequently, data from acoustic detectors often are analyzed under a detection/non-detection framework or activity patterns, with the latter often considered foraging behavior. Obviously, bats will be detected using echolocation calls at their roosts, but acoustic detection does not indicate they roost at that location.

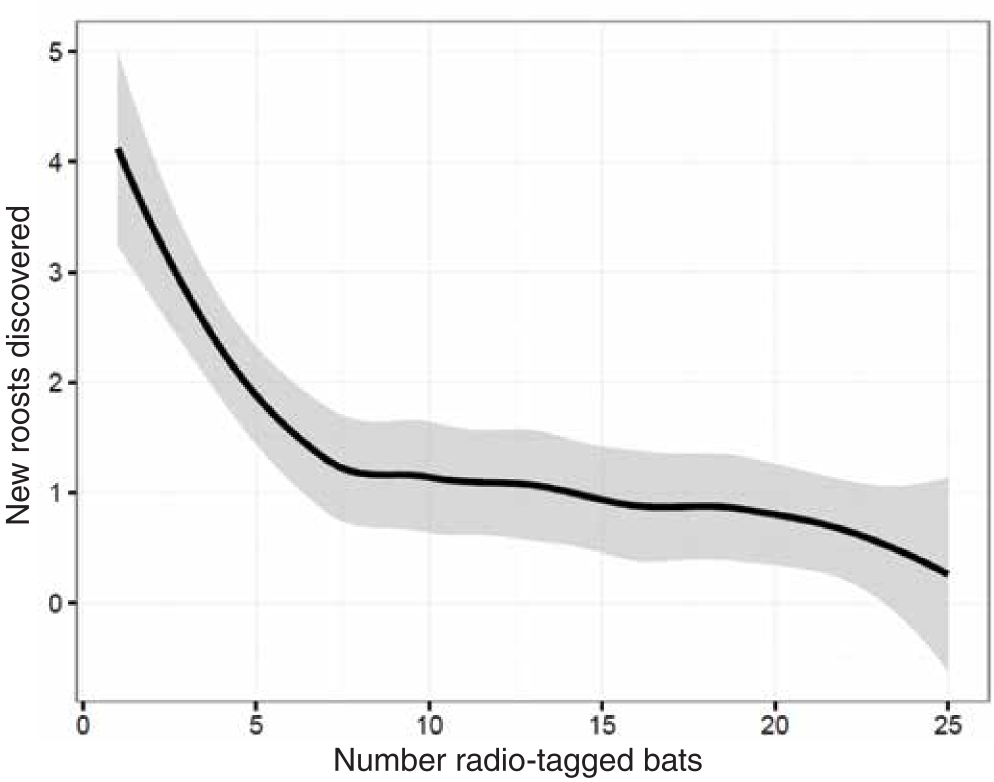

Figure 5—Smoothed mean (standard error in gray) number of new roosts discovered for every radio-tagged bat tracked. Data from three northern long-eared bat (*Myotis septentrionalis*) colonies collected over 2 years (Source: Silvis and others 2015a).

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[2] Silvis, A. [N.d.]. Unpublished data. On file with: A. Silvis, Department of Fish and Wildlife Conservation, Virginia Polytechnic Institute and State University, Blacksburg, VA 24060.

Currently, identifying *Myotis* bats in eastern North America is a contentious issue for some, as the echolocation calls of species within this genus in North America are similar with considerable overlap in echolocation metrics. Recent analysis of the performance of bat call identification software by the U.S. Geological Survey found that accuracy rates of automated identification software generally are >75 percent at the individual file level, and even better at a presence-absence level when maximum-likelihood values are considered (Ford 2014, U.S. Fish and Wildlife Service 2015a). Although many studies reviewed herein have not used the software approved by USFWS for Indiana bat surveys (http://www.fws.gov/midwest/Endangered/mammals/inba/surveys/inbaAcousticSoftware.html), many have provided estimates for call classification accuracy (derived from discriminant function analysis). It is beyond the scope of the current review to assess accuracy of all reviewed studies, and we accept results of acoustic studies as presented with the above caveats noted.

Northern long-eared bat echolocation calls range in frequency from 40 kHz to 120 kHz, but average call frequency is typically 49–53 kHz (fig. 6). Echolocation calls of this species are of low intensity relative to many other species in their frequency range. Nothing currently is known about characteristics of social vocalizations made by this species or whether call characteristics vary across its range. Little acoustic work has focused directly on the northern long-eared bat. However, it does appear that intra-night patterns of acoustic activity differ among reproductive periods and may vary among habitat types (Johnson and others 2011).

Stand and landscape condition—At the landscape level, presence of northern long-eared bats may be positively related to amount of forest cover and negatively related to amount of urban/rural cover (Johnson and others 2008, Starbuck and others 2015) and small stem density (Starbuck and others 2015), with activity levels higher in forested than urban and rural landcover types (Johnson and others 2008). However, these results are equivocal, as

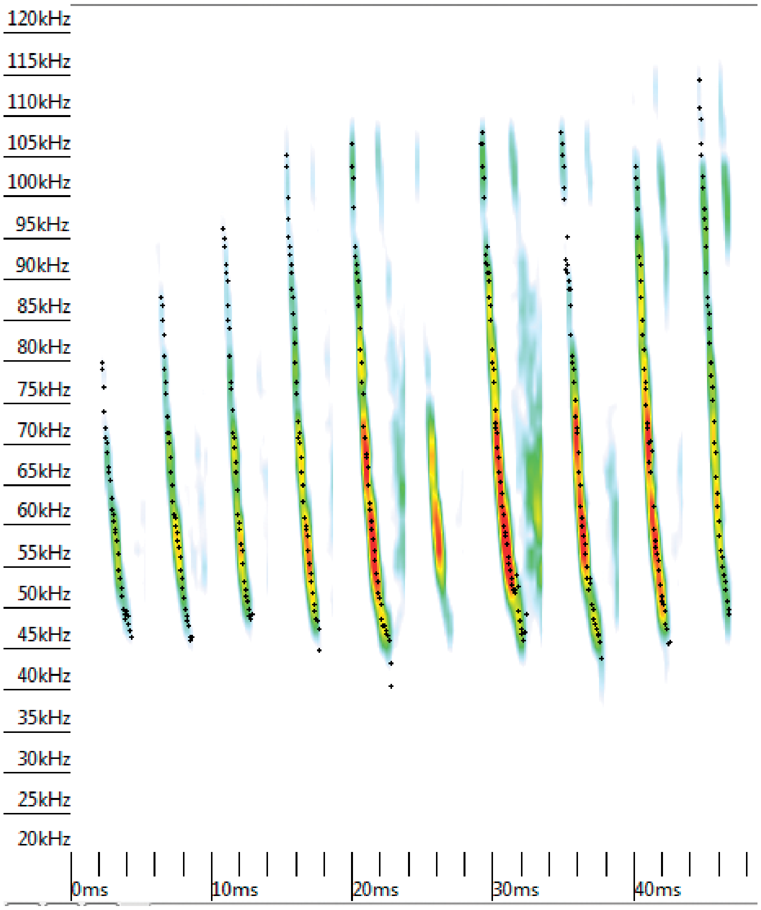

Figure 6—Echolocation calls recorded from a captured and hand-released northern long-eared bat (*Myotis septentrionalis*) showing both full spectrum and zero-crossing data. (File courtesy of M.B. Fenton; edited for space)

fragmentation amount has been found to have no negative impact on presence in forest stands (Ethier and Fahrig 2011). Independent of forest amount, forest fragmentation may have positive effects by reducing travel times between foraging and roosting sites (Ethier and Fahrig 2011); several studies have found high levels of activity at forest edges in fragmented forest-agricultural landscapes (Jantzen and Fenton 2013, Mills and others 2013).

Forest type (deciduous, coniferous, mixed) may not impact presence or activity levels (Patriquin and Barclay 2003), but it is clear that forest conditions and local landscape features are related to activity patterns (Brooks 2008, Brooks and Ford 2005, Dodd and others 2012b, Ford and others 2005, Loeb and O'Keefe 2006). In forests, activity levels appear to be greater in more open than cluttered conditions (Brooks 2008, Loeb and O'Keefe 2006). Activity may be greater in open stands, including partially harvested single-tree, shelterwood, and seed-tree harvested stands (Dodd and others 2012b). However, decreased activity levels in fields (Jantzen and Fenton 2013) suggest a limit to the level of openness tolerated for foraging. Using radiotelemetry, Owen and others (2003) found northern long-eared bats selected for partially harvested stands (30–40 percent of BA removed), but avoided leave-tree, two-aged harvests, and young clearcuts. Accordingly, contiguous canopy conditions appear to be somewhat important (Brooks and Ford 2005, Ford and others 2005).

Forested wetlands, riparian areas, and vernal pools often are considered important landscape features for bats, particularly the Indiana bat (Carter 2006, Fulton and others 2014). Several studies have investigated activity patterns of northern long-eared bats in such locations. Henderson and Broders (2008) found foraging areas were concentrated along forested riparian zones. Other studies have indicated that pools and streams under closed canopy conditions are preferred to more open streams and pools (Brooks and Ford 2005, Johnson and others 2010a), but pool size alone is unimportant (Ford and others 2005). Activity levels in riparian corridors have been found to be similar (Ford and others 2005) or greater than that of uplands (Owen and others 2004); use of forests with contiguous canopy but a relatively uncluttered and open midstory suggests a relatively complex relationship with forest stand characteristics.

Foraging area and habitat—Data from radio-tagged individuals indicate that foraging areas used by northern long-eared bats are larger than roosting areas. Broders and others (2006) report minimum mean foraging areas of 46.2 (± 44.4 SD) ha for females and 13.5 (± 8.3 SD) ha for males, and Owen and others (2003) report average home ranges of 65 (± 5.2 SE) ha for females. In fragmented agricultural landscapes, foraging and movement were limited to forest-covered corridors and tree-lined hedgerows, with open areas used less and forested areas used more than expected (Henderson and Broders 2008). In forested landscapes, foraging preference has been reported for diameter-limit harvests, intact forests, and road corridors (Owen and others 2003), and it does not appear that bats preferentially forage in either deciduous or coniferous forests (Broders and others 2006). Relative to roosting areas, foraging areas may be closer to forested riparian zones, and have lower canopy heights and higher structural complexity (Henderson and Broders 2008). Foraging areas appear to be located close to or contain roosting areas (Broders and others 2006), with maximum movement distances of up to 1770 m (Broders and others 2006, Henderson and Broders 2008).

