Chapter 10
Bats and Gaps: The Role of Early Successional Patches in the Roosting and Foraging Ecology of Bats

Susan C. Loeb and Joy M. O'Keefe

Abstract Early successional habitats are important foraging and commuting sites for the 14 species of bats that inhabit the Central Hardwood Region, especially larger open-adapted species such as hoary bats (*Lasiurus cinereus*), red bats (*L. borealis*), silver-haired bats (*Lasionycteris noctivagans*), and big brown bats (*Eptesicus fuscus*). Forest gaps, small openings, and the edges between early successional patches and mature forest are especially important habitats because they are used by both open-adapted and clutter-adapted species. Several bat species select roosts in close proximity to early successional patches, perhaps to minimize foraging and commuting costs. Future research on effects of early successional patch size, shape, vegetation structure, and connectivity on bat use, and the distribution of early successional habitats in relation to mature forest, roosting sites, and water sources will assist managers in providing the optimal types and distribution of early successional patches on the landscape.

10.1 Introduction

Fourteen species of bats inhabit the forests of the Central Hardwood Region, USA (Whitaker and Hamilton 1998, Fig. 1.1, Table 10.1). These bats rely on forest ecosystems for resources essential for survival and reproduction, including day and

S.C. Loeb (✉)
Research Ecologist with the Upland Hardwood Ecology and Management Research Work Unit, USDA Forest Service, Southern Research Station, Department of Forestry and Natural Resources, Clemson University, Clemson, SC 29634, USA
e-mail: sloeb@fs.fed.us

J.M. O'Keefe
Department of Biology, Indiana State University, 600 Chestnut Street, Terre Haute, IN 47809, USA
e-mail: Joy.O'Keefe@indstate.edu

C.H. Greenberg et al. (eds.), *Sustaining Young Forest Communities*, Managing Forest Ecosystems 21, DOI 10.1007/978-94-007-1620-9_10,

Table 10.1 Bats of the Central Hardwood Region and their primary roosting and foraging habitats

Common name	Scientific name	Summer roosting habitat	Winter roosting habitat	Major foraging areas
Rafinesque's big-eared bat	*Corynorhinus rafinesquii*	Caves, mines, or large hollow trees	Caves, mines, or large hollow trees	Oak-hickory forests
Ozark big-eared bat	*C. townsendii ingens*	Caves	Caves	Upland hardwood forests, edges
Virginia big-eared bat	*C. townsendii virginianus*	Caves	Caves	Cliffs and mixed mesophytic forests
Big brown bat	*Eptesicus fuscus*	Live and dead hardwood and pine trees; buildings	Caves, mines, rock outcrops, buildings	Forests, edges, and openings
Silver-haired bat	*Lasionycteris noctivagans*	Live and dead trees	Live trees and rock outcrops	Open areas
Red bat	*L. borealis*	Live hardwoods	Live hardwoods and leaf litter	Forests, forest edges, openings
Hoary bat	*L. cinereus*	Live hardwoods and pines	Live hardwoods and leaf litter[a]	Forest edges and openings; above canopy
Southeastern bat	*Myotis austroriparius*	Large hollow trees	Caves	Riparian areas, bottomland hardwoods
Gray bat	*M. grisescens*	Caves	Caves	Riparian areas
Small-footed bat	*M. leibii*	Talus slopes, cliff faces, bridges	Caves, mines, talus slopes, artificial structures	Closed canopy forest
Little brown bat	*M. lucifugus*	Buildings and snags	Caves and mines	Riparian areas, open canopy forests
Northern long-eared bat	*M. septentrionalis*	Hardwood and pine snags	Caves and mines	Closed canopy forests
Indiana bat	*M. sodalis*	Hardwood and pine snags	Caves and mines	Forest interior, edges, and open areas
Evening bat	*Nycticeius humeralis*	Live and dead trees	Live and dead trees	Riparian areas
Tri-colored bat	*Perimyotis subflavus*	Live hardwoods	Caves, mines, artificial structures	Forest interior, edges, and open areas

[a] No studies on winter roost habits – assume similar to red bats based on anecdotal information

night roosts (Barclay and Kurta 2007; Carter and Menzel 2007; Ormsbee et al. 2007), foraging sites (Lacki et al. 2007), and drinking water (Hayes and Loeb 2007). In turn, bats play an important role in forest ecosystem function (Marcot 1996). Eastern bats consume large amounts of insects per day (e.g., Kurta et al. 1990); many of these are important agricultural and forest pests (Jones et al. 2009). Bats also redistribute nutrients across the landscape and can create nutrient hotspots below their tree roosts (Duchamp et al. 2010). Because tree roosts are often near gaps or openings (Kalcounis-Rueppell et al. 2005), nutrient hotspots may be important in forest regeneration. Thus, understanding how management of forested ecosystems, including early successional habitats, affects bats is critical for the conservation and management of these species and for maintaining forest ecosystem health.

Many of the bats that inhabit the Central Hardwood Region are of conservation concern. The Indiana bat (*Myotis sodalis*), gray bat (*M. grisescens*), Ozark big-eared bat (*Corynorhinus townsendii ingens*), and Virginia big-eared bat (*C. t. virginianus*) are federally listed endangered species (USDI Fish and Wildlife Service 1984; 2007) and Rafinesque's big-eared bat, eastern small-footed bat, and southeastern bat are considered species of special concern (Harvey et al. 1999). Factors leading to the decline of these species include habitat loss and fragmentation, and disturbance and destruction of winter hibernation sites and summer maternity sites. Recently, these species and many other bats in the eastern USA have been facing additional threats. Since winter 2006–2007, five cave associated bats [the little brown bat (*M. lucifugus*), northern long-eared bat (*M. septentrionalis*), Indiana bat, small-footed bat (*M. leibii*), and tri-colored bat (*Perimyotis subflavus*)] have experienced severe population declines in the northeastern USA due to white-nose syndrome (Blehert et al. 2009). The big brown bat (*Eptesicus fuscus*) has also been affected by white-nose syndrome and the gray bat, Virginia big-eared bat, Ozark big-eared bat, Rafinesque's big-eared bat, and southeastern bat (*M. austroriparius*) may be at risk as this disease moves south and west (Szymanski et al. 2009). While non-cave hibernating bats such as the hoary bat (*Lasiurus cinereus*), red bat (*L. borealis*), and silver-haired bat (*Lasionycteris noctivagans*) have not been affected by white-nose syndrome to date, they are being impacted by wind energy development, particularly in the Appalachians (Arnett et al. 2008). For example, based on current mortality rates and projected number of turbines, estimated mortalities in the year 2020 in the mid-Atlantic region range from 33,000 to 110,000 individuals (Kunz et al. 2007). Because bats have low reproductive rates (Barclay and Harder 2003), population recovery will likely be slow (Racey and Entwistle 2003).

Although all bats in the eastern USA are insectivorous, they vary considerably in body size, wing morphology, and life history characteristics (Whitaker and Hamilton 1998). For example, body size ranges from 4 to 6 g for the small-footed bat and tri-colored bat to more than 25 g for the hoary bat. Some species are year round residents in an area (e.g., Rafinesque's big-eared bats) while others are short-distance migrants (e.g., tri-colored bats), regional migrants (e.g., Indiana bats, little brown bats), or long-distance migrants (hoary bat, red bat, and silver-haired bat). Further, some species rely on trees as their primary roosts while others roost in caves, mines, or artificial structures (Table 10.1). Thus, an examination of the responses of bats to

early successional communities or vegetation structure requires consideration of this variation in morphology and life history strategies.

Given concerns over the decline of early successional habitats (Greenberg et al., Chap. 1), combined with considerable concern over the viability of bats in the Central Hardwood Region, it is important to assess how forest management and the creation of early successional habitats may affect bats. Thus, our objective was to evaluate the use and importance of early successional habitats to bats in the Central Hardwood Region. Although there has been a substantial increase in research on bats in forest ecosystems in the past 15 years (Brigham 2007), there are still limited data on bats in the Central Hardwood Region. Thus, we drew upon research in other forest ecosystems to make inferences about the possible importance of early successional habitats for bats in the Central Hardwood Region. We primarily considered early successional habitats such as recently clearcut forests, wildlife openings, meadows, forest gaps, and grassy forest roads. We first considered use of early successional patches for foraging and commuting and then in roost site selection; we concluded with sections on managing early successional areas for bats in the Central Hardwood Region. We also recommend future research directions, including the importance of considering early successional habitats within the context of the larger landscape matrix.

