

A REVIEW OF FIRE EFFECTS ON BATS AND BAT HABITAT IN THE EASTERN OAK REGION

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Abstract.—Fire is increasingly being used in oak forests to promote oak regeneration, improve wildlife habitat, and reduce hazardous fuel loads. Although recent research has begun to shed light on the relationships among fire, bats, and bat habitat, these interactions are not yet fully understood. Fire may affect bats directly through heat and smoke during the burning process or indirectly through modifications in habitat. Studies suggest fire generally has beneficial effects on bat habitat by creating snags, reducing understory and midstory clutter, creating more open forests, and possibly increasing abundance of flying insects. Direct effects of fire on bats during the burning process are still largely unknown. These potential direct effects likely differ for each species or roosting guild of bats, and may also vary by season and reproductive condition.

BACKGROUND

Fires ignited by lightning and Native Americans historically maintained a mosaic of forests, grasslands, savannas, and open woodlands throughout the eastern United States, including the eastern oak (*Quercus* spp.) region (Abrams 1992, Lorimer 2001). Prior to European settlement, fire frequencies ranged from every 3 to 19 years within this region (Guyette and others 2006). European settlement, logging, and clearing for agriculture altered these landscapes during the 18th and 19th centuries. During the 20th century, fire suppression caused many forests that were previously open and park-like to succeed to dense closed-canopy forests where fire-adapted plant species were replaced by shade-tolerant and fire-sensitive vegetation (Lorimer 2001, Nowacki and Abrams 2008, Van Lear and Harlow 2002). It is assumed that bats adapted to fire across these landscapes over thousands of years of frequent fire. However, changes in bat populations resulting from fire suppression-induced changes in habitat over the past century are difficult to differentiate from other anthropogenic

effects such as disturbance of cave roosts, pesticides, habitat destruction, fragmentation, urbanization, and indiscriminant killing of bats that also occurred during portions of this period.

Fire may affect bats directly through heat, smoke, and carbon monoxide, or indirectly through modifications in habitat and changes in their food base (Dickinson and others 2009). Although use of fire by land managers has increased substantially in recent years, researchers have just begun to study the effects of fire on bats and bat habitat. Recent reviews have summarized the state of knowledge on the relationship between bats and fire. Carter and others (2002) provided a general review on effects of fire on bats in the southeastern United States and Mid-Atlantic States, and Keyser and Ford (2006) reviewed effects of fire on mammals (including bats) in eastern oak forests. A comprehensive review of direct and indirect effects of fire on bats, with an emphasis on Indiana bats (see Table 1 for scientific names of species), was presented by Dickinson and others (2009). My

Table 1.—Summer and winter roosting locations for bats found in the eastern oak region

Species	Summer Roosting	Winter Roosting
Eastern red bat (<i>Lasiurus borealis</i>)	Foliage, mostly hardwood canopies	Foliage, trees, low shrubs, leaf litter
Seminole bat (<i>L. seminolus</i>) ¹	Foliage, mostly pine canopies	Foliage, trees, low shrubs, leaf litter
Hoary bat (<i>L. cinereus</i>)	Foliage, pine and hardwood canopies	Unknown
Tri-colored bat (<i>Perimyotis subflavus</i>)	Foliage, mostly dead leaves in hardwoods, structures ² , caves, mines	Caves, mines, structures
Big brown bat (<i>Eptesicus fuscus</i>)	Tree cavities, under bark, structures, caves, mines	Caves, mines, structures
Rafinesque big-eared bat (<i>Corynorhinus rafinesquii</i>)	Tree cavities, under bark, structures, caves, mines	Caves, mines, structures, tree cavities
Southeastern bat (<i>Myotis austroriparius</i>)	Tree cavities, structures, caves, mines	Caves, mines, structures, tree cavities
Evening bat (<i>Nycticeius humeralis</i>)	Tree cavities, under bark, structures	Tree cavities, under bark, ground-level ³
Silver-haired bat (<i>Lasionycteris noctivagans</i>)	Tree cavities, under bark	Tree cavities, under bark, caves, mines, structures, ground-level
Northern long-eared bat (<i>M. septentrionalis</i>)	Tree cavities, under bark, structures	Caves, mines
Little brown bat (<i>M. lucifugus</i>)	Tree cavities, under bark, structures	Caves, mines
Indiana bat (<i>M. sodalis</i>)	Tree cavities, under bark, structures	Caves, mines
Gray bat (<i>M. grisescens</i>)	Caves, mines	Caves, mines
Ozark big-eared bat (<i>C. townsendii ingens</i>)	Caves, mines	Caves, mines
Virginia big-eared bat (<i>C. t. virginianus</i>)	Caves, mines	Caves, mines
Eastern small-footed bat (<i>M. leibii</i>)	Caves, mines, under bark, structures, rock crevices	Caves, mines
Brazilian free-tailed bat (<i>Tadarida brasiliensis</i>) ⁴	Caves, mines, structures	Caves, mines, structures

¹ Associated primarily with southern pine forests, rare in most of eastern oak region.