Prey selection—Northern long-eared bats are insectivores that forage both by gleaning and aerial hawking (Ratcliffe and Dawson 2003). Dietary analyses have indicated that northern long-eared bats prey on at least seven orders of insects and Arachnida (Carter and others 2003, Dodd and others 2012a). Lepidoptera are a preferred prey resource as indicated by total volume and frequency of occurrence in fecal samples from a variety of locations throughout the species' range (Brack and Whitaker 2001, Dodd and others 2012a, Whitaker 2004). Coleoptera and Diptera also appear to be commonly consumed (Brack and Whitaker 2001, Carter and others 2003, Dodd and others 2012a, Feldhamer and others 2009, Whitaker 2004). Pre-WNS, bats provided an estimated $3.7 billion per year in insect control of agricultural pests (Boyles and others 2011); northern long-eared bats are known to consume a variety of forest-insect pests including eastern tent caterpillar (*Malacosoma americanum*); a variety of leaf rollers and tiers; and fruit, stem, and root borers (Dodd and others 2012a).

Response to Forest Management

A variety of forest management activities may occur across a landscape, including treatments to forest stands (e.g., thinning, midstory reduction, clearcutting, shelterwood harvest, single- and group-tree select harvest, and prescribed fire) and other activities such as road construction and right-of-way clearing. Management regimes can be widely divergent, ranging from custodial management with minimal disturbances to intensive management with frequent disturbances. Few studies have conducted controlled experiments to determine the effects of forest management on northern long-eared bats, and where information is available, it does not adequately cover the full range of forest management techniques available to forest landowners. However, sufficient work has been completed to infer broad patterns in the response of this species to both timber harvest and prescribed fire.

Timber harvest—As noted earlier, northern long-eared bats roost (Johnson and others 2009, 2012; Owen and others 2002; Perry and Thill 2007a) and forage in harvested or otherwise thinned forest stands (Badin 2014, Ford and others 2005, Grindal and Brigham 1998, Owen and others 2004). Indeed, the species even has been documented to preferentially select partially harvested and burned forested conditions for roosting (Perry and others 2008). Use of partially harvested stands for roosting does not answer questions about proximate effects of roost loss on maternity colonies, and unfortunately, little information is available on this topic. However, Silvis and others (2015a) conducted a small-scale, targeted roost-removal study that provided some insight into effects of roost loss on a short timescale. Their results suggest that loss of a primary roost has little impact on colony location, roost selection, social structure, fragmentation, or roost-use patterns, but a loss of ~17 percent of roosts may begin to cause colony fragmentation, a finding consistent with a previous simulation (Silvis and others 2014a). Although there is a considerable gap in understanding the effects of forest harvest on snag and roost loss rates across the species range (e.g., Perry and Thill 2013), it is evident that at least in the mid- to long-term, forest thinning may create suitable habitat for northern long-eared bats.

Fire—Three studies have investigated direct effects of prescribed fire on northern long-eared bats. These studies indicate that northern long-eared bats may move roosting areas into or closer to burned areas in both the immediate and short term (Dickinson and others 2009, Johnson and others 2009, Lacki and others 2009b). Further, changes in habitat conditions resulting from fire do not impact roost switching rates or overall roosting area size (Johnson and others 2009, Lacki and others 2009b). Adult northern long-eared bats apparently are able to arouse from torpor in late April and exit roost trees during prescribed fires before roost trees are surrounded or consumed by fire, and may resume roosting and foraging in burned areas within 6 days after fire (Dickinson and others 2009). However, how non-volant bats and adults with offspring respond to fire is unknown. Foraging patterns after burning appear to be more related to stand type and topographic position than burn history (Dickinson and others 2009, Lacki and others 2009b).

Considerable proportions of roosts used by colonies after fire may be within burned areas, with Lacki and others (2009b) reporting 73 percent and Johnson and others (2009) reporting 38 percent of located roosts being in burned areas. Perry and Thill (2007a) found 73 percent of female roosts and 54 percent of male roosts in areas that had been burned 1–5 years previous. Similarly, colony sizes and nightly activity patterns at roosts also appear to be unaffected by burning (Johnson and others 2011). Roost selection may be variable in response to changes in habitat structure, particularly canopy openness. Johnson and others (2012) found that in burned areas, bats were more likely to use cavity trees of smaller diameter where the canopy was interrupted by fire-related mortality. In contrast, roosts in unburned areas were nearer the tops of larger cavity trees. Lacki and others (2009b) similarly found that roost selection differed pre- and post-fire; roosts used post-fire were in trees with a greater number of cavities and a higher percentage of bark cover, whereas roosts used pre-fire were taller in height and in earlier stages of decay than random snags. Because inter-annual patterns in roost selection have been poorly studied, changes in roost-selection preference should be regarded with some caution (Silvis and others 2015b).

Based on the above, it appears that prescribed fire may benefit northern long-eared bats, despite actual (Dickinson and others 2009) or potential roost loss and habitat disturbance. This may be because increases in habitat quality following burning may provide an adequate trade-off for short-term roost loss. Although the exact mechanisms for tolerance to roost loss are unclear, flexible roost selection criteria (Silvis and others 2015b), frequent roost switching, and social structure (Silvis and others 2015a), may play a role, as might landscape disturbance dynamics. Ford and others (2016) found that, although abundance of preferred roosting species may decline post-fire, recruitment rate of alternate species may be three times greater than the loss of preferred species.

Threats

Although relatively common and locally abundant before WNS, northern long-eared bats now are of conservation concern and listed as threatened under the Endangered Species Act. Population declines of this species following WNS have been substantial, and risk of local extinction is believed to be substantially greater for northern long-eared bats than other WNS-impacted species and unrelated to number of bats within hibernacula pre-WNS (Frick and others 2015). Consequently, the greatest threat to this species is WNS. Additive mortality resulting from habitat loss or disturbance during the maternity season should also be considered a threat to local populations. Habitat loss or disturbance resulting from forest management are probably not substantial threats *per se*, as numerous studies have found that northern long-eared bats will preferentially and opportunistically use managed forest stands for roosting and foraging (Ford and others 2006b, Johnson and others 2012, Menzel and others 2002b, Owen and others 2003). Moreover, because the decline in population size is due to WNS rather than habitat loss, it may be assumed that habitat availability is not a limiting factor for the species across most of its range, except in highly agricultural areas of the Midwestern United States and the forest-prairie transition zone on the western periphery of its range. Avoidance of habitat manipulation and tree removal that affects known occupied roost trees during the active maternity season (mid-May through early August) could reduce risk of mortality related to tree-felling in maternity areas where northern long-eared bats are known to be present. The limited proportion of most landscapes that are harvested in any given year makes it unlikely that loss of a small number of roost trees would cause negative population-level impacts.

Research Questions and Needs

Many questions remain unanswered relative to northern long-eared bat ecology. Research priorities include:

- **Effective treatment for WNS infections.** The greatest threat to survival of the species is WNS. Unless northern long-eared bats are capable of rapid adaptation to this disease, they could become functionally extinct over a large portion of their range without an effective treatment.

- **More effective models to predict locations of potential roost trees.** Current information is insufficient and not standardized to allow accurate prediction over managed forest landscapes. In particular, more information is needed on how parameters often recorded by forest managers (i.e., basal area, midstory density) relate to potential roost locations.

- **Effects of roost-site disturbance, including roost loss, during all life history phases.** Studies are needed to document specific effects of roost loss due to harvest, both short- and long-term. Understanding the effects of roost-site disturbance will benefit land managers for forest planning. Potential for disturbance to roosting bats from management activities, such as harvest or burning during the summer maternity season, also needs further investigation.

- **Effects of long-term changes in habitat conditions.** Given the wide breadth of habitats used by this species and relatively stable forest ownership and management trends in the United States (Oswalt and others 2012), significant loss of habitat for this species from ongoing forest management operations seems unlikely. A greater concern is how long-term changes in habitat structure and forest community composition, and changes in cave hibernacula conditions resulting from climate change, may shift distribution of the species.

- **How northern long-eared bats use forested landscapes near hibernacula during spring staging and fall swarming.** Preparation for hibernation and emergence from hibernation are critical for ensuring survival.

Regulations

Due to declines from WNS, northern long-eared bats were listed as federally threatened in April 2015 (50 CFR 17 FWS–R5–ES–2011–0024). Using a provision under section 4(d) of the Endangered Species Act of 1973 (hereafter, Act), the USFWS has enacted measures that are “necessary and advisable to provide for the conservation of the northern long-eared bat…” (hereafter, 4(d) rule; 50 CFR 17 FWS–R5–ES–2011–0024; 4500030113). Invocation of section 4(d) of the Act allows specific management actions to be exempt from the regulatory prohibited “take.” “Take” is defined as “to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture or collect” individuals of the species (50 CFR part 17). “Take” may be purposeful (e.g., intentional killing, harassing, harming, capture or handling of individuals) or incidental (take is incidental to, and not the purpose of, an otherwise lawful activity, such as tree harvest). The final 4(d) rule, published in January 2016, makes several provisions to exempt forest management from “take” within the designated WNS zone. Outside the designated WNS zone, incidental take is allowed, but purposeful take is prohibited. In the WNS zone, incidental take of bats is prohibited in and around the hibernacula, including activities that may alter the hibernacula at any time of the year, such as alterations of the entrance or interior environment that may adversely affect bats. Prescribed fire and timber harvesting are exempted from incidental take, provided that:

> (1) Known, occupied, maternity roost trees may not be destroyed, and no other tree removal may take place within a 45-m radius of known occupied maternity roosts during the pup season. As defined in the 4(d) rule, the pup season is June 1 through July 31. Known occupied maternity roost trees are “trees that have had female northern long-eared bats or juvenile bats tracked to them or the presence of female or juvenile bats is known as a result of other methods.” A tree will remain a known, occupied maternity roost “as long as the tree and surrounding habitat remain suitable for northern long-eared bats” (page 1,911).
>
> (2) No removal of trees may take place within a 0.4-km radius of known northern long-eared bat hibernacula if take may occur. However, timber management may be allowed if it is conducted at a time when bats are unlikely to be roosting in trees within the buffer (e.g., winter), the activity does not adversely affect the hibernacula’s climate, or the activity does not change the suitability of the area for bat foraging. Local USFWS Ecological Services Field Offices (http://www.fws.gov/offices) should be consulted prior to activities to evaluate the potential for incidental take of northern long-eared bats.

INDIANA BAT

(*Myotis sodalis*)

Introduction

The Indiana bat is a small to medium-sized colonial species of forest-dwelling bat in the family Vespertilionidae. Although listed as endangered, Indiana bats are distributed widely from eastern Oklahoma and Kansas to New Hampshire, south from the Great Lakes to Tennessee, with apparently limited numbers in northern Mississippi, northern Georgia, and the upper Coastal Plain of Alabama (fig. 7). As of 2015, maternity colonies also have been identified in the Coastal Plain of Virginia,[3] and it is possible that populations may exist in the Coastal Plain of northeastern North Carolina. Indiana bats are distinguished from the physically similar little brown bat by their keeled calcar and short toe-hairs. Adult body mass averages 7.1–7.5 grams. Total wingspan may be as much as 240–267 mm, with forearms between 36.0 and 40.6 mm (Thomson 1982). Sympatric species include the northern long-eared bat, little brown bat, big brown bat, and tri-colored bat.