10.2 Use of Early Successional Patches for Foraging and Commuting

Understanding and predicting bat foraging and commuting habitat is greatly aided by considering echolocation call structure and ecomorphology. Using these characteristics, bats can generally be placed along a continuum of open to closed canopy specialists (Norberg and Rayner 1987; Fenton 1990). Species adapted to open environments are fast, agile flyers and have high aspect ratios (long, narrow wings), high wing loading (large body relative to wing area), and pointed wing tips. Their echolocation calls are usually high intensity, low frequency, and narrowband (Fig. 10.1a). In contrast, species with low aspect ratios, low wing loading, and rounded wingtips are slow but maneuverable flyers. Their echolocation calls are usually high frequency, lower intensity broadband calls (Fig. 10.1b). These species are better adapted to foraging in cluttered environments (i.e., those with many physical and acoustical obstructions such as branches and leaves). Species that are intermediate in these characteristics are often found using edges. Bats of the Central Hardwood Region can be generally placed along this continuum (Table 10.2). For example, hoary bats and silver-haired bats are considered open-space species, whereas Rafinesque's big-eared bats and northern long-eared bats are more likely to be found in cluttered spaces.

Most studies of bat foraging activity and habitat use have used acoustic detectors, although some studies have used radio-telemetry (Fig. 10.2). While the use of acoustic detectors over the past two decades has advanced our understanding of habitat use by bats (Brigham 2007; Lacki et al. 2007), there are many pitfalls and

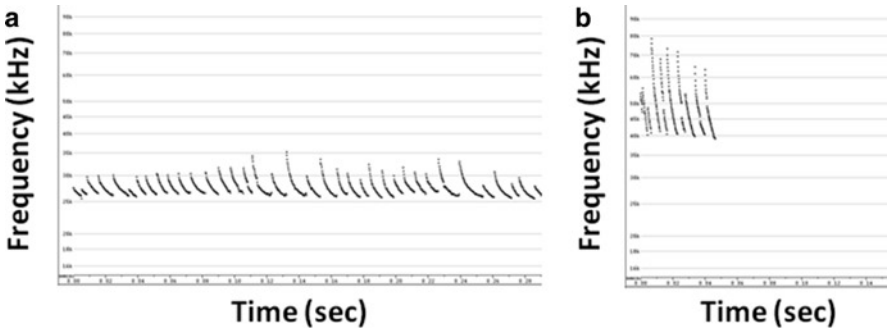

Fig. 10.1 The search phase echolocation calls of (**a**) a big brown bat, *Eptesicus fuscus*, and (**b**) a northern long-eared bat, *Myotis septentrionalis*

Table 10.2 Wing morphology indices from Norberg and Rayner (1987) and echolocation call structures of bats in the Central Hardwood Region

Species	Wing aspect ratio	Wing loading	Wingtip shape index	Echolocation call
Hoary bat *(Lasiurus cinereus)*	8.1	16.5	1.60	Narrow band, high intensity
Red bat *(L. borealis),*	6.7	14.0	1.26	Broad band, medium intensity
Big brown bat *(Eptesicus fuscus)*	6.4	9.4	1.09	Narrow band, high intensity
Evening bat *(Nycticeius humeralis)*	6.8	10.7	1.01	Broad band, medium intensity
Silver-haired bat *(Lasionycteris noctivagans)*	6.6	8.2	1.68	Narrow band, high intensity
Gray bat *(M. grisescens),*	6.4	8.2	1.79	Broad band, medium intensity
Tri-colored bat *(Perimyotis subflavus)*	6.2	5.6	2.05	Broad band, medium intensity
Small-footed bat *(Myotis leibii)*	6.1	6.7	2.96	Broad band, low intensity
Little brown bat (*M. lucifugus)*	6.0	7.5	3.20	Broad band, medium intensity
Northern long-eared bat *(Myotis septentrionalis)*	5.8	6.8	2.24	Broad band, low intensity
Indiana bat *(Myotis sodalis)*	5.4	6.5	5.56	Broad band, medium intensity
Rafinesque's big-eared bat *(Corynorhinus rafi nesquii)*	5.9	5.9	–	Broad band, very low intensity
Virginia and Ozark big-eared bat *(C. t. virginianus)*	5.9	7.2	2.31	Broad band, very low intensity

High aspect ratios indicate long narrow wings, high wing loadings indicate heavier body size relative to wing size, and higher wingtip shape indices indicate more rounded wingtips. Species are listed from top to bottom along the open-closed canopy continuum based on ecomorphology and echolocation call characteristics. No data are available for the southeastern bat

assumptions of the technique (Hayes 2000; Gannon et al. 2003). For example, it is not possible to distinguish age and sex of bats detected by recorders and thus, we must assume that habitat use is consistent among all sub-populations. Because there is currently no way to tell whether multiple recordings of a species at a site represent one individual detected multiple times or several individuals, the number of calls recorded cannot be used as an index of abundance (Weller 2007). It is also difficult to infer habitat selection or preference based on acoustic data because bat detectors

Fig. 10.2 Techniques used to determine use of different habitat types by bats. (**a**) An Anabat II bat detector system, (**b**) the Anabat II system deployed in the field, (**c**) an Indiana bat with a radio transmitter, and (**d**) tracking a bat with an antenna and receiver

measure resource use by populations and not individuals (Miller et al. 2003). If differential detectability among species and habitat types is not taken into account, areas where detection is best (e.g., open areas) may appear to be favored or species with higher intensity calls may appear to be more active (MacKenzie 2006). Finally, it is not possible to use acoustic detectors to assess foraging and commuting behavior for species with very low intensity echolocation calls, like big-eared bats (*Corynorhinus* spp.) (Fenton 2003). Nonetheless, acoustic detectors yield considerable data on relative activity of bats in early successional habitats and other habitat types, and allow researchers to examine use by multiple species in a variety of habitat types at the same time, thus controlling for factors such as weather, time of night, and stage of the reproductive cycle.

Much of the information on bat use of early successional habitats comes from studies that have examined the effects of timber harvesting on bat activity. In general, these studies have shown that overall activity and foraging activity are greater in recent clearcuts than in adjacent forest (Erickson and West 1996; Krusic et al. 1996; Grindal and Brigham 1998, 1999; Ellis et al. 2002). However, responses to harvesting often vary by species and in accordance with predictions based on ecomorphology and echolocation call structure. For example, open-space species such as silver-haired bats and hoary bats are more active in recently clearcut stands (2–8 years post-harvest) than in mature forests whereas clutter-adapted bats such as *Myotis* spp. are more active in mature forests than in recent clearcuts (Patriquin and Barclay 2003; Owen et al. 2004; Morris et al. 2010). However, some small species such as northern long-eared bats, Indiana bats, and tri-colored bats use open areas as well as mature forests (Ellis et al. 2002; Sparks et al. 2005; O'Keefe 2009).

While relative adaptations to clutter may influence use and avoidance of early successional habitats by large and small bats, predation risk and food availability may also contribute to the observed pattern. Faster flight might enable larger bats to evade predators in open areas while smaller bats might need the protective cover provided by forest canopy (Rydell et al. 1996). Food availability can also play a role although there are few data to support this. In some areas, nocturnal insect abundance is greater in early successional forest than mature forest (Lunde and Harestad 1986), while in other areas it is the same or greater in mature forest than in clearcuts (Kalcounis and Brigham 1995; Grindal and Brigham 1998; Burford et al. 1999; Grindal and Brigham 1999; Dodd et al. 2008; Morris et al. 2010). Some studies have found that bat activity is positively related to insect abundance (Kalcounis and Brigham 1995; Tibbels and Kurta 2003), while others have found no relationship between bat activity and insect abundance (Lunde and Harestad 1986; Grindal and Brigham 1999; Obrist et al. 2011). Morris et al. (2010) concluded that insect availability can be important in determining bat habitat use in an intensively managed forest landscape in the North Carolina Coastal Plain, but it plays a secondary role to stand structural characteristics. However, it should be noted that most studies have only identified potential prey to Order or Family and thus, factors such as prey size or preference have not been investigated. There is a positive relationship between bat body size and insect prey size, although larger bats take both large and small prey items (Aldridge and Rautenbach 1987; Barclay and Brigham 1991). If larger insects are restricted to open areas or are more vulnerable to capture by bats in open areas, then larger bats may select these areas because of the availability of preferred prey items. Conversely, smaller insects may seek the protective cover of forest, thus attracting small bats to late seral stage forests. We are not aware of any studies that have examined the relationship between insects and their habitat associations relative to body size or vulnerability to capture, but these types of studies are necessary to fully understand bat foraging in relation to early and late successional habitats.