² Structures include buildings, bridges, culverts, water tanks, wells, and other man-made structures.

³ Ground-level includes small mammal burrows, rock crevices, under tree roots, and other cavities or crevices on the ground.

⁴ Resides primarily south of the eastern oak region.

objectives here are to expand upon those reviews and update information provided by recent studies. In the life history of bats, roosts and food are the two most important resources known to affect bat distribution and abundance (Kunz and Lumsden 2003). Therefore, I focus primarily on how fire in forests potentially affects these two resources. This discussion focuses on understory burning typically used for management purposes (not stand-replacing wildfire) and the effects of fire intensities typically found during prescribed burns.

Similar to birds, many species of bats undertake short (<500 km) or long-range (>1000 km) migrations between summer and winter use areas. Consequently, range maps often depict a species occurring throughout a wide area, but a species may occur only in portions of their range during each season (e.g., Cryan and Veilleux 2007). Furthermore, the ecology of bats often differs substantially among seasons. Thus, fire affects different species in different ways during each season, and burns conducted during winter will likely affect various species in different ways from those conducted between spring and fall.

ROOSTING AND FIRE

Bats may spend over half their lives in roosts, and roosts provide protection from predators and the weather (Kunz and Lumsden 2003). Therefore, adequate roost sites are critical to the survival of bats. Bats that occur in the eastern oak region use different types of roosts, and the type of roost used often differs between summer and winter (Table 1). The 17 bat species that occur or potentially occur in the region can be classified loosely into three guilds: foliage-roosting species; species that roost in cavities, crevices, or under bark of trees during all or part of the year (cavity- and bark-roosting species hereafter); and cave obligates. Many bats use different types of roosts between summer and winter. For example, red bats and tri-colored bats in forests roost mostly in foliage during summer; however, during winter, red bats continue to roost in forests whereas tri-colored bats

retreat to caves or mines for hibernation. Therefore, differences in the natural history of each species determine how fire affects that species, and direct effects of fire on individual bats is likely dependent on season and intensity of fire, sex and age of bat, and reproductive condition of bat. Most tree-roosting bats switch roosts every 2-4 days (e.g., Lewis 1995); thus, an abundant supply of potential roost locations is needed to provide suitable roosting habitat within a forest stand.

Growing Season Fires and Foliage-Roosting Bats

During late spring, summer, and early fall (summer hereafter), four species that occur in the region roost in foliage (leaves or needles of trees and shrubs) during the day, including red bats, hoary bats, Seminole bats, and tri-colored bats (Table 1). Lasiurine bats (red, hoary, and Seminole bats) typically roost 15-19 m above the ground in the canopies of overstory trees (Hein and others 2008; Hutchinson and Lacki 2000; Menzel and others 1998; Perry and Thill 2007a, 2007b; Perry and others 2007a). Seminole bats roost primarily in the needles of pines, red bats roost mostly in deciduous foliage such as oaks, and hoary bats use both pines and hardwoods (Hein and others 2008; Hutchinson and Lacki 2000; Menzel and others 1998; Perry and Thill 2007a, 2007b; Perry and others 2007a; Willis and Brigham 2005). Tri-colored bats roost in a variety of locations during summer, including caves, mines, and buildings (Fujita and Kunz 1984). However, in forests lacking these substrates, they roost in foliage of trees (often oaks), and mostly in dead leaves or suspended clusters of dead pine-needles (Perry and Thill 2007d, Veilleux and others 2003).

Direct effects of growing-season burns on foliage-roosting bats are largely unknown. Because they typically roost relatively high (15-19 m) in the canopies of overstory trees during the warm season, it is unlikely that burning during the growing season leads to direct mortality. Further, carbon monoxide levels at roosting heights are unlikely a concern when flame lengths (fire intensity) are less than 1.6 m, which

is typically the most intense fires observed during most prescribed burns (Dickinson and others 2010). 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 the 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 suggest models used to predict foliage scorch during prescribed burns (Reinhardt 2003) may potentially be useful as surrogates for predicting injury to bats.