Menzel and others (2001) provided a comprehensive review of the ecology of the Indiana bat. Herein, we provide a review of literature published since 2001, with particular focus on research in more diverse landscapes and on topics not addressed in the Menzel and others (2001) review.

Growing Season Roost Ecology

Similar to northern long-eared bats, Indiana bats rarely use anthropogenic or artificial structures such as bat boxes (Belwood 2002, Butchkoski and Hassinger 2002, Whitaker and others 2006), although they readily use artificial bark roosts (Adams and others 2015). During summer (May–July), females form maternity colonies under loose bark or in crevices or cavities of snags or declining live trees, whereas males roost solitarily (fig. 8) (Britzke and others 2003, 2006; Kurta and others 1993, 2002; Timpone and others 2010). Colonies larger than 100 are reported (Kniowski 2011, Kurta 2005), but average colony size is probably between 50 and 90 (Adams and others 2015, Britzke and others 2006, Callahan and others 1997, Harvey 2002, Kurta and others 2002). Individual colonies may use numerous roosts, with reports of over 30 roosts (Bergeson and others 2015, Silvis and others 2014b). In some cases, number of roosts used by a colony appears to be relatively small (Johnson and others 2009), but it is unclear if this is an artifact of sampling. Although maternity colonies by definition contain mother-offspring pairs, no studies have identified whether colonies themselves follow matrilines across years, how nearby colonies are related, or the population genetic structure in general.

Figure 7—Approximate Indiana bat (*Myotis sodalis*) range. Range data modified from National Atlas North American bat ranges (U.S. Geological Survey 2014).

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[3] Germain, M. St. [N.d.]. Unpublished data. On file with: M. St. Germain, Department of Fish and Wildlife Conservation, Virginia Polytechnic Institute and State University, Blacksburg, VA 24060.

Figure 8—Solitary male Indiana bat (*Myotis sodalis*) roosting under loose bark of a 20-cm d.b.h. pine snag during the fall. (Photo by Stephen Brandebura, Arkansas State University)

Roost switching occurs an average of every 2 to 6 days. There is some evidence that roost switching may be less frequent in more challenging environments, like those at relatively high elevations in mountainous terrain (Britzke and others 2003), but this has not been thoroughly tested. Although only addressed in a single study, maternity colonies of Indiana bats exhibit a fission-fusion social dynamic associated with roost switching, which may also carry over during foraging (Silvis and others 2014b). Social structure of maternity colonies appears to be variable among years, but factors that drive this variability are unclear. It is commonly accepted that maternity colonies of Indiana bats use multiple roosts, with some being "primary" and others "secondary." Primary roosts receive consistent use, use by a large number of bats relative to other roosts used by the colony, or both (Britzke and others 2003, Callahan and others 1997, Miller and others 2002). However, network analysis suggests that bats probably do not view roosts in binary fashion (primary or alternate), but rather on a continuum. Moreover, roost importance within colony networks may change across years, and former primary roosts may decrease in status or may not be used (Britzke and others 2006, Silvis and others 2014b). Not all individuals within a maternity colony will hibernate together (Kurta and Murray 2002), which raises questions about how maternity colonies form and how migration routes are chosen.

Overall annual adult survival was estimated to be 64.2 percent pre-WNS, with little difference between males and females, although caution is urged when interpreting this estimate given biases inherent to the study design (Boyles and others 2007, Humphrey and Cope 1977). It is unknown what inter-annual survival rates are now that WNS is causing decreased over-winter survival.

Stand and landscape condition—In the agricultural Midwestern United States, roosts of Indiana bats commonly are found in bottomland hardwood forests, riparian forests, and otherwise hydric forest types (Bergeson and others 2013, Carter 2006, Kniowski 2011, Timpone and others 2010). In the Appalachian Mountains and the periphery of their range, Indiana bats have been found in more upland areas (Britzke and others 2006, Hammond 2013, Johnson and others 2010b, Johnson and Gates 2009) and in somewhat xeric forest types despite availability of hydric forests (Jachowski and others 2016). As noted by Carter (2006), location of suitable roosts in relation to other habitat features probably is more important than habitat type alone in determining roosting locations. Indeed, landscape-scale analyses have found that forest area and configuration are better predictors of roosting than distance to stream or water alone (Jachowski and others 2016, Pauli and others 2015a, Watrous and others 2006, Weber and Sparks 2013). However, distance to stream and area in hydric forest still may be important predictors (Bergeson and others 2015, Carter and others 2002, Pauli and others 2015a, Watrous and others 2006).

Across studies, reported landscape composition ≥1 km around roosts ranges from 8 to 62 percent forested, 33 to 55 percent agricultural and open field, 8 to 19 percent wetland, 6 to 23 percent urban and residential, and 0.9 to 3 percent open water (Bergeson and others 2015, Kurta and others 2002, Miller and others 2002, Sparks and others 2005, Watrous and others 2006). Proportion of forest within local landscapes has been found to have positive effects (Watrous and others 2006, Weber and Sparks 2013), negative effects (Pauli and others 2015a), or no relationship (Farmer and others 2002) with likelihood of Indiana bat presence. A positive relationship between amount of forest on the landscape and presence of Indiana bat roosts is consistent with the overall requirement for forest roosts, but the negative relationship between forest amount and presence identified by Pauli and others (2015a) is difficult to explain. It is possible that landscape configuration has differential effects on habitat selection by Indiana bats, as the best predictors of summer habitat have been found to differ between forested and agricultural areas (Weber and Sparks 2013). The apparent positive effect of moderate amounts of forest edge in agricultural areas also could be suggestive that Indiana bats actually prefer moderately forested landscapes (Watrous and others 2006, Weber and Sparks 2013). This may help explain why roost switching is relatively less common and colony sizes are smaller in the mostly forested Appalachian Mountains and other sites on the periphery of their distribution (Britzke and others 2006, Carter 2006). Preference for only moderately forested landscapes at large scales is consistent with selection for diverse land cover types (Watrous and others 2006), but may also be an artifact of landscape configuration within the core of the species range. Reproductive maternity colonies are known to persist in habitat fragments across years (Silvis and others 2014b) (fig. 9), suggesting that even if moderately forested landscapes are not preferred, colonies are able to persist and reproduce therein.

Forest stands used by Indiana bats in the Midwestern and Northeastern United States are typically deciduous (Brack 2006, Britzke and others 2006, Carter and others 2002, Carter and Feldhamer 2005, Johnson and others 2010b, Johnson and Gates 2009, Kniowski 2011, Kurta and others 2002, Timpone and others 2010, Watrous and others 2006), possibly because of limited availability of mixed or pine-dominated stands. In more southerly areas, the species roosts in mixed pine-hardwood stands[3] (Britzke and others 2003) or stands otherwise containing pine trees (Brack 2006, Gumbert and others 2002, Hammond 2013, Perry and others 2016). There is apparent selection preference for larger forest stands in fragmented landscapes (Jachowski and others 2016). Among stands, density of suitable roost trees (Farmer and others 2002), basal area, and density of large trees may be better predictors of roost-site selection than distance to hydric features (Jachowski and others 2016, Miller and others 2002), with increased likelihood of presence with increased availability of large trees and potential roosts. However, forest patches in the Midwestern United States used by Indiana bats for roosting often contain considerable percentages of bottomland hardwoods and wetlands (Carter and others 2002, Watrous and others 2006).

Roost characteristics—Indiana bats have consistently been found to roost in trees larger than surrounding trees and in moderate to large canopy gaps; nearly all studies have found statistically significant differences in these factors between roosts and random trees (Bergeson and others 2015; Brack 2006; Britzke and others 2003, 2006; Carter and Feldhamer 2005; Johnson and others 2010b; Johnson and Gates 2009; Kniowski 2011; Kurta and others 2002; Miller and others 2002; Timpone and others 2010; Watrous and others 2006) (fig. 10). Loose or exfoliating bark is by far the primary roost type, with only limited crevice and cavity roosting reported (Bergeson and others 2015; Brack 2006; Britzke and others 2003, 2006; Carter and Feldhamer 2005; Jachowski and others 2016; Johnson and others 2010b; Kniowski 2011; Kurta and others 2002; Miller and others 2002; Timpone and others 2010; Watrous and others 2006). Roost tree decay stage is generally advanced, but availability of roosting substrate appears to be more important (Bergeson and others 2015; Brack 2006; Britzke and others 2003, 2006; Carter and Feldhamer 2005; Jachowski and others 2016; Johnson and others 2010b; Kniowski 2011; Kurta and others 2002; Miller and others 2002; Timpone and others 2010; Watrous and others 2006).