Edges between early successional patches and stands in mid to late seral stages appear to be particularly important to medium- and small-sized bat species. For example, in Alberta and British Columbia, overall bat activity is greater along the edges of forests adjacent to recently clearcut patches than in the center (Crampton and Barclay 1996; Grindal and Brigham 1999). In a similar study in Alberta,

Hogberg et al. (2002) found that activity of *Myotis* spp. was also greater along edges of clearcuts than in the center. Hoary bats, red bats, and *Myotis* spp. are positively associated with edge in Ontario, Canada (Furlonger et al. 1987) as are bats of five genera in intensively managed forests in the Coastal Plain of South Carolina (Hein et al. 2009a). Activity of hoary bats, Brazilian free-tailed bats (*Tadarida brasiliensis*), tri-colored bats, big brown bats, evening bats (*Nycticeius humeralis*), and red bats is significantly greater at forest edges than in interior forest in the Coastal Plain of North Carolina (Morris et al. 2010). In Oklahoma, adult female Ozark big-eared bats forage in open areas, edges, and intact forests, but not all habitat types are used equally; edges are selected and interior forests are avoided, particularly during the post-lactation period (Clark et al. 1993). Radio-telemetry studies of Indiana bats and northern long-eared bats also suggest that edges are important for commuting (Murray and Kurta 2004; Henderson and Broders 2008).

Wind, insect availability, predation risk, and navigation may drive bats' preferences for edges (Verboom and Spolestra 1999). Foraging and commuting are more efficient along leeward edges, which are more protected from wind than open areas. Insects also tend to concentrate along leeward edges (Lewis 1970; Whitaker et al. 2000) making them particularly rich foraging grounds. Edges may also serve as navigation aids for short-distance movements (Verboom et al. 1999) and long-distance migration (Furmankiewicz and Kucharska 2009). Although several authors have suggested that edges provide protection from predators (Clark et al. 1993; Walsh and Harris 1996; Verboom and Spolestra 1999), Lesiński et al. (2009) found that tawny owl (*Strix aluco*) predation on bats was greater along forest edges than in forest interiors or open areas. Thus, the protective nature of edges needs further investigation.

Small openings or gaps within interior forests also appear to be important foraging and commuting areas (Hayes and Loeb 2007). For example, bat activity in wildlife openings or logging decks larger than 0.25 ha in red pine (*Pinus resinosa*) stands in Michigan is significantly greater than in adjacent thinned or unthinned stands (Tibbels and Kurta 2003) and bat activity in bottomland hardwood forests in South Carolina is significantly greater in 0.03 ha and 0.50 ha gaps than in 70-year-old forest (Menzel et al. 2002). Several studies in the Appalachian Mountains have also found that small openings and gaps are important foraging and commuting sites (Ford et al. 2005; Loeb and O'Keefe 2006; Schirmacher et al. 2007). In the upper Piedmont and mountains of South Carolina, big brown bats, red bats, tri-colored bats, and northern long-eared bats are more likely to be recorded at sample points with open vegetation regardless of stand age class than at points with medium or dense vegetation, indicating that they are using small gaps within mature forest as well as recently harvested stands and open fields (Loeb and O'Keefe 2006). In the Central Appalachians of West Virginia, occurrence of big brown bats, red bats, hoary bats, and little brown bats is positively related to gap width (Ford et al. 2005), and in the Allegheny Plateau presence of big brown bats, little brown bats, and tri-colored bats is positively associated with forest openings (Schirmacher et al. 2007). Bats may be attracted to small gaps and openings within mature forest for several reasons. Similar to recent clearcuts and other large early successional habitats, structural and acoustic clutter are lower in gaps than in intact forest and insect availability may also be greater in gaps

(Tibbels and Kurta 2003). Further, many bats select roost structures close to gaps (see sect. 10.3) either for thermal benefits from increased solar exposure or access to foraging sites (e.g., Willis and Brigham 2005; Perry et al. 2007a; O'Keefe et al. 2009). Forest roads and trails are also important foraging and commuting habitats. Several studies in Australia have found that bat activity is significantly greater on trails than in mature forest, even when the trails traverse dense regrowth forests (Law and Chidel 2001, 2002; Adams et al. 2009). Similarly, Zimmerman and Glanz (2000) found that bat activity in Maine was positively associated with gravel roads that functioned as edge between forests and open areas. In an intensively managed forest in the Coastal Plain of South Carolina, the odds of big brown bat, tri-colored bat, and Seminole bat (*L. seminolus*) occurrence were over five times greater if a road was present (Hein et al. 2009a). Forest trails and roads may be important because they combine the features of small gaps (i.e., reduced clutter) and edges (i.e., navigational aids and potential cover from predators).

To illustrate relative use of various early successional areas and mature forest by bats, we present data collected on the Nantahala National Forest in southwestern North Carolina. We used AnabatII bat detectors and zero-crossings interface modules (Titley Electronics, Australia) to passively record bat activity for two full nights each in one 80 year-old yellow-poplar-oak (*Liriodendron tulipifera-Quercus* spp.) forest, three gated roads 6–10 m wide, and three wildlife openings ≤ 3 ha. Gated forest roads and wildlife openings were planted in grasses and clover and maintained by annual or biennial mowing. Bat activity was far greater on gated roads and in wildlife openings than in the forested site (Fig. 10.3a). However, as in many other studies, use of roads and openings varied by species or phonic group. Hoary bats, which are open-space bats (Table 10.2), used wildlife openings to a much greater extent than roads (Fig. 10.3b). Clutter-adapted northern long-eared bats, which have echolocation calls and body morphology designed for gleaning insects from vegetation (Faure et al. 1993), rarely used openings but often used roads (Fig. 10.3b). Big brown bats, red bats, and tri-colored bats appeared to be more flexible in their use of early successional habitats than open or closed canopy specialists.

Many studies have examined the relationship between seral stage and bat activity at the stand level, but findings from recent landscape scale studies suggest that the importance of early successional patches may vary with scale. In the Ozark Highlands of Missouri, occupancy by big brown bats is positively associated with non-forested areas such as pastures or grasslands at the site level, but negatively associated with the percent of non-forested area in the surrounding landscape, whereas red bats are positively associated with non-forested habitat at both site and landscape scales (Amelon 2007). Site level characteristics have insignificant effects on little brown bat occupancy but the amount of non-forested habitats and pine forest in the surrounding landscape has a positive effect on their presence (Amelon 2007). Site occupancy of Indiana bats in Missouri is also positively related to the proportion of non-forested habitats in the surrounding landscape (Yates and Muzika 2006).

All early successional habitats are not equivalent and several factors may affect their relative use by bats including size, vegetation type, and position on the landscape. For example, big brown and hoary bat activity is greater in open fields with

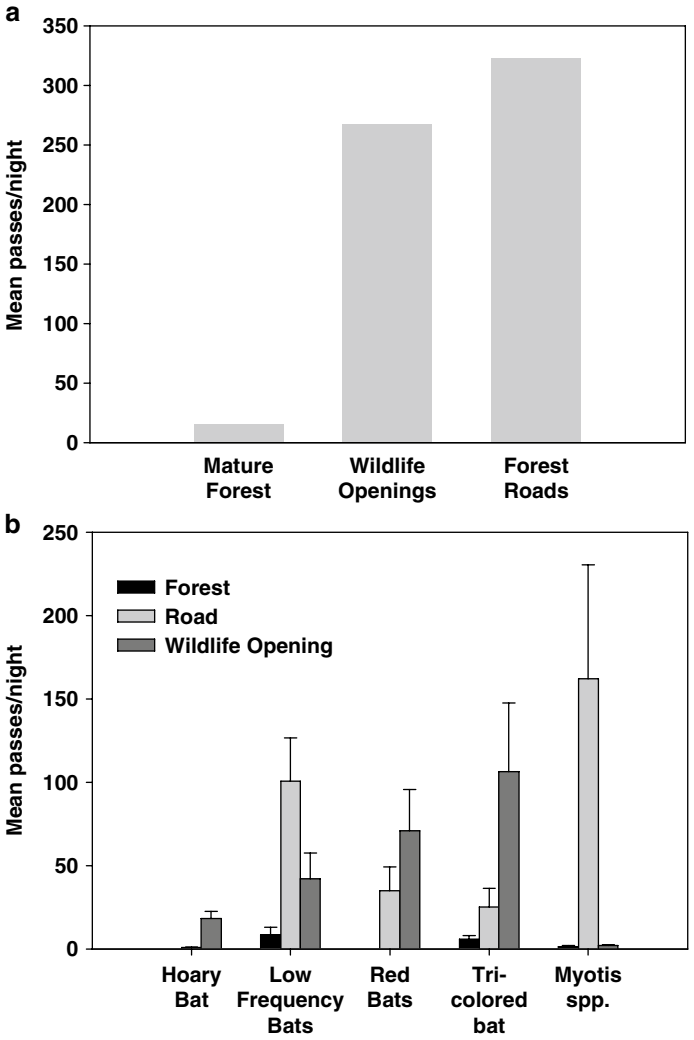

Fig. 10.3 Bat activity in intact forest, gated roads, and wildlife openings on the Nantahala National Forest, North Carolina in summer 2004. (**a**) Mean number of bat passes recorded per night for all species. (**b**) Mean number of passes per night by species or species group. Low frequency bats consisted of big brown bats and silver-haired bats and *Myotis* spp. consisted of northern long-eared bats, little brown bats, and small-footed bats