When temperatures associated with fires are below lethal thresholds, heat and smoke could potentially disturb foliage-roosting bats regardless of roost height, causing them to relocate to other trees. However, foliage is not a limited substrate in most forests, and a substantial supply of alternative roosts is likely available if bats are disturbed (Carter and others 2002). Tri-colored bats, which tend to have great site fidelity to particular dead leaf clusters in hardwood forests (Perry and Thill 2007d, Veilleux and others 2003), may have more difficulty locating alternative roosts that provide adequate cover from predators after disturbance. Furthermore, because male tri-colored bats occasionally roost in suspended dead leaves close to the ground (<5 m high), they may be more susceptible to direct effects of fire than many other bats during summer (Perry and Thill 2007d).

Temperate, insectivorous bats undergo periods of torpor during which their metabolism is reduced and body temperatures may be similar to ambient air temperature. Bats control energy expenditure by regulating the frequency, depth, and duration of torpor (Speakman and Thomas 2003). Torpor lasting multiple days or weeks is considered hibernation. Because torpor can slow fetal development and reduce milk production (Racey 1973, Wilde and others 1999), females during the gestation and lactation

periods of summer may spend less time in torpor than nonreproductive females or males (Cryan and Wolf 2003, Hamilton and Barclay 1994, Kurta and Fujita 1988, Solick and Barclay 2006). Because females are less likely to be in torpor during the reproductive season, they are likely able to escape fire more readily than males or non-reproductive females. However, non-volant young may not have the ability to escape heat and smoke from intense fires during the reproductive season. Nevertheless, females of many species (including most bats in the region) often carry non-volant young when roost switching, especially when disturbed (Davis 1970), and likely have the ability to escape oncoming heat if given sufficient warning.

Low-intensity burns during the reproductive season would likely have few negative effects on bats roosting in relatively tall (19-25 m) overstory trees. Furthermore, active bats maintain body temperatures of approximately 32-38 °C (90-100 °F) and may remain active above temperatures of 30 °C (86 °F) (Barclay and others 1996, Herreid and Schmidt-Neilsen 1966). Thus, bats may not be in torpor or may only be in shallow torpor during periods of relatively high ambient temperatures, which would allow for quick escape during fires. Dickinson and others (2010) suggested bats may arouse and escape fire in less than 10 minutes when temperatures are 25 °C (77 °F).

Dormant-Season Fires and Foliage-Roosting Bats

In southern portions of the eastern oak region, red bats and Seminole bats may be active during winter nights when temperatures are above freezing. During winter, red bats roost on the ground (under leaf litter) or 1-6 m above the ground in the lower branches of eastern red cedars or in persistent dead leaves of oaks or shrubs (Mormann and Robbins 2007). Red bats typically roost in trees when temperatures exceed 10 °C during winter (Mormann 2005). Seminole bats roost in the canopies of overstory pines and hardwoods, in understory vegetation, pine needle clusters suspended above the ground, or in pine litter on the forest floor during

winter (Hein and others 2008). Evidence suggests hoary bats occur in the region during winter (Cryan 2003), but little is known about their winter roosting habits. Furthermore, little is known about the winter roosting habits of tri-colored bats outside hibernacula (caves, mines, and man-made structures), and it is not known if they use tree roosts or are active during winter in southern portions of the region.

Potential effects of dormant-season burning on species that use forests during winter are likely affected by ambient air temperatures. During colder periods of winter, lasiurine bats and some cavity- and bark-roosting species may retreat to roosts on or near the ground where temperatures are more stable (Boyles and others 2005, Flinn 2009, Hein and others 2008, Mormann and Robbins 2007, Perry and others 2010, Saugey and others 1998). For example, Mormann and Robbins (2007) found red bats switched from tree roosts to leaf litter roosts when temperatures approached freezing, and Flinn (2009) found most roosts of red bats in leaf litter when the maximum daytime temperature was $<14^{\circ}\text{C}$ (57°F). Hein and others (2008) found that Seminole bats roosted extensively on or near the forest floor when minimum nightly temperatures were below 4°C (39°F). Thus, on days when the previous night's temperature is below approximately 5°C (41°F), these bats are expected to be located in roosts more vulnerable to fire. Studies suggest that during winter, red bats roost in litter mostly on south-facing slopes where radiant heating may provide greater temperatures than other areas across a landscape (Flinn 2009, Mormann and Robbins 2007), whereas one study suggested red bats may roost more on north slopes where lower temperatures allow deeper torpor (Saugey and others 1989).