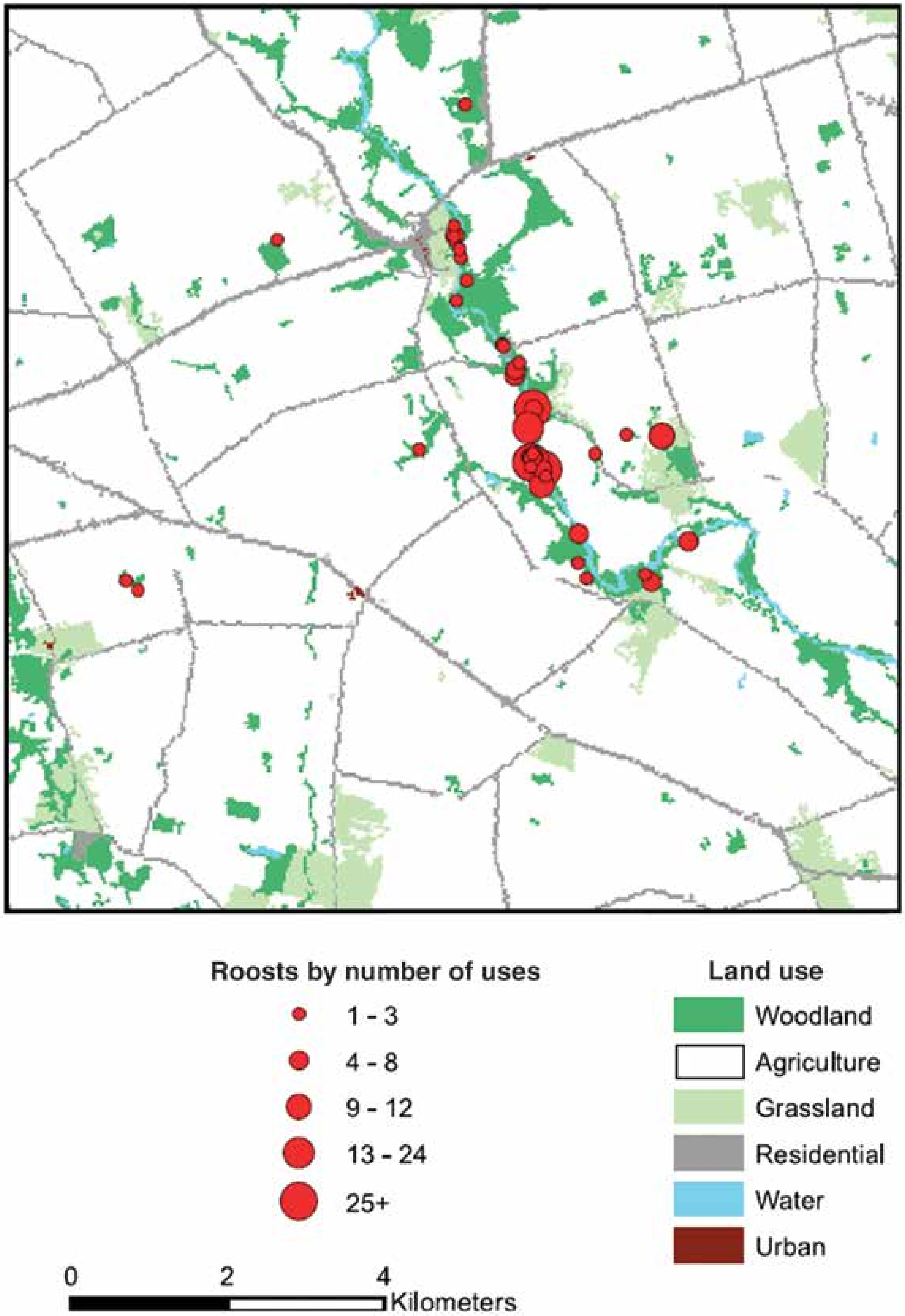

Figure 9—Indiana bat (*Myotis sodalis*) roost locations in a highly fragmented agricultural landscape in Pickaway County, Ohio (Source: Kniowski 2011).

Figure 10—Representative Indiana bat (*Myotis sodalis*) roost. Note size relative to surrounding trees and canopy gap. (Photo by Andrew Kniowski, Virginia Polytechnic Institute and State University)

Virtually all studies suggest that selection for canopy gaps is beneficial for increasing solar exposure, but no studies have assessed whether solar exposure increases recruitment or juvenile growth rate. Furthermore, benefits of increased solar exposure to non-reproductive females and males are unknown. Roosts may be located on south-facing aspects and mid-slope, which also provides increased solar exposure (Britzke and others 2003, Jachowski and others 2016), although this is not universal and may be offset by other factors (Johnson and others 2010b). In North Carolina, Indiana bats selected roosts on the upper portion of ridges on south-facing slopes in mixed pine-hardwood forests (Hammond 2013). However, Gardner and others (1991) found that roost temperatures at sites with intense solar radiation may reach potentially lethal levels (e.g., 44 °C) in mid- to late-summer, forcing bats to move to less-exposed and better insulated roosts, and Indiana bats may use sites with more shade during warm weather (Callahan and others 1997). Perry and others (2016) found males during the fall roosted mostly in lower slope positions in the higher elevation portions of study areas. Cooler temperatures resulting from cold air drainage into lower slopes (Perry 2013) may have allowed deeper torpor and greater energy conservation during the critical pre-hibernation period (Perry and others 2016). There does not appear to be a substantial difference in roost selection among reproductive conditions or sexes, although this has not been thoroughly studied. Similarly, although some studies have found that "primary" roosts are larger and receive more solar exposure than "secondary roosts" (Britzke and others 2003, Kniowski 2011), this is not always the case (Miller and others 2002).

Diameter of live trees and snags used for roosting varies from 4.3 to 86.6 cm d.b.h. (Britzke and others 2003, Menzel and others 2001, Perry and others 2016), which suggests flexibility in tree sizes used. Although studies suggest many species of bats (including Indiana bats) prefer trees larger than random for roosting, these studies are biased by minimum sizes used to calculate random trees. For example, when minimum diameter of random trees are set ≤15 cm d.b.h., Indiana bats preferred trees larger than random, but did not prefer trees larger than random when minimum size of random trees included in analysis are set at ≥18.5 cm d.b.h. (U.S. Fish and Wildlife Service 2007). Therefore, Indiana bats likely prefer overstory trees, but not necessarily the largest overstory trees. Males during fall may use trees ≥20 cm d.b.h. at a higher proportion than their availability, and trees smaller than this at less than their availability (Perry and others 2016). Overstory age of forest stands is an important factor for roost selection by Indiana bats (and other bat species), as trees must be large enough (older) to provide adequate rooting substrate. In Arkansas, 98 percent of male roosts were in stands with an overstory ≥38 years old, suggesting this may be an important age threshold for roost selection, likely due to the development of adequate tree size and surrounding forest structure (Perry and others 2016).

Tree species used/preferred—Indiana bats have been reported using at least 31 species or genera of trees (Kurta 2005) (table 5), and likely use many more. Preference, or intense use, has been reported for silver (*Acer saccharinum*) and sugar maples (*A. saccharum*) (Kurta and others 2002, Timpone and others 2010), oaks (Bergeson and others 2015, Carter and Feldhamer 2005, Timpone and others 2010), shagbark hickory (*Carya ovata*) (Brack 2006, Britzke and others 2006), pines (Britzke and others 2003, Gumbert and others 2002, Hammond 2013), and green ash (*Fraxinus pennsylvanica*) (Carter and Feldhamer 2005). Regionally, deciduous species dominate across the Midwestern United States, but pines appear to be selected in southern areas, mountainous regions, and along the east coast (Brack 2006, Britzke and others 2003, Carter and Feldhamer 2005, Gumbert and others 2002, Hammond 2013, Menzel and others 2001, Perry and others 2016). Live shagbark hickory tends to be used whenever it is an available species (Menzel and others 2001), possibly due to its longevity (roost stability) compared to snags as well as its unique exfoliating bark characteristics (Perry and others 2016). Selection for tree species has not been thoroughly investigated, but all tree species preferred or intensely used are notable for being susceptible to developing loose bark. Regional preference for tree species is clearly constrained by the local assemblage of available tree species and likely with habitat type. For example, based on species reported as preferred or strongly used, it appears that in xeric sites, oaks, hickory, and pines may be selected, whereas in mesic sites, maples and ash are selected. In both cases, preference for tree species is also likely constrained by stand history and the resulting availability of suitable roosts.

Table 5—Tree species (or species groups) used as roosts by Indiana bats (*Myotis sodalis*)[a]

Species	Preferred
American beech (*Fagus grandifolia*)	
Ash (*Fraxinus* spp.)	X
American basswood (*Tilia americana*)	
Birch (*Betula* spp.)	
Black locust (*Robinia pseudoacacia*)	
Eastern hemlock (*Tsuga canadensis*)	
Elm (*Ulmus* spp.)	X
Flowering dogwood (*Cornus florida*)	
Green ash (*Fraxinus pennsylvanica*)	X
Hackberry (*Celtis occidentalis*)	
Hickory (*Carya* spp.)	
Hophornbeam (*Ostrya virginiana*)	
Honey locust (*Gleditsia triacanthos*)	
Maple (*Acer* spp.)	X
Mockernut hickory (*Carya tomentosa*)	
Oak (*Quercus* spp.)	X
Pines (*Pinus* spp.)	X
Poplar (*Populus* spp.)	
Quaking aspen (*Populus tremuloides*)	
Sassafras (*Sassafras albidum*)	
Shagbark hickory (*Carya ovata*)	X
Shortleaf pine (*Pinus echinata*)	X
Sourwood (*Oxydendrum arboretum*)	
American sycamore (*Platanus occidentalis*)	
Sweet birch (*Betula lenta*)	
Tuliptree (*Liriodendron tulipifera*)	
Walnut (*Juglans* spp.)	
White ash (*Fraxinus americana*)	
White pine (*Pinus strobus*)	
Yellow birch (*Betula alleghaniensis*)	
Yellow-poplar (*Liriodendron tulipefera*)	

X = Preference or intense use was observed.

[a] List is not comprehensive due to lack of reporting in some studies.

Roosting area space use—Maternity colonies may be >500 km away from hibernacula (Kurta and Murray 2002, Winhold and Kurta 2006), with southerly hibernacula having greater catchment areas than northerly hibernacula (Britzke and others 2012). However, distances moved from hibernacula may also be quite small, with some recorded distances <40 km (Britzke and others 2006). Indiana bats exhibit site fidelity to roosting areas (Gumbert and others 2002, Silvis and others 2014b), both within (Brack 2006, Butchkoski and Hassinger 2002, Gumbert and others 2002, Silvis and others 2014b) and between years (Gumbert and others 2002, Silvis and others 2014b). It is unclear how long bats may continue to use roost areas, but some roost areas have been used up to 4 years (Kniowski 2011, Kurta and Murray 2002). Colony areas may shift slightly between years, possibly in response to roost suitability and survival (Gumbert and others 2002, Kurta and Murray 2002, Silvis and others 2014b). Overall inter-annual return rates for colony members are unknown and difficult to predict. Return rates could be high given relatively high pre-WNS yearly survival estimates, or low given that not all members of maternity colonies hibernate together (and thus may be free to join new colonies).

Roost area home range (not including foraging area) is inconsistently reported in the literature, and where reported, differences in method and sample size complicate cross-study comparisons. Nonetheless, whole-colony roost areas have been reported between 174.9 and 1704.0 ha (Carter and Feldhamer 2005, Silvis and others 2014b). Silvis and others (2014b) reported that roost area may vary considerably in size between years and provided an observed difference of 1529.1 ha between consecutive years in the agricultural Midwest.

Maximum reported distance moved between a capture location and a roost is 40 km, but this was recorded during spring when bats were emerging from caves and may not be the norm; mean recorded distance moved during this time was 26.9 km (Britzke and others 2006). In contrast, Johnson and Gates (2009) reported maximum distance between capture site and roost as 2.6 km during the maternity season. Rommé and others (2002) reported a mean maximum distance of 4.3 (± 2.8 SD) km, and Perry and others (2016) reported distances up to 11.6 km from capture sites (hibernacula) to tree roosts during fall. Distances moved between sequentially used roosts may be considerable, as Carter and Feldhamer (2005) and Bergeson and others (2015) report maximum distances of 4.6 and 8.2 km, respectively. However, average distance moved between roosts is probably considerably smaller with reported means of 686 and 1079 m (Bergeson and others 2015, Kurta and others 2002). There have been no formal comparisons of distances moved by bats in different reproductive conditions.