herbaceous vegetation maintained by mowing than in clearcut areas with regenerating saplings (Brooks 2009), and ponds in 0.4 ha fields are used more than ponds in 6.2–18.2 ha clearcuts <10 years old (Huie 2002). Differential use of open spaces may be due to differences in patch characteristics. For example, vegetation type and management history can affect insect abundance and diversity (Swengel 2001),

and there is some indication that patch size can affect bat activity. Grindal and Brigham (1998) found that bat activity in British Colombia tends to decrease with increasing clearcut size (from 0.5 to 1.5 ha); in the Coastal Plain of South Carolina, foraging activity of hoary bats is greater in small gaps (0.03 ha) but activity of other species does not differ between large and small gaps (Menzel et al. 2002). Patch size effects may be related to the reluctance of some bats to cross large open areas. Swystun et al. (2001) found that edges of isolated forest patches were not used as often as edges of forest patches close to mature forest, and the close adherence of northern long-eared bats and Indiana bats to hedgerows while commuting suggests that some bats may avoid large open spaces (Murray and Kurta 2004; Henderson and Broders 2008). Thus, position on the landscape and connectivity may be important factors affecting bat activity in early successional patches. However, we are unaware of any studies that relate use of early successional patches to their distribution on the landscape.

Unlike early successional habitats, forests in mid-seral stages (e.g., closed canopy sapling-pole stage) are rarely used by bats (Crampton and Barclay 1996; Erickson and West 1996; Krusic et al. 1996; Law and Chidel 2001; Ellis et al. 2002; Loeb and O'Keefe 2006; Adams et al. 2009). Thus, early successional habitats that are allowed to regenerate to closed canopy forest will likely become unsuitable bat foraging and commuting habitat for a given period. However, the horizontal edges created by the canopies of mid-successional forests may be attractive to bats and thinning may be used in mid-successional closed canopy forest to minimize the time these stands are unsuitable (Guldin et al. 2007) and create more bat-suitable stand structures (Humes et al. 1999; Loeb and Waldrop 2008).

10.3 Early Successional Habitats and Roost Site Selection

Bat roosts have many critical functions including serving as sites for social interactions and rearing young, and providing protection from the elements and predators (Kunz and Lumsden 2003). Bats that roost in trees during the non-hibernation period can be divided into those that roost in crevices or cavities (including those that roost between the bark and bole) and those that roost in foliage (Kunz and Lumsden 2003). Both groups are represented in the Central Hardwood Region (Table 10.1).

Over the past 15–20 years many studies have investigated use and selection of day roosts by tree-roosting bats during the summer reproductive period; however, less work has been conducted on foliage-roosting species (Barclay and Kurta 2007; Carter and Menzel 2007). Most studies have focused on tree and stand level features and less attention has been given to relationships between larger-scale features and roost site selection (Kalcounis-Rueppell et al. 2005). In general, tree-roosting bats select roosts within mature forests (Barclay and Brigham 1996) and avoid using recently harvested stands and other open areas even when roost trees may be available (e.g., Arnett and Hayes 2009). However, there are some exceptions. In some areas of the Pacific Northwest, western long-eared bats (*M. evotis*) roost in stumps in 8–9 year old clearcuts (Vonhof and Barclay 1997) or rock crevices in open areas

close to forest edges (Rancourt et al. 2005). In the Southern Appalachians, red bats occasionally roost in < 5 year-old hardwood stands (O'Keefe et al. 2009) and in the Piedmont of South Carolina they have been found roosting in pastures and yards (Leput 2004). Though maternity colonies of northern long-eared bats usually roost in large dead trees in mature stands, a few colonies in the Southern Appalachians were found roosting in leave trees within 2–4 year old shelterwood cuts (O'Keefe 2009). Small canopy gaps in mature forest are also important roost sites for bats. For example, Indiana bats in Missouri and Illinois primarily roost within or on the edges of forest openings (Callahan et al. 1997; Carter and Feldhamer 2005) and silver-haired bats in northeastern Washington roost exclusively in forest gaps (Campbell et al. 1996). In general, cavity or crevice-roosting bats tend to select roosts in areas with lower canopy cover than the surrounding forest (Kalcounis-Rueppell et al. 2005), presumably for increased solar radiation and, thus, reduced thermoregulatory costs (Barclay and Kurta 2007).

Although early successional patches other than small gaps are not important for roosting per se, their distribution on the landscape may be important for roost site selection. Because early successional habitats are important foraging and commuting sites for many bat species, and because flight is an expensive mode of locomotion (Altringham 1996), bats may try to minimize their commuting costs by selecting roosts that are close to early successional habitats. However, it should be noted that some authors have suggested that commuting costs are trivial compared to other energetic demands (Kurta et al. 2002; Lumsden et al. 2002).

Despite considerable variation within and among species, there is evidence that some bats select roosts based on proximity to early successional patches. For example, red bats which are often considered to be an open-adapted species (Table 10.2), use edges, forests, and open areas for foraging (Elmore et al. 2005; Ford et al. 2006; Amelon 2007; Morris et al. 2010). Thus, it is not surprising that they have been found to roost closer than expected to edges, particularly forest roads in a variety of forest types (Mager and Nelson 2001; Leput 2004; Perry et al. 2008; O'Keefe et al. 2009). However, in some forest landscapes red bats avoid roosting near edges and open areas. For example, in an intensively managed pine landscape in Mississippi, red bats roost farther from 0 to 8 year-old clearcut edges than expected (Elmore et al. 2004) and in mature second-growth mixed mesophytic forests in Kentucky, they roost an average of 277 m from the forest edge (Hutchinson and Lacki 2000). Evening bats fall closer to the center of the clutter continuum (Table 10.2) but, like red bats, vary in their response to early successional habitats in the surrounding landscape with regards to roosting. In Arkansas and coastal Georgia, evening bats select roosts in landscapes with more open areas such as fields, wildlife openings, clearcuts < 8 years of age, and group selection cuts (Miles et al. 2006; Perry et al. 2008), but in coastal South Carolina evening bats roost farther from openings (fields, wildlife openings, and clearcuts < 5 years old) than expected (Hein et al. 2009b).

Variation in roost site selection relative to early successional habitats is also seen among some of the more clutter-adapted species, with responses varying with the amount and configuration of early successional patches on the landscape. In a landscape dominated by mature hardwood forests in the Southern Appalachians, adult

male tri-colored bats roost closer than expected to small nonlinear openings and recent (≤5 years) 2-aged shelterwood harvests than expected (O'Keefe et al. 2009) and in Indiana woodlands, adult female tri-colored bats roost close (52 m) to the forest edge, though non-reproductive females roost significantly closer to edges than reproductive females (Veilleux et al. 2004). In contrast, tri-colored bats in a managed forest in Arkansas roost farther than expected from roads, but are more likely to use areas with small openings (i.e., group selection harvests, Perry et al. 2008) which corresponds with our finding that tri-colored bat activity was greater in nonlinear openings than along roads (see Fig. 10.3). Northern long-eared bats are considered to be clutter specialists (Faure et al. 1993), but proximity to early successional habitats may affect landscape-scale roost site selection for this species. In Arkansas, northern long-eared bats select roosts in areas with more group selection harvests within 250 m, though this same population tends to roost farther from roads than expected (Perry et al. 2008). In Kentucky, lactating female northern long-eared bats select roosts that are close to roads, but pregnant and post-lactating females do not (Lacki and Schwierjohann 2001).

Several factors may be driving the considerable variation in roost site selection relative to early successional habitats. Studies of eastern red bats have been conducted in forests undergoing a wide range of forest management activities (Elmore et al. 2004; Leput 2004; Perry et al. 2007b; O'Keefe et al. 2009), in large contiguous tracts of non-managed forest (Hutchinson and Lacki 2000), and in urban areas (Mager and Nelson 2001; Limpert et al. 2007). Thus, variation in the amount and distribution of early successional habitats on the landscape may account for the differences among the various studies. Even among forested landscapes, the distribution of early successional patches on the landscape can be quite variable due to both geography and land use history (e.g., forest management practices, agriculture, and urbanization). Historically, large scale disturbances such as hurricanes and fires have been more important in the creation of early successional habitats in the Coastal Plain and grassland biomes in the eastern USA, whereas small scale disturbances are more important in creating early successional habitats in upland hardwood forests of the Central Hardwoods Region (Runkle 1990; White et al., Chap. 3). Further, in the pine forests of the Coastal Plain final harvests tend to be clearcuts, whereas there is greater reliance on partial cuts and natural regeneration in upland hardwood systems (Wear and Greis 2002). In addition, small gaps are very difficult to map and may often be ignored in coarser, landscape scale studies. Thus, influences of early successional habitats on roost site selection may be underrepresented in landscapes where small gaps represent the primary form of early successional habitats. In contrast, where large scale forest disturbances are more common such as the Coastal Plain, early successional habitats are more available and are easier to map and include in roost-related landscape studies.