Many bats may take from 30 to 60 minutes to arouse from torpor when ambient temperature is 5°C (Thomas and others 1990), and red bats roosting in leaf litter may take up to 30 minutes to arouse (Layne 2009). Furthermore, lower ambient air temperatures correspond with longer arousal times. However, when

temperatures fall to near or below freezing ($<5^{\circ}\text{C}$ or $<41^{\circ}\text{F}$), red bats increase their metabolisms or arouse to prevent freezing (Dunbar and Tomasi 2006). Thus, a bat may not have sufficient time to arouse and flee from approaching flames on cold days ($>5^{\circ}\text{C}$), but may be in a lesser state of torpor when temperatures are below freezing. Data on lightning strikes from the Interior Highlands suggest natural fire ignitions peak in July-September, with a smaller peak in March-April (USDA FS 1999). Historical accounts also suggest Native Americans ignited fires mostly in September and November (USDA FS 1999). This led Carter and others (2002) to suggest that bats using forests burned during winter may not be fully adapted to winter burning.

Hein and others (2008) recommended caution when conducting prescribed burns on days when temperatures the previous nights are $<4^{\circ}\text{C}$. However, Layne (2009) suggested temperature from sunrise to the onset of the fire had a higher correlation value with red bat recovery times than night-before temperatures. Furthermore, Layne (2009) recommended conducting winter fires on days when temperatures are greater than 10°C and starting the fire on north-facing slopes to give red bats a chance to passively rewarm and react to approaching fire. Nevertheless, if or how these bats escape injury during winter fire remains unclear, and it is unknown what temperatures these bats experience under the leaf litter.

Reports of red bats exiting leaf litter or located on the ground attempting to flee during dormant-season burns suggests they may arouse during winter fires (Moorman and others 1999, Saugey and others 1989). Furthermore, dormant-season burns are typically ignited in late morning or early afternoon when humidity is lower and temperatures are higher. For example, unpublished data on ignition times and temperatures of days when dormant-season burns were conducted (November-early March) in the Interior Highlands of Arkansas indicated average temperature 2 hours before ignition was 7.7°C , and average temperature at time of ignition was 12.3°C

(Table 2). Further, 36 percent of burns were conducted when temperatures 2 hours before ignition measured below 5 °C. Only 13 percent of burns were initially ignited when temperatures were below 5 °C, and many of these burns took hours to complete. Thus, in southern portions of the eastern oak region, dormant-season burns often take place at times when ambient temperatures allow for quicker arousal.

Scesny (2006) reported red bats aroused (22 minutes at 5 °C) when exposed to smoke and the sound of fire, suggesting fire provides cues that cause these bats to arouse. However, other studies suggest individual bats of other species may not arouse when exposed to nontactile stimuli such as sound and light (Speakman and others 1991), and bats in torpor may not be able to perceive sound when temperatures fall below 12 °C (Harrison 1965). Arousal from fire sounds and smoke may be a species-specific response of red bats adapted to roosting close to the ground in fire-prone areas, but additional study is warranted. Nevertheless, possible arousal from fire stimuli, along with the warmer temperatures just prior to many burns may enable red bats to arouse and escape oncoming flames during many dormant-season burns. Head fires typically move in the direction of the wind and may deliver smoke over the area to be burned for substantial periods prior to the arrival of fire. When head fires and slower-moving back fires are used simultaneously, smoke from the head fire may cover the area prior to arrival of the back fire. Thus, substantial smoke may inundate the area prior to arrival of fire, providing cues for bats to arouse. Further study is needed on the interactions of ambient temperature, torpor, arousal times, fire stimuli, and escape behaviors by bats.

Growing Season Fires and Cavity- and Bark-Roosting Species

In forested areas lacking buildings or manmade structures, eight species roost primarily in cavities or crevices of trees during summer (Table 1). In forests, this guild roosts under exfoliating bark, in hollow trees, and in small cavities of damaged or diseased trees (Ford and others 2006; Lacki and Schwierjohann

Table 2.—Ambient temperatures (°C) for days when 372 controlled burns were conducted during November-March in the Interior Highlands of Arkansas, 2007-2010. Ignition time was estimated at 11 am for all days based on consensus from fire management officers.