Acoustic Activity Patterns and Foraging Ecology

USFWS guidance recently have allowed summer surveys for Indiana bats to use acoustic methodology (U.S. Fish and Wildlife Service 2015a). Indiana bat echolocation calls range in frequency from 40 kHz to 69 kHz, but average call frequency is typically 47-51 kHz (fig. 11). Although identification of *Myotis* bats from their echolocation calls is currently a contentious issue, particularly when done using automated identification software, empirical reviews of software suggest that echolocation calls of Indiana bats can be distinguished relatively reliably from those of other *Myotis* species, particularly when maximum likelihood values are used (Britzke and others 2002, 2011; U.S. Fish and Wildlife Service 2015a).

Stand and landscape condition—In a mostly forested landscape, occupancy of forest patches by Indiana bats has been found to be positively related to mean patch size but negatively related to proportion of landscape in

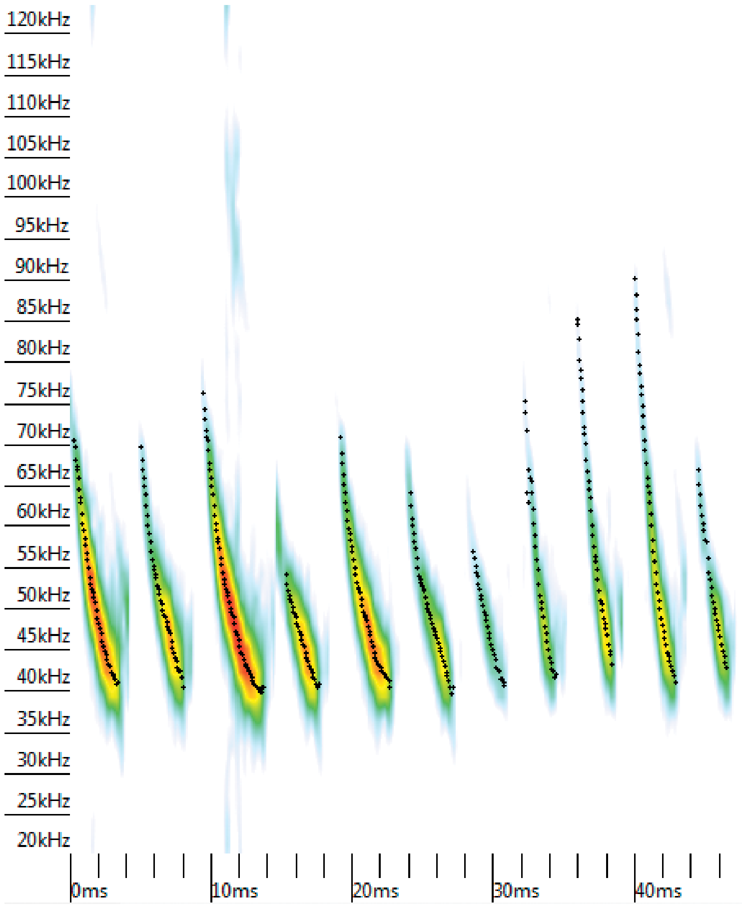

Figure 11—Echolocation call recorded from a hand-released Indiana bat (*Myotis sodalis*) showing both full spectrum and zero-crossing data.

forested cover types (Yates and Muzika 2006); this is consistent with observations of roosting areas (Pauli and others 2015a). In largely forested landscapes, probability of presence has been found to be positively related to riparian stream order and canopy cover (Ford and others 2005), and basal area of snags (Yates and Muzika 2006). Among forest stands, activity levels are greater in riparian forests than upland forests (Owen and others 2004), with overall activity levels positively associated with canopy cover over waterways, smaller streams, and elevation (which may be correlated) (Johnson and others 2010a). In riparian areas, activity has been found to be negatively related to percent wetland and open water (Johnson and others 2010a).

Foraging area and habitat—Foraging areas used by maternity colonies of Indiana bats apparently are considerably larger than roosting areas, with Silvis and others (2014b) providing an estimate between 3555.3 and 3609.0 ha; foraging areas appeared stable between years. Mean home range for individual Indiana bats is consistently reported between 200 and 400 ha, but may be variable within a given locality or among bats within a maternity colony (max reported SD = 994 ha) (Bergeson and others 2013, Brack 2006, Butchkoski and Hassinger 2002, Jachowski and others 2014b, Johnson and Gates 2009, Kniowski and Gehrt 2014, Menzel and others 2005a, Rommé and others 2002). Home range size may decrease throughout summer (Bergeson and others 2013), but there is no apparent difference in home range area among different reproductive conditions (Womack and others 2013a). Reported fall home ranges may be larger than summer home ranges (Rommé and others 2002), and the smallest reported average home range is 130.5 ha (Jachowski and others 2014b). Home ranges of individuals roosting in buildings may be smaller than those of individuals roosting in trees (Butchkoski and Hassinger 2002). Largest reported average home range size is 1137 ha (Womack and others 2013a). Indiana bats may travel over 4 km from roosts while foraging (Butchkoski and Hassinger 2002, Murray and Kurta 2004, Rommé and others 2002).

At the landscape scale, Indiana bats consistently prefer hydric and forested habitat types, and avoid agricultural and developed land cover types (Bergeson and others 2013, Brack 2006, Butchkoski and Hassinger 2002, Johnson and Gates 2009, Kniowski and Gehrt 2014, Menzel and others 2005a, Sparks and others 2005, Womack and others 2013b). Preferred habitat may change across seasons, with Brack (2006) noting increasing use of deciduous forest in the pre-hibernation period. Within home ranges, habitat use is similar to that of the landscape scale, with increased likelihood of use of forested wetland, and decreased use of shrub wetlands and developed lands (Jachowski and others 2014b). Depending on landscape configuration, Indiana bats may traverse agricultural areas using forest edges (Murray and Kurta 2004), or fly across fields (Kniowski and Gehrt 2014). The decision to fly across fields or traverse edges probably is tied to energetic costs and possibly exposure to predators, and use of forest edges probably is more likely when forest availability is greater.

Prey selection—Indiana bats are insectivores that are believed to forage primarily by aerial hawking. Dietary analyses have found that they prey on insects of the orders Lepidoptera, Coleoptera, Trichoptera, Diptera, Hymenoptera, Hemiptera, Homoptera, and Neuroptera; they also consume spiders (Caylor 2011, Feldhamer and others 2009, Lee and McCracken 2004, Tuttle and others 2006). Lepidopterans are a preferred food based on percent volume and frequency (Caylor 2011, Feldhamer and others 2009, Lee and McCracken 2004, Tuttle and others 2006).

Response to Forest Management

Perhaps due to complications of conducting manipulative experiments with endangered species, there are few direct studies on effects of forest management and no systematic investigation of effects of different forest management techniques on Indiana bats. Consequently, available information is derived from occasions when Indiana bats were found on managed landscapes.

Timber harvest—Indiana bats have been found in managed forest systems (Jachowski and others 2014b, Johnson and others 2010b) and may display a positive association between foraging and managed forest conditions (Womack and others 2013b). Indiana bats are often found roosting in a variety of managed forests during fall, including stands that have been selectively cut, clearcut, shelterwood cut, and burned (Brack 2006, Perry and others 2016). However, Indiana bat activity has also been found to be lower 2 to 4 years after forest thinning compared to pre-thinning, although activity levels may be greater in uneven-aged treatments than in either even-aged treatments or unharvested controls (Caylor 2011).

Dietary composition has been found to vary after forest management treatments, possibly related to changes in insect availability (Caylor 2011). Simulations of effects of timber harvest on Indiana bats suggest that creation of suitable foraging habitat may be maximized under low intensity timber-harvest scenarios such as single-tree and patch-cutting, with short-term availability of roosting habitat maximized using selection harvests (Pauli and others 2015b). However, single-tree selection over the long term (>1 cutting entry) leads to cluttered, uneven-aged structure, and no studies have examined long-term effects of this silvicultural system on bats. Although evidence is limited, preference for managed forests, greater activity in partially harvested areas, and simulation results suggest that Indiana bats are at least tolerant to many forest management practices and may benefit from careful application of forest management techniques. It is possible that forest management activities that remove moderate amounts of basal area and promote development of potential roosting habitat may benefit Indiana bats, but robust documentation of potential positive effects would require considerable future study.

Fire—Few studies have investigated the effects of fire on Indiana bats. Johnson and others (2010b) found that in a landscape containing both burned and unburned forest, male Indiana bats readily used burned stands for roosting, and roost switching behavior did not differ between burned and unburned stands. In burned stands, Indiana bats roosted in fire-killed red and sugar maples, whereas in unburned stands, they roosted primarily in live hickories, oaks, and maples (Johnson and others 2010b). Selection for fire-killed maples corresponds with findings of Ford and others (2016) who suggested that prescribed fire increased overall availability of roosting opportunities for northern long-eared bats, which mitigated loss of roosts caused by fire. In 1 of 3 study areas in Arkansas, Perry and others (2016) found male Indiana bats during the fall preferred mature forest stands (≥50 years old) that had been recently burned and stands burned multiple times over the previous 10 years for roosting, whereas mature forests that were not burned were used at a lower proportion than their availability (fig. 12). MacGregor and others (1999) found male Indiana bats during the fall roosted twice as often as expected in an area burned frequently for red-cockaded woodpeckers (*Leuconotopicus borealis*) during 1 of 2 years of sampling. Johnson and others (2010b) found that roosts in burned stands occupied larger canopy gaps than roosts in unburned stands. Given the commonly held supposition that increased solar radiation is beneficial for bats, it may be that burning increases overall roost suitability in burned stands, at least for females during the summer maternity season.

Figure 12—Snag used by male Indiana bats (*Myotis sodalis*) during fall in an open pine stand burned frequently. (Photo by Stephen Brandebura, Arkansas State University)

Direct effects of growing-season burns on roosting bats are unknown, as no published studies have reported these effects. Average height of roost entrance for Indiana bats (summarized from 16 separate studies) was 5–16 m (U.S. Fish and Wildlife Service 2007), which may be high enough to avoid direct mortality during low-intensity fires. Bats roosting under pieces of bark, which are typically closed at the top but open at the bottom, may be more affected by rising heat and smoke, whereas bats in cavities are likely more protected (Guelta and Balbach 2005). Bats roosting in well insulated cavities located relatively high in the trees are unlikely to be subjected to injury during low-intensity prescribed burns (Perry 2012).