Sex and reproductive condition of bats may also contribute to variation in roost selection relative to early successional habitats. During the reproductive period, females have high energy demands related to gestation and lactation (Kurta et al. 1989, 1990). Because daily torpor can delay gestation and growth of young (Racey and Swift 1981), pregnant and lactating females use torpor less often than adult

males and non-reproductive females (Hamilton and Barclay 1994). Thus, reproductive females often select warmer roosts that allow them to maintain higher body temperatures while minimizing energetic costs (Lausen and Barclay 2006; Willis 2006), regardless of distance to foraging sites. In contrast, thermal considerations may be less important for males and non-reproductive females and distance to foraging areas may be a more important factor in their choice of roost sites. For example, O'Keefe et al. (2009) found that tree and stand characteristics are not important factors determining roost selection by male red bats and tri-colored bats, but males of both species roost closer to openings than expected. In contrast, studies of female red bats have found that tree and stand characteristics are important factors influencing roost site selection (Hutchinson and Lacki 2000; Veilleux et al. 2003; Elmore et al. 2005; Perry and Thill 2007; Perry et al. 2007a). Similarly, in southeastern Australia, pregnant and lactating female lesser long-eared bats (*Nyctophilus geoffroyi*) roost in large diameter snags in floodplain forests despite the fact that these snags are 4–10 km from foraging sites in a farmland mosaic whereas males, which do not rely on large-diameter snags, roost within 2 km of foraging sites in the same farmland mosaic (Lumsden et al. 2002).

Roost permanency, abundance and distribution of suitable roosts, predation risk, and social factors are also important in roost site selection by bats (Kunz and Lumsden 2003; Miller et al. 2003; Kalcounis-Rueppell et al. 2005) and may determine whether bats roost in or near early successional habitats. Some bats may avoid roosting in or near early successional habitats because trees in these sites are more exposed to predators (Russo et al. 2007) or to wind and rain (Callahan et al. 1997). Further, because bats commonly move among several roosts within a relatively small area (Barclay and Kurta 2007; Carter and Menzel 2007), the abundance of suitable roosts within a site may also be a more important factor governing roost selection.

10.4 Management of Early Successional Habitats for Bats in the Central Hardwood Region

It is generally agreed that roosts are the most limiting factor for bats in forested landscapes and conservation strategies should focus on protecting existing roosts and ensuring the availability of future roosts (Hayes 2003; Duchamp et al. 2007). Because most tree roosting bats use large trees or snags in mature forests (Kalcounis-Rueppell et al. 2005), creation and maintenance of early successional patches would seem counter to wise conservation strategies for bats. However, as we have illustrated, early successional habitats are important foraging and commuting sites for many species and the distribution of early successional patches may influence roost site selection. Nonetheless, the importance of roosts to survival and reproductive success of bats and reliance of so many bat species on large trees and snags must be kept in mind when considering management of early successional habitats in the Central Hardwood Region.

Early successional habitats, particularly in the form of gaps, small openings, and forest roads are important foraging sites for many species of bats and many species roost in, or at the edge, of gaps. Thus, creating many small gaps within mature forest may benefit bats as well as birds (Blake and Hoppes 1986) and reptiles (Greenberg 2001; Moorman et al., Chap. 11). Conserving or creating potential roost trees in or at the edge of small gaps will provide valuable roosting habitat, particularly for maternity colonies. Although retaining relict, cull, and dead trees is often counter to many silvicultural goals and may be perceived as a safety hazard, there are various ways to manage stands in which these structures are retained while minimizing the impact on subsequent regeneration (Guldin et al. 2007) and safety.

Because many bats are reluctant to cross large expanses of open area (e.g., Murray and Kurta 2004; Henderson and Broders 2008) and edges are often the preferred foraging site within clearcuts (e.g., Crampton and Barclay 1996; Grindal and Brigham 1999; Hogberg et al. 2002), most bats will probably benefit from smaller-sized cuts (<10 ha). Small cuts will increase the amount of edge relative to the amount of open area and minimize the distances bats will have to fly to traverse open spaces. Smaller cuts may also benefit other wildlife, particularly amphibians (Moorman et al., Chap. 11). However, as cut areas regenerate to dense closed-canopy second growth forest, the interior portion of these forests will cease to serve as bat foraging habitat, at least until the stands are thinned or mature into more suitable forest structures. Further, we have often observed a strong increase in bat activity one year after silvicultural treatments such as thinning and 2-age shelterwood cuts, with declines in activity in subsequent years (Loeb and Waldrop 2008; O'Keefe 2009). Thus, the benefits of regeneration cuts for bats may be short-term, at least at the stand scale. But, if regeneration cuts are conducted at a sustained rate over time across the landscape, harvesting may provide long-term benefits at larger spatial scales.

Bats in fragmented habitats often fly along tree lines and hedgerows (Murray and Kurta 2004; Henderson and Broders 2008), so leaving strips of mature trees within shelterwood cuts or using group selection harvests may facilitate bat movements in cuts, make cuts more desirable foraging sites, and provide current or future roost sites near foraging habitats. However, creation of many small cuts or group selection harvest may have some indirect negative impacts on bats and other organisms due to a higher rate of soil erosion resulting from multiple re-entries (Hood et al. 2002). Leaving too many trees may also interfere with regeneration of shade-intolerant trees (Guldin et al. 2007). In riparian areas, leaving trees in streamside management zones may be sufficient for providing adequate cover and roosting habitat (Hayes and Loeb 2007; O'Keefe 2009).

Although heavily traveled roads can impede movement of some bat species (Kerth and Melber 2009) and are sources of mortality for other species (Lesiński 2007, 2008; Russell et al. 2009), our data and those of several others (Zimmerman and Glanz 2000; Law and Chidel 2001, 2002; Adams et al. 2009; Hein et al. 2009a) demonstrate that gated or lightly traveled forest roads are often important foraging and commuting sites for bats. Forest roads may be particularly important in densely forested habitats by serving as commuting routes between roosting and foraging sites. However, roads may have negative impacts on forest ecosystems (e.g., sedimentation), but impacts can

be minimized through best management practices such as road closure, revegetation, and sediment control (Swift and Burns 1999; Grace and Clinton 2007).

Because bats are so mobile and use a variety of habitat types for foraging, roosting, and commuting, habitat management for bats requires a landscape approach and consideration of both spatial and temporal factors (Duchamp et al. 2007). Unfortunately, there is considerable variation among species in the Central Hardwoods Region in roost structure use (Table 10.1) and movement patterns (Lacki et al. 2007), which may make planning at the landscape scale more difficult. Thus, providing a diversity of habitat types of varying age classes and forest structures across the landscape (especially mature forest structures for roosting) while ensuring good connectivity among them, may be the best strategy for maintaining viable bat populations.

10.5 Future Research

There are still many questions about the use of early successional habitats by bats and the best ways to manage these habitats to meet the needs of bats. One of the first areas of research concerns the applicability of existing knowledge to times outside the summer reproductive period. Most research has been conducted during summer, a critical period for reproduction and growth of the young. Spring and fall also are critical due to energetic demands of migration and hibernation, but little is known about bat roosting and foraging habitat needs and how management activities may affect them during these times (Cryan and Veilleux 2007). Bats lose approximately 15%–30% of their body weight during hibernation (Hall 1962; Thomas et al. 1990; Johnson et al. 1998) and must regain some of that weight upon emergence in spring. Replenishing fat reserves is particularly important for females who must migrate to summer maternity sites and prepare for the reproductive period. During late summer and fall, bats must put on sufficient fat to migrate to hibernation sites and meet the physiological demands of winter. Foraging resources may be particularly critical during migration periods, yet we know little about the foraging habitats used by bats during these periods.

Species that do not hibernate in caves face increased energy demands during late summer and early fall because they often migrate up to 1,000 km from their summer range to more southerly areas where they roost in trees, bushes, and leaf litter (Cryan and Veilleux 2007). However, many individuals either remain within the Central Hardwood Region or migrate from more northerly climes to the Central Hardwood Region. While some research has been conducted on roost site selection of long distance migrants during winter (Saugey et al. 1998; Boyles and Robbins 2006; Mormann and Robbins 2007), no studies have examined the relationship between winter roost sites and early successional habitat types. Further, many bats in the Central Hardwood Region are active during warm nights in winter and at least some species (red bats, silver-haired bats, big brown bats, hoary bats) feed during arousals (Boyles et al. 2006; Dunbar et al. 2007). Thus, it is important to determine whether early successional habitats are important for foraging bats in the Central Hardwood Region during winter.