Parameter	Min	Max	Average
Low temp previous night (6 am)	-10.6	19.4	2.0±0.34
Temp 2 hours before ignition (9 am)	-8.3	21.7	7.7±0.33
Temp at time of ignition (11 am)	-6.1	25.0	12.3±0.34

2001; Perry and Thill 2007c, 2008). Individual species may roost mostly in snags or live trees, and some species may use cavities more than loose bark. For example, evening bats tend to roost more in cavities than under bark (Boyles and Robbins 2006, Menzel and others 2001a, Perry and Thill 2008), whereas Indiana bats tend to roost mostly under exfoliating bark of live trees or snags (Foster and Kurta 1999, Menzel and others 2001b). However, bats may exhibit regional preferences for tree species and roost types based on the composition of available tree species and previous forest disturbances such as disease outbreaks, ice storms, fires, and tornados that create abundant snags or defects in particular tree species. Within this guild, reproductive females typically roost in colonies during summer, whereas adult males and nonreproductive females usually roost alone.

Female maternity colonies in this guild are typically found in relatively tall trees with abundant solar exposure during summer (Brigham and Barclay 1996) where warmer roost temperatures promote fetal and juvenile growth (Speakman and Thomas 2003). Among this guild, roosts in trees for both sexes combined average around 5-10 m above the ground (Lacki and others 2009a, Menzel and others 2002b, Perry and Thill 2008). However, males of some cavity- and bark-roosting species often roost in smaller snags or closer to the ground than females during summer (Broders and Forbes 2004, Kurta 2005, Lacki and Schwierjohann 2001, Perry and Thill 2007c). For example, Perry and Thill (2007c)

found 21 percent of roosts of male northern long-eared bats were located in small (<10 cm diameter at breast height [d.b.h.]) midstory trees and snags during summer, whereas <2 percent of female roosts were in these trees. Consequently, for some cavity- and bark-roosting species, males may be more susceptible than females to direct effects of fires during summer because of their closer proximity to the ground and thinner insulation provided by small diameter trees. Males may also enter torpor more frequently than reproductive females (Speakman and Thomas 2003), which could make arousal and escape from fire more difficult for males during cooler periods of summer.

Many of the factors associated with potential injury to foliage-roosting bat species during summer (e.g., height of roosts and fire intensity) may also affect cavity- and bark-roosting species. However, the types of roosts used by cavity- and bark-roosting species may affect vulnerability to injury from fire. 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). Thus, bats roosting in well insulated cavities located relatively high in the trees are unlikely to be subjected to injury. It is unknown how smoke affects bats in these roosts or if different types of roosts reduce or enhance smoke exposure to roosting bats.

Little is known of the direct effects of fire on this guild, and few studies have examined escape behaviors, direct mortality, or potential reductions in survival associated with effects of fire. Dickinson and others (2009) monitored two northern long-eared bats (one male and one female) in roosts during a controlled summer burn. Both bats exited their roosts within 10 minutes of ignition near their roosts and flew in areas where the fire was not occurring. Among four bats they tracked before and after burning, all switched roosts during the fire, but no mortality was observed. Likewise, Rodrigue and others (2001) reported flushing of a *Myotis* bat from an ignited snag during an April controlled burn in West Virginia.

Dormant Season Fires and Cavity- and Bark-Roosting Species

Many cavity- and bark-roosting species hibernate for extended periods during winter in northern portions of the region, often in caves or abandoned mines. Thus, many of these species are not directly vulnerable to dormant-season burns, with the possible exception of smoke intrusions into hibernacula (see below). In southern areas, some species including big brown bats, southeastern bats, Rafinesque big-eared bats, and evening bats, may be active and forage during warmer days of winter or may roost in trees (Barbour and Davis 1969, Boyles and Robbins 2006, Humphrey and Gore 1992). Furthermore, silver-haired bats are long-range migrants that can be found throughout most of the region during winter (Cryan 2003) where they roost in trees in southern portions of the region (Perry and others 2010).

Similar to the foliage-roosting species, some cavity- and bark-roosting bats that remain active during winter may roost on or near the ground during colder periods (<5 °C) of winter. For example, evening bats may use small mammal burrows during colder winter days (Boyles and others 2005), and silver-haired bats may be under tree roots, in rock crevices, or in tree cavities at ground level during colder winter days (Perry and others 2010). Thus, these species may use roosts that are more protected from excessive heat associated with fires than the foliage-roosting species during winter. For bats roosting in the ground, soil temperatures may not exceed 44 °C (111 °F) during prescribed burns at soil depths below 5 cm (Raison and others 1986). However, soil temperatures may exceed 200 °C (392 °F) at a depth of 9.5 cm under heavy fuel loads such as slash piles (Roberts 1965). Furthermore, smoke and CO₂ levels in ground cavities may be benign during controlled burns (O'Brien and others 2006).