Dickinson and others (2010) created models predicting potential burns to ears, wings, or other non-furred parts of bats based on roost heights, fire intensity (flame length), and wind speed. Winds may reduce temperature and gas concentrations at roosting heights by distorting fire plumes. They suggest that bats roosting at heights above 12 m (wind speeds of 2 m/sec [4.5 mph]) to 22 m (wind speeds of 0 m/sec) would not be injured during intense controlled burns (flame lengths approximately 1.6 m high). Furthermore, they suggested models used to predict foliage scorch during prescribed burns may potentially be useful as surrogates for predicting injury to bats. Carbon monoxide levels at roosting heights are unlikely a concern when flame lengths (fire intensity) are <1.6 m, which are typically the most intense fires observed during most prescribed burns (Dickinson and others 2010). Models for carbon monoxide suggest that critical levels of blood carboxyhemoglobin may be reached during intense fires, but only in close proximity to flames, which limits potential danger to lower-height roosts.

If applied outside of the active season, it seems likely that prescribed fires may affect bats similarly to timber harvest, creating appropriate conditions for both roosting and foraging. Studies suggest fire generally has beneficial effects on bats by creating snags, reducing understory and midstory clutter, creating more open forests, and possibly increasing abundance of flying insects (Perry 2012). However, as with effects of timber harvest, additional study is suggested.

Threats

Federally endangered before WNS, the Indiana bat has been a species of conservation concern since 1967. Pre-WNS, populations of this species were increasing, largely as a result of comprehensive habitat management measures that protected both hibernacula and summer maternity habitat. Populations are once again on the decline as a result of WNS (Thogmartin and others 2012, 2013). Given effectiveness of pre-WNS habitat conservation efforts, the greatest threat to this species is WNS. Additive mortality resulting from habitat loss or disturbance during maternity season may be a threat to local populations, but effective conservation measures already in place should limit risk. As with all species experiencing rapid declines, loss of genetic diversity following a potential WNS-related population bottleneck may lead to further population declines. Secondarily, over the next several centuries, changes in climate may also reduce total available habitat across the species' range and shift populations to the Northeastern United States and the Appalachians Mountains (Loeb and Winters 2013). Climate change also is likely to shift roost preference, as a recent analysis has shown that range-wide variation in bat roost selection is related to mean summer temperature (Fabianek and others 2015).

Research Questions and Needs

Much is known about the Indiana bat, but many questions remain unanswered. Research priorities include:

- **Effective treatment for WNS infections.** The greatest threat to survival of the species is WNS. Although declines in Indiana bats due to WNS have not been as dramatic as other bat species, unless this species can adapt to WNS, an effective treatment for the disease may be required to prevent it from becoming functionally extinct over much of its range.

- **Effects of long-term changes in habitat conditions and availability.** Maintaining adequate roosting habitat will continue to be a challenge for land managers. However, given the wide breadth of habitat types used, loss of habitat seems unlikely except for fragmentation in the Midwestern United States. A greater concern is whether long-term changes in habitat structure and forest community composition will have additive impacts with WNS. Additionally, changes in cave hibernacula environments resulting from climate change may affect the species' distribution.

- **More effective models to predict locations of potential roost trees.** Current information is insufficient and not standardized to allow accurate prediction over managed forest landscapes. In particular, more information is needed on how the parameters often recorded by forest managers (i.e., basal area, midstory density) relate to potential roost locations.

- **Studies on effects of forest management on Indiana bats are few.** Consequently, information is needed on effects of various silvicultural systems and prescribed burning on Indiana bat roosting and foraging.

- **How Indiana bats use forested landscapes near hibernacula during spring staging and fall swarming.** Preparation for hibernation and emergence from hibernation are critical for ensuring subsequent survival.

Regulations

Under the National Environmental Policy Act, individual Federal projects must be assessed for potential effects on endangered species that may be present in an area. This act covers Federal lands and projects funded with Federal money. For example, on National forests and military installations where land and range management routinely occurs, each site has a comprehensive plan (e.g., forest plan) that outlines standards for management. In addition, most sites within the range of the Indiana bats have formally consulted with USFWS in development of their plans and have received non-jeopardy biological opinions and incidental take statements (Krusac and Mighton 2002). These formal consultations are intended to balance the need to conduct land management activities and the need to minimize but not eliminate "take" of Indiana bats (Dickinson and others 2009). Because most Federal entities negotiate separately with their local USFWS field office, management standards (e.g., snag retention guidelines, smoke guidelines, buffers around hibernacula) for Indiana bats may differ among sites (Dickinson and others 2009). Activities that deviate from established and approved plans may require additional formal consultation with USFWS.

Similar to Federal lands, non-Federal and private landowners may negotiate with USFWS to develop habitat conservation plans (HCPs). Under an HCP, incidental take statements are issued by USFWS after consultation, again with the goal of balancing the need for land management and minimizing take.

TRI-COLORED BAT

(*Perimyotis subflavus*)

Introduction

The tri-colored bat (*Perimyotis subflavus*), formerly known as the eastern pipistrelle (*Pipistrellus subflavus*), is a small forest-dwelling bat in the family Vespertilionidae (Fujita and Kunz 1984). This species is distributed from southeastern Canada to Honduras and reaches as far west as Oklahoma (fig. 13). Evidence suggests that its range is expanding westward (Armstrong and others 2006, Geluso and others 2005, Kurta and others 2007). Tri-colored bats are the second smallest bat species in eastern North America, with a body mass ranging from 3.3 to 8.0 grams, a total length of 77 to 89 mm, and a forearm length of 31.4 to 34.1 mm (Fujita and Kunz 1984, Whitaker and Hamilton 1998) (fig. 14). Sympatric species over much of the species' range in the Eastern United States include the Indiana bat, little brown bat, northern long-eared bat, and big brown bat. Due to a paucity of research, little is known about the ecology of the tri-colored bat in forests, especially when compared to the better-studied northern long-eared and Indiana bats.

Growing Season Roost Ecology

Brack and Mumford (1984) speculated that the tri-colored bat range is constrained by geographic distribution of hibernacula. However, there is little robust evidence for this as stable isotope data indicate that this species is a regional migrant (Fraser and others 2012) and acoustic data indicate their ability to cross long geographic distances such as the Great Lakes (Thorne 2014). Furthermore, tri-colored bats are found hibernating in culverts, old bunkers, and other man-made structures in areas without caves from Texas across the Southeastern United States (Jones and Pagels 1968, Sandel and others 2001), and its distribution extends into tropical regions of Central America and southern Mexico. Exact distances migrated are unknown, but it appears that males migrate longer distances than females (Fraser and others 2012). Patterns of acoustic detection during the late summer and early fall suggest that migration may be in mid-August (Dzal and others 2009, Thorne 2014), with bats in the Midwestern United States entering hibernacula sometime between late-September through mid-October (Damm and Geluso 2008).

Figure 13—Approximate tri-colored bat (*Perimyotis subflavus*) range. Range data modified from National Atlas North American bat ranges (U.S. Geological Survey 2014).

Tri-colored bats may begin forming maternity groups as early as mid- to late April. During the summer maternity season (generally April–July), tri-colored bats are known to roost in buildings (Jones and Suttkus 1973), live and dead foliage, other vegetation (including lichens and Spanish moss), and exfoliating bark (Farrow and Broders 2011, Poissant and others 2010, Veilleux and others 2004, Veilleux and Veilleux 2004). In southern locations, summer roosts may also serve as hibernacula (Jones and Suttkus 1973). Tri-colored bats form small maternity

Figure 14—An adult tri-colored bat. (Photo by Andrew Kniowski, Virginia Polytechnic Institute and State University)

colonies, with a maximum reported colony size of 29 individuals (Whitaker 1998), and mean colony sizes of 10–18 (Poissant 2009, Whitaker 1998). Although colonies are generally believed to contain primarily females, in at least one instance, adult males have been found in almost equal proportion to females within colonies (Jones and Suttkus 1973).

Although the social structure of maternity colonies has not been assessed, colonies appear to be distinct social groups with little to no interchange of individuals among groups (Poissant 2009). Roost switching may occur as often as every 2.5 days (Poissant 2009), but may occur less often[1], with individual bats using multiple roosts (Perry and Thill 2007a, Veilleux and Veilleux 2004). Compared to other temperate foliage-roosting species, tri-colored bats have greater roost-site fidelity during summer, with individuals remaining in the same roost for a maximum of 17–33 consecutive nights (Perry and Thill 2007b, Veilleux and others 2003). Movement of all colony members is common (Poissant 2009, Whitaker 1998). Most of the time in roosts (77 percent) is spent resting, with 16 percent of time spent in an alert condition (Winchell and Kunz 1996).

Historic estimates suggest survival peaks at approximately 3.5 years with males having greater survival than females (Davis 1966), although the method used to assess survival was not robust by current analytical standards. Litter size is larger than those of similarly sized bats in eastern North America, with a reported average litter size of 1.93–1.96 (Hoying and Kunz 1998). Parturition occurs between late May and early July (Whitaker 1998). Juvenile body mass and growth are closely related to ambient and roost temperature, rainfall, and availability of insect prey (Hoying and Kunz 1998). Volancy generally is attained by approximately 4 weeks of age (Whitaker 1998). Adult females may abandon maternity roosts shortly after young are volant, although juveniles may remain longer (Whitaker 1998). Capture ratios in the Southeastern United States indicate a sex ratio of 0.4F:1M juveniles, and an adult sex ratio of 5.0F:1M (Miller 2003). It is unlikely that the adult population truly is skewed so strongly towards females, and it is relatively common in many locations to capture more males than females. Indeed, Perry and others (2010) found the opposite trend, with 1F:3M. In part, detection of skewed sex ratios may be biased by proximity of sampling to maternity colonies.

Stand and landscape condition—Range of the tri-colored bat encompasses a considerable portion of eastern North America. Although the species has been captured across diverse forest types, studies on forest associations of this species are limited. Roosting behavior of this species in forests has been documented in mixed pine-hardwood stands in the Ouachita Mountains in Arkansas (Perry and others 2007, 2008; Perry and Thill 2007a), deciduous hardwoods in western Indiana (Veilleux and Veilleux 2004), and hardwood-boreal transition Acadian forest in Nova Scotia (Farrow and Broders 2011, Poissant 2009). In the Ouachita Mountains, small-scale roost site selection (<250 m) was positively related to area of mixed pine-hardwoods >100 years old, group selection cuts, and thinned mature (>50 years old) stands. In contrast, landscape scale roost site selection (>1000 m) was negatively related to area of immature pine stands 15–29 years old and area of mixed pine-hardwoods 50–99 years old, but positively related to largest forest patch size and patch adjacency (Perry and others 2008). Additionally, roosts reported by Perry and others (2007, 2008) were farther from roads than random, and most were in unharvested 50–99 year old mixed pine-hardwood or hardwood stands. In the Acadian forests of Nova Scotia, small-scale roost site selection was positively related to number of trees with useable lichen substrate (*Usnea trichodea*), and percent softwood immediately surrounding roosts, and negatively related to distance from water. Because studies of roosting behavior are limited, it is difficult to generalize these behaviors across regions.