As touched on in previous sections, we know little about how the spatial configuration and structure of early successional patches affects use by bats. For example, far more research is needed on effects of size and shape of early successional patches before we can develop effective management plans that meet the needs of bats. Other landscape-scale factors that may affect bats' use of early successional patches include distance to other early successional patches, distance to water sources, distance to flight corridors such as roads or trails, and the age structure of the surrounding forest matrix. We also need a better understanding of how these factors affect insect use of early successional habitats, particularly the insect taxa and size classes that are preferred food items of bats. Future research should also compare use of recently harvested areas and other types of early successional habitats of similar size and shape to tease apart the effects of vegetation and other patch characteristics (e.g., size and shape). This will require that researchers clearly describe patch vegetation and structural characteristics when reporting the results of their studies.

Because gaps appear to be an important habitat component for all eastern bat species and were historically the most prevalent form of early successional habitats in the Central Hardwood Region (Runkle 1990), we need a better understanding of how bats use gaps and the relationship between roost site selection and gap dynamics. Use of new technologies such as LIDAR (Light Detection and Ranging), may provide more accurate data on small gap distribution in mature forest (e.g., Vepakomma et al. 2008), allowing researchers to better test hypotheses about the relationship between habitat selection and forest gaps.

10.6 Conclusions

Early successional habitats are just one of many habitat types used by bats in the Central Hardwood Region and other forested ecosystems. They may be important to bats for foraging but many questions remain about characteristics of early successional patches that contribute to their relative use. Because most bats roost in mature forest, the creation and management of early successional patches on the landscape must be balanced by the maintenance of sufficient mature forest with large trees and snags for roosting. Given the numerous other threats facing bats at the present time (habitat loss to urbanization, climate change, white-nose syndrome, wind energy development) and the precipitous declines in many populations, managing existing forests so that they provide all the resource needs of bats (roosts, foraging and commuting habitats, and clean water) is critical for the conservation of these important species.

Literature Cited

Adams MD, Law BS, French KO (2009) Vegetation structure influences the vertical stratification of open- and edge-space aerial-foraging bats in harvested forests. For Ecol Manage 258:2090–2100

Aldridge HDJN, Rautenbach IL (1987) Morphology, echolocation and resource partitioning in insectivorous bats. J Anim Ecol 56:763–778

Altringham JD (1996) Bats: biology and behavior. Oxford University Press Inc., New York

Amelon SK (2007) Multi-scale factors influencing detection, site occupancy and resource use by foraging bats in the Ozark Highlands of Missouri. Dissertation, University of Missouri, Columbia

Arnett EB, Hayes JP (2009) Use of conifer snags as roosts by female bats in western Oregon. J Wildl Manage 73:214–225

Arnett EB, Brown WK, Erickson WP, Fiedler JK, Hamilton BL, Henry TH, Jain A, Johnson GD, Kerns J, Koford RR, Nicholson CP, O'Connell TJ, Piorkowski MD, Tankersley RD Jr (2008) Patterns of bat fatalities at wind energy facilities in North America. J Wildl Manage 72:61–78

Barclay RMR, Brigham RM (1991) Prey detection, dietary niche breadth, and body size in bats: why are aerial insectivorous bats so small? Am Nat 137:693–703

Barclay RMR, Brigham RM (1996) Bats and forests symposium, Canada Research Branch, BC Ministry of Forestry, Victoria, p 292

Barclay RMR, Harder LD (2003) Life histories of bats: life in the slow lane. In: Kunz TH, Fenton MB (eds) Bat ecology. The University of Chicago Press, Chicago, pp 209–253

Barclay RMR, Kurta A (2007) Ecology and behavior of bats roosting in tree cavities and under bark. In: Lacki MJ, Hayes JP, Kurta A (eds) Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, pp 17–59

Blake JG, Hoppes WG (1986) Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. Auk 103:328–340

Blehert DS, Hicks AC, Behr M, Meteyer CU, Berlowski-Zier BM, Buckles EL, Coleman JTH, Darling SR, Gargas A, Niver R, Okoniewski JC, Rudd RJ, Stone WB (2009) Bat white-nose syndrome: an emerging fungal pathogen? Science 323:227

Boyles JG, Robbins LW (2006) Characteristics of summer and winter roost trees used by evening bats (*Nycticeius humeralis*) in southwestern Missouri. Am Midl Nat 155:210–220

Boyles JG, Dunbar MB, Whitaker JO Jr (2006) Activity following arousal in winter in North America. Mamm Rev 36:267–280

Brigham RM (2007) Bats in forests: what we know and what we need to learn. In: Lacki MJ, Hayes JP, Kurta A (eds) Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, pp 1–15

Brooks RT (2009) Habitat-associated and temporal patterns of bat activity in a diverse forest landscape of southern New England, USA. Biodivers Conserv 18:529–545

Burford LS, Lacki MJ, Covell CV Jr (1999) Occurrence of moths among habitats in a mixed mesophytic forest: implications for management of forest bats. For Sci 45:323–332

Callahan EV, Drobney RD, Clawson RL (1997) Selection of summer roosting sites by Indiana bats (*Myotis sodalis*) in Missouri. J Mammal 78:818–825

Campbell LA, Hallett JG, O'Connell MA (1996) Conservation of bats in managed forests: use of roosts by *Lasionycteris noctivagans*. J Mammal 77:976–984

Carter TC, Feldhamer GA (2005) Roost tree use by maternity colonies of Indiana bats and northern long-eared bats in southern Illinois. For Ecol Manage 219:259–268

Carter TC, Menzel JM (2007) Behavior and day-roosting ecology of North American foliage-roosting bats. In: Lacki MJ, Hayes JP, Kurta A (eds) Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, pp 61–81

Clark BS, Leslie DM Jr, Carter TS (1993) Foraging activity of adult female Ozark big-eared bats (*Plecotus townsendii ingens*) in summer. J Mammal 74:422–427

Crampton LH, Barclay RMR (1996) Habitat selection by bats in fragmented and unfragmented aspen mixedwood stands of different ages. In: Barclay RMR, Brigham RM (eds) Bats and forests symposium, Canada Research Branch, BC Ministry of Forestry, Victoria, pp 238–259

Cryan PM, Veilleux JP (2007) Migration and use of autumn, winter, and spring roosts by tree bats. In: Lacki MJ, Hayes JP, Kurta A (eds) Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, pp 153–175

Dodd LE, Lacki MJ, Rieske LK (2008) Variation in moth occurrence and implications for foraging habitat of Ozark big-eared bats. For Ecol Manage 255:3866–3872

Duchamp JE, Arnett EB, Larson MA, Swihart RK (2007) Ecological considerations for landscape management of bats. In: Lacki MJ, Hayes JP, Kurta A (eds) Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, pp 237–261

Duchamp JE, Sparks DW, Swihart RK (2010) Exploring the "nutrient hot spot" hypothesis at trees used by bats. J Mammal 91:48–53

Dunbar MB, Whitaker JO Jr, Robbins LW (2007) Winter feeding by bats in Missouri. Acta Chiropt 9:305–310

Ellis AM, Patton LL, Castleberry SB (2002) Bat activity in upland and riparian habitats in the Georgia Piedmont. Proc Annu Conf Southeast Assoc Fish Wildl Agen 56:210–218

Elmore LW, Miller DA, Vilella FJ (2004) Selection of diurnal roosts by red bats (*Lasiurus borealis*) in an intensively managed pine forest in Mississippi. For Ecol Manage 199:11–20

Elmore LW, Miller DA, Vilella FJ (2005) Foraging area size and habitat use by red bats (*Lasiurus borealis*) in an intensively managed pine landscape in Mississippi. Am Midl Nat 153:405–417

Erickson JL, West SD (1996) Managed forests in the western Cascades: the effects of seral stage on bat habitat use patterns. In: Barclay RMR, Brigham RM (eds) Bats and forests symposium, Canada Research Branch, BC Ministry of Forestry, Victoria, pp 215–227

Faure PA, Fullard JH, Dawson JW (1993) The gleaning attacks of the northern long-eared bat, *Myotis septentrionalis*, are relatively inaudible to moths. J Exp Biol 178:173–189

Fenton MB (1990) The foraging behaviour and ecology of animal-eating bats. Can J Zool 68:411–422

Fenton MB (2003) Science and the conservation of bats: where to next? Wildl Soc Bull 31:6–15