Fire Effects on Cavity and Snag Dynamics

Members of the cavity- and bark-roosting guild rely heavily on hollow trees, senescent trees, or snags, and availability of snags or trees with cavities may be

directly affected by fire. Snag density and population dynamics are complex and dependent on multiple factors. Age structure of stands and tree species affect snag dynamics. Natural disturbances such as insects, disease, wind and ice storms, lightning, drought, and wildfire all affect creation and destruction of snags. Snag densities are also affected by management prescriptions such as partial harvest, thinning, herbicides, and burning. Because of this complexity, managers often use models to predict snag dynamics in forest stands (McComb and Ohmann 1996, Morrison and Raphael 1993), and snag dynamics is included in the Fires and Fuels Extension of the Forest Vegetation Simulator model (FFE-FVS) (Dixon 2002).

Fire can affect the availability of roosting substrate for cavity- and bark-roosting bats by creating or consuming snags. Although stand-replacing or intense wildfires may create large areas of snags, effects of multiple, low-intensity prescribed burning on snag dynamics may be difficult to predict, especially for forests consisting mostly of fire-adapted species such as oaks. Low-intensity controlled burns with small fuel loads usually kill few or no overstory trees, but typically top-kill small (<5 cm d.b.h.) trees in the understory (personal observation). Low-intensity, ground-level fire may injure larger hardwood trees, creating avenues for pathogens such as fungi to enter and eventually form hollow cavities in otherwise healthy trees (Smith and Sutherland 2006). Fire may scar the base of trees, promoting the growth of basal cavities or hollowing of the bole in hardwoods (Nelson and others 1933, Van Lear and Harlow 2002). Consequently, repeated burning could potentially create forest stands with abundant hollow trees. Trees located near down logs, snags, or slash may be more susceptible to damage or death, and aggregations of these fuels can create clusters of damaged trees or snags (Brose and Van Lear 1999, Smith and Sutherland 2006). However, snags created by fire may not stand as long as snags created by other disturbances because these snags may be weakened at the base by fire (Morrison and Raphael 1993).

In stands with no recent history of fire, prescribed burns may initially create abundant snags by killing small trees and species that are not fire tolerant. Species with thin bark such as beech (*Fagus grandifolia*) and red maple (*Acer rubrum*), may suffer substantial damage or death, whereas oaks and hickories (*Carya* spp.) with thicker bark may suffer little or no damage (Brose and Van Lear 1999, Hare 1965). Furthermore, smaller-diameter trees are at greater risk from mortality due to fire (Hare 1965, McCarthy and Sims 1935). Although burning often creates substantial numbers of small (<15 cm d.b.h.) snags (Horton and Mannan 1988, Morrison and Raphael 1993, Stephens and Moghaddas 2005), effects on larger trees depends greatly on fire intensity, species of trees that are present, fuel loads, and past fire history. In oak savannas, frequent burning may eventually eliminate tree species that are not fire tolerant such as red maple, black cherry (*Prunus serotina*), and serviceberry (*Amelanchier* sp.) (Peterson and Reich 2001). However, long-term fire suppression can allow many relatively fire-intolerant species to grow into size-classes that are resistant to fire (Harmon 1984). Regardless, bats often take advantage of fire-killed snags. For example, Boyles and Aubrey (2006) found that initial burning of forests after years of suppression created abundant snags, resulting in extensive use of these burned areas by evening bats for roosting. Similarly, Johnson and others (2010) found that after burning, male Indiana bats roosted primarily in fire-killed maples.

Fire may consume some standing snags. For example, in forests of ponderosa pine (*Pinus ponderosa*), loss of larger snags (>20 cm d.b.h.) was 43 percent following introduction of fire and 21 percent following second fires, but net loss (including new snags created by fire) was only 12 and 3 percent, respectively (Bagne and others 2008). Furthermore, Holden and others (2006) found fewer large (>47.5 cm d.b.h.) snags in ponderosa forests burned twice compared to those burned only once, but found no difference between areas burned two or three times. Thus, initial burns

may create abundant snags and second burns may consume some of these, but further burns may not eliminate substantial numbers of large snags. However, comparable studies from eastern oak forests are not available.