Roost characteristics—Buildings reported as roosts include houses and abandoned military bunkers (Jones and Suttkus 1973, Whitaker 1998). Nonetheless, foliage roosts appear to be the preferred roost type in forests during summer (Perry and Thill 2007b, Poissant and others 2010, Veilleux and Veilleux 2004). In the Ouachita Mountains of Arkansas, all roosts were in foliage, with 50 percent of female and 91 percent of male roosts in dead leaves suspended in deciduous trees; 43 percent of maternity colonies were in dead needle clusters suspended in large, live pines (fig. 15) (Perry and Thill 2007b). In Indiana, all roosts by females were in live or dead deciduous tree foliage (Veilleux and others 2004). In the Acadian forest of Nova Scotia, female tri-colored bats roosted exclusively in beard lichen (*Usnea trichodea*) found primarily in boreal conifers (Poissant and others 2010). Dead leaf clusters used for roosting can range from a single dead leaf to clusters >30 cm in diameter, and large dead limbs containing multiple clusters of dead leaves have been documented as maternity colonies (Perry and Thill 2007b).

Trees containing female roosts in Arkansas were larger than random trees, whereas trees containing male roosts did not differ from random (Perry and Thill 2007b). It seems likely that abundance of suitable substrate is an important criterion for roost selection, as trees containing tri-colored bat roosts in Nova Scotia had a greater amount of *U. trichodea* coverage than random trees (Poissant and others 2010). Reproductive condition impacts roost selection, with reproductively active females roosting at lower levels in the forest strata, closer to permanent water sources, and farther from the nearest forest/field edge than non-reproductive females (Veilleux and others 2004).

Figure 15—Tri-colored bat (*Perimyotis subflavus*) maternity colony located in suspended dead pine needles 20 m above the ground in a live 40-cm d.b.h. pine. (Photos by S. Andrew Carter, U.S. Forest Service)

Tree species used/preferred—Few studies have assessed selection preferences for tree species used by the tri-colored bat. It is clear, however, that *U. trichodea* lichen is a preferred roost type in Nova Scotia (Poissant and others 2010). With regard to tree species used for roosting, spruce trees (*Picea* sp.) have been used extensively in Nova Scotia (Poissant and others 2010), and oaks were the most used species reported for reproductive females in Indiana (Veilleux and others 2004) and for males and females in Arkansas (Perry and Thill 2007b). Female maternity colonies in Arkansas were often found in clusters of dead pine needles in large overstory shortleaf pines (Perry and Thill 2007b).

Roosting area space use—Adult tri-colored bats exhibit inter-annual site fidelity, with juveniles exhibiting natal site fidelity (Veilleux and Veilleux 2004). However, temporal extent of this fidelity is unclear. Roosting area of individual bats appears to be relatively small (≤2.3 ha) (Veilleux and Veilleux 2004). Roosting area of maternity colonies is variable in size, with a reported range in Nova Scotia between 1.6 and 77.4 ha (mean = 22.8), and contain an average of 22.8 roosts (Poissant 2009).

Acoustic Activity Patterns and Foraging Ecology

Because acoustic detectors collect information across the bat species community, there is a relatively greater amount of acoustic information on tri-colored bats than capture and radio-tracking data. Additionally, it is worth noting that the echolocation calls of tri-colored bats are easy to distinguish from bats of the genus *Myotis* due to some diagnostic call characteristics. Echolocation calls from tri-colored bats range in frequency from approximately 40 to 49 kHz (fig. 16).

Stand and landscape condition—At the landscape level, studies have found the amount of nonforest landcover to be negatively related to activity (Farrow and Broders 2011), and the amount of forest to be negatively related with activity while fragmentation had no impact (Ethier and Fahrig 2011). In a savannah-woodland gradient in the Missouri Ozark Highlands, occupancy was found to have a weak negative relationship with both percent forest and percent urban landcover (Starbuck and others 2015). Thus, the particular effects of landscape condition on activity and presence remain unclear.

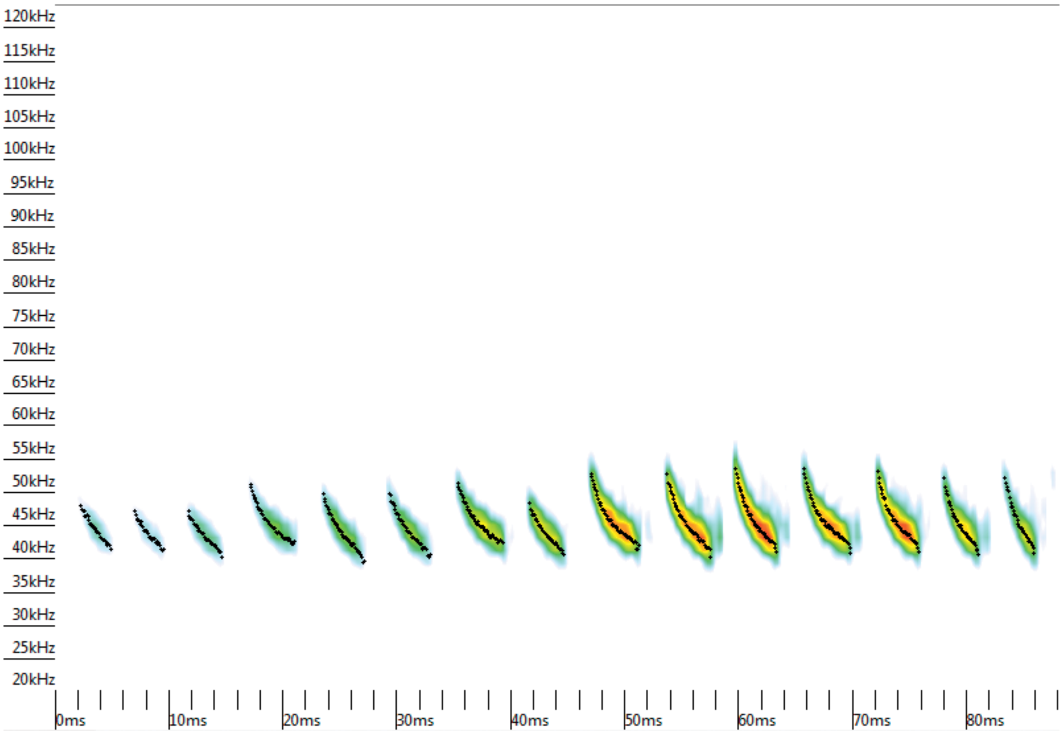

Figure 16—Echolocation call recorded from a captured and hand-released tri-colored bat (*Perimyotis subflavus*) showing both full spectrum and zero-crossing data.

At the stand level, the exact relationship between activity and forest structure is moderately well understood. Several studies have indicated a positive association between activity and canopy cover and forest age (Ford and others 2006a, Johnson and others 2010a), with activity in forests being greater at sites with low to moderate amounts of vegetation cover and density (Bender and others 2015, Ford and others 2006a, Johnson and others 2010a, Loeb and O'Keefe 2006, Yates and Muzika 2006). Activity levels were positively related to forest and corridor edge (Hein and others 2009, Morris and others 2010), and riparian areas (Broders and others 2003, Ford and others 2005, Johnson and others 2008, Owen and others, 2004, Vindigni and others 2009). Activity was low over open waterways and pools (Broders and others 2003, Johnson and others 2010a, Menzel and others 2005b, Owen and others 2004).

Foraging area and habitat—No studies have documented foraging patterns of radio-tagged tri-colored bats. However, acoustic data from the upper Coastal Plain in South Carolina suggested that feeding activity (feeding buzzes) did not differ between canopy gaps and closed canopy forests; between gaps of different sizes; between harvested or unharvested forests; or among gap edges, gap centers, and adjacent forest (Menzel and others 2002a).

Prey selection—Dietary analysis indicates that Trichoptera, Coleoptera, Diptera, and Hymenoptera form a substantial proportion of the tri-colored bat diet (Caylor 2011, Feldhamer and others 2009).

Response to Forest Management

Few studies have assessed response of tri-colored bats to forest management activities, although the species is known to occur in intensively managed landscapes throughout eastern North America (Bender and others 2015, Brooks 2008, Caylor 2011, Morris and others 2010, Owen and others 2004, Vindigni and others 2009). Activity of tri-colored bats was apparently unaffected by prescribed burning in pine stands (Loeb and Waldrop 2008), with no apparent relationship to time since burning (Armitage and Ober 2012).

In an actively managed forest landscape of Arkansas, tri-colored bats roosted only in stands with a hardwood component that retained an overstory ≥50 years old (Perry and Thill 2007b). In that study, 48 percent of male roosts were in partially harvested stands (group selection stands or stands with overstory reduction and midstory removal), but 88 percent of those roosts were located in unharvested greenbelts [including streamside management zones (SMZs) or riparian buffers] that were retained within harvested stands. No female roosts were found in partially harvested portions of stands (Perry and Thill 2007b). The common denominator among roost sites used by tri-colored bats in that study was the presence of a well-developed, hardwood-dominated midstory.

Potential direct effects of fire on tri-colored bats are unknown. Mean roost heights in forests have been reported as 17.7 m in Indiana and 12.5 m in Arkansas (Perry and Thill 2007b, Veilleux and others 2004), suggesting bats may roost high enough to avoid negative direct effects during low-intensity burning. Given the highly flammable nature of their roost substrate (elevated dead leaves), direct effects of fire could be negative, but no studies have examined this relationship.

Threats

Although relatively common and locally abundant before WNS, the tri-colored bat is now of conservation concern across its temperate distribution. Population declines of this species following WNS have been great, and risk of local extirpation is believed to be substantial (Ford and others 2011, Frick and others 2015). Given the cosmopolitan nature of their distribution, including Mexico and Central America, extinction is unlikely, but extirpation from some areas in North America is possible. The greatest threat to this species is WNS. Wind turbines also have killed significant numbers of tri-colored bats (Arnett and others 2008). Additional mortality resulting from habitat loss or disturbance during the maternity season may be a threat to local populations. In the long term, loss of genetic diversity following WNS may lead to further population declines. This may be a larger risk for the tri-colored bat than the northern long-eared bat as genetic evidence suggests that tri-colored bats survived a historically recent population bottleneck (Martin 2014). Threats from habitat loss or disturbance resulting from forest management are unknown, but use of dead foliage roosts, which generally have shorter lifespans than snags, suggests that this species is highly plastic and adaptive in response to forest habitat management at small spatial scales. Moreover, because population decline is due to WNS rather than habitat loss, and because the species range was expanding pre-WNS (Kurta and others 2007), it may reasonably be assumed that habitat availability is not a limiting factor for this species. Avoidance of habitat manipulation and tree removal that affects roost trees during the active maternity season (mid-May through early August) should be sufficient to avoid mortality related to tree-felling in maternity areas. Moreover, given the habitat plasticity demonstrated by this species, it is unlikely that tree felling operations below the landscape scale will have population-level effects.