Ford WM, Menzel MA, Rodrigue JL, Menzel JM, Johnson JB (2005) Relating bat species presence to simple habitat measures in a central Appalachian forest. Biol Conserv 126:528–539

Ford WM, Menzel JM, Menzel MA, Edwards JW, Kilgo JC (2006) Presence and absence of bats across habitat scales in the upper coastal plain of South Carolina. J Wildl Manage 70:1200–1209

Furlonger CL, Dewar HJ, Fenton MB (1987) Habitat use by foraging insectivorous bats. Can J Zool 65:284–288

Furmankiewicz J, Kucharska M (2009) Migration of bats along a large river valley in southwestern Poland. J Mammal 90:1310–1317

Gannon WL, Sherwin RE, Haymond S (2003) On the importance of articulating assumptions when conducting acoustic studies of habitat use by bats. Wildl Soc Bull 31:45–61

Grace JM III, Clinton BD (2007) Protecting soil and water in forest road management. Trans Am Soc Agric Biol Eng 50:1579–1584

Greenberg CH (2001) Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the Southern Appalachians. For Ecol Manage 148:135–144

Grindal SD, Brigham RM (1998) Short-term effects of small-scale habitat disturbance on activity by insectivorous bats. J Wildl Manage 62:996–1003

Grindal SD, Brigham RM (1999) Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. Ecoscience 6:25–34

Guldin JM, Emmingham WH, Saugey DA, Carter SA (2007) Silvicultural practices and management of habitat for bats. In: Lacki MJ, Hayes JP, Kurta A (eds) Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, pp 177–205

Hall JS (1962) A life history and taxonomic study of the Indiana bat, *Myotis sodalis*. Reading Publ Mus and Art Gallery, Reading

Hamilton IM, Barclay RMR (1994) Patterns of daily torpor and day-roost selection by male and female big brown bats (*Eptesicus fuscus*). Can J Zool 72:744–749

Harvey MJ, Altenbach JS, Best TL (1999) Bats of the United States. Arkansas Game and Fish Commission, Little Rock

Hayes JP (2000) Assumptions and practical considerations in the design and interpretation of echolocation-monitoring studies. Acta Chiropt 2:225–236

Hayes JP (2003) Habitat ecology and conservation of bats in western coniferous forests. In: Zabel CJ, Anthony RG (eds) Mammal community dynamics: management and conservation in the coniferous forests of western North America. Cambridge University Press, New York, pp 81–119

Hayes JP, Loeb SC (2007) The Influences of forest management on bats in North America. In: Lacki MJ, Hayes JP, Kurta A (eds) Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, pp 207–235
Hein CD, Castleberry SB, Miller KV (2009a) Site-occupancy of bats in relation to forested corridors. For Ecol Manage 257:1200–1207
Hein CD, Miller KV, Castleberry SB (2009b) Evening bat summer roost-site selection on a managed pine landscape. J Wildl Manage 73:511–517
Henderson LE, Broders HG (2008) Movements and resource selection of the northern long-eared myotis (*Myotis septentrionalis*) in a forest-agriculture landscape. J Mammal 89:952–963
Hogberg LK, Patriquin KJ, Barclay RM (2002) Use by bats of patches of residual trees in logged areas of the boreal forest. Am Midl Nat 148:282–288
Hood SM, Zedaker SM, Aust WM, Smith DW (2002) Universal soil loss equation (USLE)–predicted soil loss for harvesting regimes in Appalachian hardwoods. North J Appl For 19:53–58
Huie KM (2002) Use of constructed woodland ponds by bats in the Daniel Boone National Forest. Thesis, Eastern Kentucky University, Richmond
Humes ML, Hayes JP, Collopy MW (1999) Bat activity in thinned, unthinned, and old-growth forests in western Oregon. J Wildl Manage 63:553–561
Hutchinson JT, Lacki MJ (2000) Selection of day roosts by red bats in mixed mesophytic forests. J Wildl Manage 64:87–94
Johnson SA, Brack V Jr, Rolley RE (1998) Overwinter weight loss of Indiana bats (*Myotis sodalis*) from hibernacula subject to human visitation. Am Midl Nat 139:255–261
Jones G, Jacobs DS, Kunz TH, Willig MR, Racey PA (2009) Carpe noctem: the importance of bats as bioindicators. End Spec Res 8:93–115
Kalcounis MC, Brigham RM (1995) Intraspecific variation in wing loading affects habitat use by little brown bats (*Myotis lucifugus*). Can J Zool 73:89–95
Kalcounis-Rueppell MC, Psyllakis JM, Brigham RM (2005) Tree roost selection by bats: an empirical synthesis using meta-analysis. Wildl Soc Bull 33:1123–1132
Kerth G, Melber M (2009) Species-specific barrier effects of a motorway on the habitat use of two threatened forest-living bat species. Biol Conserv 142:270–279
Krusic RA, Yamasaki M, Neefus CD, Pekins PJ (1996) Bat habitat use in White Mountain National Forest. J Wildl Manage 60:625–631
Kunz TH, Lumsden LF (2003) Ecology of cavity and foliage roosting bats. In: Kunz TH, Fenton MB (eds) Bat ecology. The University of Chicago Press, Chicago, pp 3–89
Kunz TH, Arnett EB, Erickson WP, Hoar AR, Johnson GD, Larkin RP, Strickland MD, Thresher RW, Tuttle MD (2007) Ecological impacts of wind energy development on bats: questions, hypotheses, and research needs. Front Ecol Environ 5:315–324
Kurta A, Bell GP, Nagy KA, Kunz TH (1989) Water balance of free-ranging little brown bats (*Myotis lucifugus*) during pregnancy and lactation. Can J Zool 67:2468–2472
Kurta A, Kunz TH, Nagy KA (1990) Energetics and water flux of free-ranging big brown bats (*Eptesicus fuscus*) during pregnancy and lactation. J Mammal 71:59–65
Kurta A, Murray SW, Miller DH (2002) Roost selection and movements across the summer landscape. In: Kurta A, Kennedy J (eds) The Indiana bat: biology and management of an endangered species. Bat Conservation International, Austin, pp 118–129
Lacki MJ, Schwierjohann JH (2001) Day-roost characteristics of northern bats in mixed mesophytic forest. J Wildl Manage 65:482–488
Lacki MJ, Amelon SK, Baker MD (2007) Foraging ecology of bats in forests. In: Lacki MJ, Hayes JP, Kurta A (eds) Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, pp 83–127
Lausen CL, Barclay RMR (2006) Benefits of living in a building: big brown bats (*Eptesicus fuscus*) in rocks versus buildings. J Mammal 87:362–370
Law B, Chidel M (2001) Bat activity 22 years after first-round intensive logging of alternate coupes near Eden, New South Wales. Aust For 64:242–247
Law B, Chidel M (2002) Tracks and riparian zones facilitate the use of Australian regrowth forest by insectivorous bats. J Appl Ecol 39:605–617

Leput DW (2004) Eastern red bat (*Lasiurus borealis*) and eastern pipistrelle (*Pipistrellus subflavus*) maternal roost selection: implications for forest management. Thesis, Clemson University, Clemson

Lesiński G (2007) Bat road casualties and factors determining their number. Mammalia 71:138–142

Lesiński G (2008) Linear landscape elements and bat casualties on roads – an example. Ann Zool Fennici 45:277–280

Lesiński G, Gryz J, Kowalski M (2009) Bat predation by tawny owls *Strix aluco* in differently human-transformed habitats. Ital J Zool 76:415–421

Lewis T (1970) Patterns of distribution of insects near a windbreak of tall trees. Ann Appl Biol 65:213–220

Limpert DL, Birch DL, Scott MS, Andre M, Gillam E (2007) Tree selection and landscape analysis of eastern red bat day roosts. J Wildl Manage 71:478–486

Loeb SC, O'Keefe JM (2006) Habitat use by forest bats in South Carolina in relation to local, stand, and landscape characteristics. J Wildl Manage 70:1210–1218

Loeb SC, Waldrop TA (2008) Bat activity in relation to fire and fire surrogate treatments in southern pine stands. For Ecol Manage 255:3185–3192

Lumsden LF, Bennett AF, Silins JE (2002) Location of roosts of the lesser long-eared bat *Nyctophilus geoffroyi* and Gould's wattled bat *Chalinolobus gouldii* in a fragmented landscape in south-eastern Australia. Biol Conserv 106:237–249

Lunde RE, Harestad AS (1986) Activity of little brown bats in coastal forests. Northwest Sci 60:206–209

MacKenzie DI (2006) Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. J Wildl Manage 70:367–374

Mager KJ, Nelson TA (2001) Roost-site selection by eastern red bats (*Lasiurus borealis*). Am Midl Nat 145:120–126