Season of burning and topography also affect potential damage or death of overstory trees in hardwood stands. Winter burns tend to cause the least overstory damage because of cooler ambient temperatures and the dormant state of trees (Brose and Van Lear 1999). Spring burns may cause the greatest damage to overstory trees because of higher ambient temperatures, sunlight on boles, and fully hydrated vascular tissues that may reach lethal temperatures when burned (Brose and Van Lear 1999). Summer burns tend to be less damaging than spring burns, likely because of bole shading and lower intensity of fires (Brose and Van Lear 1999). Dry, upland sites on ridge tops and steep slopes tend to burn more intensely, and trees in these locations may be more susceptible to damage during fires.

Fire and Forest Structure for Roosting

Aside from creating snags, periodic prescribed burning may reduce the number of woody shrubs, understory trees, and midstory trees (10-25 cm d.b.h.) in the short term (Blake and Schuette 2000, Hutchinson and others 2005). Longer-term applications of prescribed fire may reduce stand density (Hutchinson and others 2005, Peterson and Reich 2001) and complexity (clutter). Repeated low-intensity fire reduces clutter in the midstory and understory and creates more open forests, which may provide more favorable roosting (and foraging) conditions for many bat species, especially females during the reproductive season. Studies often find roost trees (mostly female) further from other overstory trees (Betts 1998, Brigham and others 1997b) and less canopy cover at roost sites compared to random locations (Kalcounis-Rüppell and others 2005). Canopy gaps created by fire may provide favorable roosting sites with greater solar exposure during summer for maternity colonies of some cavity- and bark-roosting species (Johnson and

others 2009). Furthermore, maternity roosts may be located in areas with few midstory trees or relatively lower tree densities, which may provide both greater solar exposure and more open areas immediately around and below roosts that would otherwise impede inexperienced juvenile flyers (Perry and Thill 2007c). Thus, burned areas may have lower tree densities, less structural clutter, more open canopy, and greater numbers of snags, which may provide favorable roosting areas for many species.

Studies often find bats favor burned areas for roosting. For example, Perry and others (2007b) found five of six species, including red bats, Seminole bats, northern long-eared bats, big brown bats, and evening bats roosted disproportionately in stands that were thinned and burned 1-4 years prior but that still retained large overstory trees. Boyles and Aubrey (2006) found evening bats used burned forest exclusively for roosting. Furthermore, Johnson and others (2009) found that for northern long-eared bats, roost-switching frequency, duration at roosts, and distance between successive roosts were similar between burned and unburned forests.

Caves and Mines

Bats of 13 species may use caves during all or part of the year. Three bats (gray bat, Ozark big-eared bat, and Virginia big-eared bat) are year-round cave obligates (Table 1). Little is known of the effects of fire on adjacent cave and mine habitats used by bats, but these effects may be especially important in karst areas of the eastern oak region. Fire could alter vegetation surrounding entrances, which could potentially modify airflow (Carter and others 2002, Richter and others 1993). Smoke and noxious gases could enter caves, depending on air-flow characteristics of individual caves or mines and weather conditions such as temperature (Carter and others 2002, Tuttle and Stevenson 1977). Fire may not cause levels of gases high enough to be toxic to bats in caves or mines, but gases could potentially cause arousals during hibernation (Dickinson and others 2009). Caviness (2003) noted smoke intrusion into hibernacula

during winter burning in Missouri, but no arousal of hibernating bats was observed. No quantitative studies have examined smoke intrusions into caves and mines or smoke effects on hibernating cave bats, but this is an area that needs to be studied.

FORAGING AND FIRE

Fire and Forest Structure for Foraging

Various factors can affect bat use, activity, and foraging within forests stands. Although studies often find the greatest levels of bat activity in forested riparian areas (Carter 2006, Ford and others 2005, Grindal and others 1999, Zimmerman and Glanz 2000), bat activity and foraging may be greatly influenced by forest clutter. Studies throughout North America suggest that most bats avoid highly cluttered areas and prefer to forage and travel in areas with less clutter (Brigham and others 1997a, Erickson and West 2003, Hayes and Loeb 2007, Humes and others 1999). Bats are often more active in early- and late-seral stages which are usually less cluttered than in intermediate forest stages (e.g., Burford and Lacki 1995a, Erickson and West 2003, Humes and others 1999, Loeb and O'Keefe 2006, Menzel and others 2005). Thinning may reduce clutter and lead to increased bat activity (Erickson and West 2003, Lacki and others 2007), although some studies suggest no response by bats to thinning (Tibbels and Kurta 2003).