Research Questions and Needs

Many questions remain unanswered relative to the ecology of the tri-colored bat. Research priorities include:

- **Effective treatment for WNS infections.** The greatest threat to survival of the species is WNS. If tri-colored bats are unable to adapt to this disease, an effective treatment for WNS may be one of the few options to prevent tri-colored bats from becoming functionally extinct over portions of their range.

- **Forest-habitat relationships.** Significant study is suggested to fully understand the life history and ecology of this species.

- **Effects of forest management.** Studies are needed to document the specific effects of forest management at both the short and long term. Understanding effects of roost-site disturbance could be highly beneficial to land managers for forest planning.

- **Effects of long-term changes in habitat conditions and availability:** Studies are needed to understand how long-term changes in habitat structure and forest community composition, and changes in cave hibernacula conditions resulting from climate change might shift the distribution of this species.

- **Range-wide genetic diversity of the species.** Limited genetic data are available on this species. Efforts to understand the genetic diversity of the tri-colored bat could be beneficial for long-term planning of population recovery and assessment of species extinction risk.

- **How tri-colored bats use forested landscapes near hibernacula during spring staging and fall swarming.** Preparation for hibernation and emergence from hibernation are critical for ensuring subsequent survival.

CONCLUSIONS

Northern long-eared, tri-colored, and Indiana bats are forest-obligate species, but display different relationships within the forests they inhabit. Despite unique relationships between each species and forests, all display variability in behavior across their range, with great degrees of flexibility in habitat selection. Recent work with bat habitat selection and behavior indicates that some variability in roost selection (Fabianek and others 2015) and roost switching behavior (Patriquin and others, in press) may be related to local climatic conditions. At the larger, distribution-wide scale, differences in habitat selection are closely tied to local landscape configuration and forest structural condition.

Historically, ecology of northern long-eared bats has been considered similar to Indiana bats, primarily due to overlap in roost-tree characteristics. However, several factors have been found to differ between the two species. First, although both species have defined social structures and both use roosts in a hierarchical fashion, it is not apparent that social structure and behavior are identical (Silvis and others 2014a, 2014b). Additionally, size of area used for roosting and foraging differs substantially between these two species, with Indiana bats using space at scales nearly an order of magnitude greater than those of northern long-eared bats (Silvis and others 2014a, 2014b). Indiana bat roost selection also varies subtly from that of northern long-eared bats (Carter and Feldhamer 2005, Foster and Kurta 1999, Timpone and others 2010). Although both species typically select roost trees larger than surrounding trees and sites with canopy gaps, roost trees used by Indiana bats are generally larger than those used by northern long-eared bats. Roost type also varies, with Indiana bats using exfoliating bark as roosts more consistently than northern long-eared bats, which typically use cavities to a greater extent. Moreover, northern long-eared bats may roost further away from aquatic areas than Indiana bats (Jung and others 2004). In general, roost selection and landscapes used by the Indiana bat are more consistent across the species' range than that of the northern long-eared bat. Relative to the above characteristics, tri-colored bats are substantially different from both species. In particular, tri-colored bats use foliage roosts and form smaller and less intensely social groups than either northern long-eared or Indiana bats.

All three species reviewed are capable of persisting in fragmented landscapes that consist of variable mixtures of forest, agriculture, and to some extent, exurban development. Based on the studies reviewed, Indiana bats may be better suited to fragmented environments than tri-colored or northern long-eared bats. It is important to note that this perceived tolerance may be due to study-location bias, as many bat researchers studied Indiana bats in small woodlots in fragmented landscapes. Relatively little is known about how changing landscape configuration affects these three species of bats, particularly when changes consist of large-scale conversion of forests and mixed landscapes to more-intensive agricultural or developed land use. However, it is apparent from a number of studies that these three species may benefit from heterogeneous forest landscapes such as those created by active forest management, when heterogeneity encompasses forest type, age, and structural characteristics (fig. 17). Benefits of heterogeneous forest landscapes to bats may arise from beneficial juxtaposition of roosting and foraging areas.

Although northern long-eared bats do not appear as tolerant of landscape fragmentation as Indiana bats, this species is plastic in selection of forest stands and roosting habitat. They may capitalize on beneficial changes in habitat near existing roosts, as demonstrated by females shifting roosting and foraging areas to stands recently treated with prescribed fire (Ford and others, in press; Johnson and others 2009; Lacki and others 2009b). Further, both simulations and experimental manipulations suggest that northern long-eared bats may be tolerant of some limited to moderate level of roost loss (Silvis and others 2014a, 2015a). Simulation results suggest that

Figure 17—A 70-percent overstory retention shelterwood harvest in an oak-hickory forest, Richland Furnace State Forest, Ohio. (Photo by Alexander Silvis, Virginia Polytechnic Institute and State University)

Indiana bats also may be tolerant of roost loss, but that response to roost loss may be less predictable (Silvis and others 2014b). Differences in responses between northern long-eared bats and Indiana bats to roost loss are unsurprising because these species differ in social roosting behaviors, roost switching, and numbers of roosts used per individual. In contrast, virtually nothing is known about the effects of roost loss on tri-colored bats. It seems reasonable to suspect that effects of roost loss on tri-colored bats are limited, given their preference for an abundant and highly ephemeral roosting resource (i.e., foliage that lasts for days to weeks rather than years). In all cases, tolerance to roost loss is predicated on avoidance of direct mortality resulting from roost loss or alteration.

Despite the ecological differences among these three species, there are a number of forest management approaches that could broadly benefit these and other bat species. Activities such as prescribed burning and harvesting are often constrained by numerous and sometimes conflicting objectives, including favorable burning parameters, public health and safety, site conditions, market conditions, and ecological objectives. For example, maintaining habitat for endangered red-cockaded woodpeckers may require burning during periods that may be less favorable for bats. Nonetheless, the following approaches could be used to improve roosting and foraging habitat and to reduce potential negative impacts on bats. It should be noted that these management options are not regulatory and do not supersede local, State, and Federal regulations, but will likely improve habitat conditions for bats. However, some items, such as hazard tree removal and timing of timber harvest, are explicitly mentioned in the 4(d) rule. Also, as noted above, response of bats to most forest management actions has largely not been studied; these suggestions should be viewed with this in mind:

- Where feasible during vegetation management operations, retain snags (especially those ≥20 cm d.b.h.) except where human safety or property may be jeopardized or when disease or insects associated with dead trees could pose a forest health threat.

- When possible, conduct hazard tree removal during the dormant season unless an immediate threat to human safety or property exists.

- Consider installing artificial roosts in areas lacking adequate roost structure, especially adjacent to ponds and along riparian areas. Artificial bark roosts have been found to be particularly effective for Indiana bats (Adams and others 2015).

- During timber marking and harvest, consider retaining some mature trees of species known to be preferred for roosting, such as live shagbark hickory. Retain trees that show signs of cavities, basal openings, or hollowing of the bole. Plan timber harvests to avoid the pup-rearing season (e.g., June–July as designated in the current 4(d) rule stipulations for northern long-eared bat), when feasible.

- Unless ecological or silvicultural objectives or limited burn windows require growing-season burns, consider conducting prescribed burns during the dormant season. Avoid burning during the pup-rearing season (e.g., June–July), when feasible.

- During spring and fall when bats are roosting in trees, consider minimizing prescription and use of intense burns when temperatures are <10 °C (50 °F) or when winds <8 kph (5 mph). To minimize potential impacts, conduct spring and fall burns during afternoons when ambient temperatures are greatest (fig. 18).

- In areas with continuous canopy cover, consider maintaining small (<2 ha) forest openings with abundant snags, especially in close proximity to hibernacula.

- Protect and maintain forest cover and snags in riparian areas. Consider maintaining continuous canopy cover over water sources and create ponds in areas lacking water sources.

- Consider maintaining diverse landscapes that include early successional patches, abundant edges, woodlands, savannas, and mature to older forest stands. Within mature forests, maintaining or encouraging a diversity of composition and structure (e.g., variable overstory basal area and midstory densities) could provide for diverse bat communities and benefit a wide array of other taxa.

Figure 18—Low intensity prescribed fire being applied to a 50-percent overstory retention shelterwood harvest in Richland Furnace State Forest, Ohio, to promote oak regeneration. (Photo by Andrew Kniowski, Virginia Polytechnic Institute and State University)

- Consider using thinning to limit length of time regenerating stands remain in dense, closed-canopy conditions and to accelerate stands from the stem-exclusion to the understory re-initiation phase. Consider midstory reductions in some mature stands to improve foraging habitat conditions and to promote canopy gap heterogeneity. Planting rows of seedlings farther apart during reforestation operations may extend the time to canopy closure and thin as operationally and economically feasible.
- Consider protecting cave and abandoned mine hibernacula from entry during the fall swarm through hibernation and spring emergence to prevent disturbance. Try to avoid activities such as dozer operations, tree felling, fire-line construction, or blasting in close proximity (within 0.4 km) to hibernacula during these periods. Consider hibernacula as smoke-sensitive areas during winter prescribed burns. Try to avoid activities in any season that might alter or change hibernacula airflow.

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Forest management activities can have substantial effects on forest structure and community composition and response of wildlife therein. Bats can be highly influenced by these structural changes, and understanding how forest management affects day-roost and foraging ecology of bats is currently a paramount conservation issue. With populations of many cave-hibernating bat species in eastern North America declining as a result of white-nose syndrome (WNS), it is increasingly critical to understand relationships among bats and forest-management activities. Herein, we provide a comprehensive literature review and synthesis of: (1) responses of northern long-eared (*Myotis septentrionalis*) and tri-colored (*Perimyotis subflavus*) bats—two species affected by WNS that use forests during summer—to forest management, and (2) an update to a previous review on the ecology of the endangered Indiana bat (*Myotis sodalis*).

Keywords: Bat conservation, forest management, forestry, habitat relationships, Indiana bat (*Myotis sodalis*), North America, northern long-eared bat (*Myotis septentrionalis*), roost, tri-colored bat (*Perimyotis subflavus*), white-nose syndrome.

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