Marcot BG (1996) An ecosystem context for bat management: a case study of the interior Columbia River Basin, USA. In: Barclay RMR, Brigham RM (eds) Bats and forests symposium, Canada Research Branch, BC Ministry of Forestry, Victoria, pp 19–36

Menzel MA, Carter TC, Menzel JM, Ford WM, Chapman BR (2002) Effects of group selection silviculture in bottomland hardwoods on the spatial activity patterns of bats. For Ecol Manage 162:209–218

Miles AC, Castleberry SB, Miller DA, Conner LM (2006) Multi-scale roost-site selection by evening bats on pine-dominated landscapes in southwest Georgia. J Wildl Manage 70:1191–1199

Miller DA, Arnett EB, Lacki MJ (2003) Habitat management for forest-roosting bats of North America: a critical review of habitat studies. Wildl Soc Bull 31:30–44

Mormann BM, Robbins LW (2007) Winter roosting ecology of eastern red bats in southwest Missouri. J Wildl Manage 71:213–217

Morris AD, Miller DA, Kalcounis-Rueppell MC (2010) Use of forest edges by bats in a managed pine forest landscape. J Wildl Manage 74:26–34

Murray SW, Kurta A (2004) Nocturnal activity of the endangered Indiana bat (*Myotis sodalis*). J Zool 262:197–206

Norberg UM, Rayner JMV (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philos Trans R Soc Lond B 316:335–427

Obrist MK, Rathey E, Bontadina F, Martinoli A, Conedera M, Christe P, Moretti M (2011) Response of bat species to sylvo-pastoral abandonment. For Ecol Manage 261:789–798

O'Keefe JM (2009) Roosting and foraging ecology of forest bats in the Southern Appalachian Mountains. Dissertation, Clemson University, Clemson

O'Keefe JM, Loeb SC, Lanham JD, Hill HS Jr (2009) Macrohabitat factors affect day roost selection by eastern red bats and eastern pipistrelles in the Southern Appalachian Mountains, USA. For Ecol Manage 257:1757–1763

Ormsbee PC, Kiser JD, Perlmeter SI (2007) Importance of night roosts to the ecology of bats. In: Lacki MJ, Hayes JP, Kurta A (eds) Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, pp 130–151

Owen SF, Menzel MA, Edwards JW, Ford WM, Menzel JM, Chapman BR, Wood PB, Miller KV (2004) Bat activity in harvested and intact forest stands in the Allegheny Mountains. North J Appl For 21:154–159

Patriquin KJ, Barclay RMR (2003) Foraging by bats in cleared, thinned and unharvested boreal forest. J Appl Ecol 40:646–657

Perry RW, Thill RE (2007) Tree roosting by male and female eastern pipistrelles in a forested landscape. J Mammal 88:974–981

Perry RW, Thill RE, Carter SA (2007a) Sex-specific roost selection by adult red bats in a diverse forested landscape. For Ecol Manage 253:48–55

Perry RW, Thill RE, Leslie DM (2007b) Selection of roosting habitat by forest bats in a diverse forested landscape. For Ecol Manage 238:156–166

Perry RW, Thill RE, Leslie DM Jr (2008) Scale-dependent effects of landscape structure and composition on diurnal roost selection by forest bats. J Wildl Manage 72:913–925

Racey PA, Entwistle AC (2003) Conservation ecology of bats. In: Kunz TH, Fenton MB (eds) Bat ecology. The University of Chicago Press, Chicago, pp 680–743

Racey PA, Swift SM (1981) Variation in gestation length in a colony of pipistrelle bats (*Pipistrellus pipistrellus*) from year to year. J Reprod Fertil 61:123–129

Rancourt SJ, Rule MI, O'Connell MA (2005) Maternity roost site selection of long-eared myotis, *Myotis evotis*. J Mammal 86:77–84

Runkle JR (1990) Gap dynamics in an Ohio *Acer-Fagus* forest and speculations on the geography of disturbance. Can J For Res 20:632–641

Russell AL, Butchkoski CM, Saidak L, McCracken GF (2009) Road-killed bats, highway design, and the commuting ecology of bats. End Spec Res 8:49–60

Russo D, Cistrone L, Jones G (2007) Emergence time in forest bats: the influence of canopy closure. Acta Oecol 31:119–126

Rydell J, Entwistle AC, Racey PA (1996) Timing of foraging flights of three species of bats in relation to insect activity and predation risk. Oikos 76:243–252

Saugey DA, Crump BG, Vaughn RL, Heidt GA (1998) Notes on the natural history of *Lasiurus borealis* in Arkansas. J Ark Acad Sci 52:92–98

Schirmacher MR, Castleberry SB, Ford WM, Miller KV (2007) Habitat associations of bats in south-central West Virginia. Proc Annu Conf Southeast Assoc Fish Wildl Agen 61:46–52

Sparks DW, Ritzi CM, Duchamp JE, Whitaker JO Jr (2005) Foraging habitat of Indiana myotis (*Myotis sodalis*) at an urban/rural interface. J Mammal 86:713–718

Swengel AB (2001) A literature review of insect responses to fire, compared to other conservation managements of open habitat. Biodivers Conserv 10:1141–1169

Swift LW Jr, Burns RG (1999) The three Rs of roads. J For 97:40–44

Swystun MB, Psyllakis JM, Brigham RM (2001) The influence of residual tree patch isolation on habitat use by bats in central British Columbia. Acta Chiropt 3:197–201

Szymanski JA, Runge MC, Parkin MJ, Armstrong M (2009) White-nose syndrome management: report on structured decision making initiative. USDI Fish and Wildlife Service, Fort Snelling

Thomas DW, Dorais M, Bergeron J-M (1990) Winter energy budgets and cost of arousals for hibernating little brown bats, *Myotis lucifugus*. J Mammal 71:475–479

Tibbels AE, Kurta A (2003) Bat activity is low in thinned and unthinned stands of red pine. Can J For Res 33:2436–2442

USDI Fish and Wildlife Service (1984) A recovery plan for the Ozark big-eared bat and Virginia big-eared bat. USDI Fish and Wildlife Service, Fort Snelling, 119 p

USDI Fish and Wildlife Service (2007) Indiana bat (*Myotis sodalis*) draft recovery plan: first revision. USDI Fish and Wildlife Service, Fort Snelling, 258 p

Veilleux JP, Whitaker JO Jr, Veilleux SL (2003) Tree-roosting ecology of reproductive female eastern pipistrelles, *Pipistrellus subflavus*, in Indiana. J Mammal 84:1068–1075

Veilleux JP, Whitaker JO Jr, Veilleux SL (2004) Reproductive stage influences roost use by tree roosting female eastern pipistrelles, *Pipistrellus subflavus*. Ecoscience 11:249–256

Vepakomma U, St-Onge B, Kneeshaw D (2008) Spatially explicit characterization of boreal forest gap dynamics using multi-temporal LIDAR data. Remote Sens Environ 112:2326–2340

Verboom B, Spolestra K (1999) Effects of food abundance and wind on the use of tree lines by an insectivorous bat, *Pipistrellus pipistrellus*. Can J Zool 77:1393–1401
Verboom B, Boonman AM, Limpens HJGA (1999) Acoustic perception of landscape elements by the pond bat (*Myotis dasycneme*). J Zool 248:59–66
Vonhof MJ, Barclay RM (1997) Use of tree stumps as roosts by the western long-eared bat. J Wildl Manage 61:674–684
Walsh AL, Harris S (1996) Foraging habitat preferences of verspertilionid bats in Britain. J Appl Ecol 33:508–518
Wear DN, Greis JG (eds) (2002) Southern forest resource assessment. Gen Tech Rep SRS-53, USDA Forest Service Southern Research Station, Asheville
Weller TJ (2007) Assessing population status of bats in forests: challenges and opportunities. In: Lacki MJ, Hayes JP, Kurta A (eds) Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, pp 264–291
Whitaker JO Jr, Hamilton WJ Jr (1998) Mammals of the eastern United States. Cornell University Press, Ithaca
Whitaker DM, Carroll AL, Montevecchi WA (2000) Elevated numbers of flying insects and insectivorous birds in riparian buffer strips. Can J Zool 75:740–747
Willis CKR (2006) Daily heterothermy by temperate bats using natural roosts. In: Zubaid A, McCracken GF, Kunz TH (eds) Functional and evolutionary ecology of bats. Oxford University Press, New York, pp 38–55
Willis CKR, Brigham RM (2005) Physiological and ecological aspects of roost selection by reproductive female hoary bats (*Lasiurus cinereus*). J Mammal 86:85–94
Yates MD, Muzika RM (2006) Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests. J Wildl Manage 70:1238–1248
Zimmerman GS, Glanz WE (2000) Habitat use by bats in eastern Maine. J Wildl Manage 64:1032–1040