Responses to clutter differ among bat species. Differences in bat size (mass), bat morphology, and the echolocation frequencies used among species are believed to make some species more adapted to foraging in cluttered habitats, whereas others are more adapted to foraging in open habitats (Aldridge and Rautenbach 1987, Norberg and Rayner 1987). Species such as big brown bats likely forage more in open forests (Ford and others 2005, Ford and others 2006), whereas northern long-eared bats and Indiana bats may readily utilize cluttered forests (Broders and others 2004, Ford and others 2005, Owen and others 2003, Schirmacher and others 2007), and red bats may use both cluttered and uncluttered habitats

(Carter and others 2004, Menzel and others 2005). However, associations between individual species and levels of tolerable clutter are not concrete, and further study on foraging-habitat associations is needed. Total bat activity may be greater above the forest canopy than below, and some species, such as hoary bats and big brown bats, may be more active above the forest canopy (Menzel and others 2005). Reproductive condition may also affect bat foraging; less-maneuverable pregnant females may be less able to forage in cluttered habitats than nonpregnant bats (Aldridge and Brigham 1988).

In general, within forest stands, fire reduces clutter that theoretically would provide favorable foraging habitat for some species. Similar to thinning, fire may reduce tree densities and create more open forest canopies. However, thinning and midstory removal may reduce structural clutter substantially more than burning alone, and bats may respond to thinning more strongly than simply burning. For example, in the Piedmont of South Carolina, Loeb and Waldrop (2008) found overall bat activity greater in thinned stands than unthinned controls, whereas activity in thinned and burned stands was intermediate. Fire may also kill small groups of trees, creating small gaps in the forest canopy. Small openings, such as tree gaps and group openings, often have higher activity than the surrounding forest (Menzel and others 2002a, Tibbels and Kurta 2003). Quantitative studies have found bat activity response to burned forests is generally favorable or not discernable. For example, following spring burns, Lacki and others (2009b) found home-range sizes and core areas of northern long-eared bats during late spring to summer were unaffected by burn-induced changes in habitat, but bats foraged more in burned habitats than unburned areas. Alternatively, Loeb and Waldrop (2008) found no difference in bat activity levels in burned and unburned habitats.

Fire and Insect Abundance

All species of bats found in the eastern oak region are voracious insectivores. An individual can consume from 40 to 100 percent of its body mass in insects

nightly (Kunz and others 1995). Most bats in the region consume insects in flight, although some species such as big brown bats and northern long-eared bats may glean insects off foliage (Faure and others 1993, Stamper and others 2008). Consequently, abundance of nocturnal flying (and to a lesser extent, foliar) insects may have a direct effect on fitness of individual bats, but short- and long-term effects of prescribed burning on abundance of nocturnal flying insects remain unclear.

Arthropod communities consist of numerous orders, families, and species that vary in natural history and include detritivores, herbivores, and predators. Therefore, responses of the overall insect community to fire are complex. Among individual insect taxa, fire and fire frequency may affect species groups differently, with some families increasing in burned areas and other families decreasing in richness or abundance depending on season and intensity of burns. Insect communities may differ between burned and unburned areas (Swengel 2001). Some flying insects (at least 40 species, mostly beetles) are attracted to fires, and the subgenus *Melanophila* use infrared sensors to locate fires where they lay eggs on burnt woody debris immediately after cooling (Hart 1998).

Although many studies have examined effects of burning on insects, these studies are often not directly applicable to the insects available to bats in eastern oak forests subjected to burning. Most previous studies in North America have focused on effects of burning on insect abundance and diversity in grasslands or agricultural lands. Previous studies often include taxa that are not readily available to bats or combine taxa such as ground-dwelling and flying species. Furthermore, sampling methods used to determine effects of burning may affect observed responses. For example, pitfalls and litter sampling techniques often sample ground-dwelling insects that are not part of the food base for bats. Also, many studies of volant insect abundances examined diurnal insect abundance, and it is unclear if patterns of abundance for nocturnal insects mirror those of diurnal insects. Relatively few

studies have examined effects of burning in a way that would provide insight into the specific groups of insects that bats utilize as food (i.e., nocturnal flying insects).

Aside from the limitations of previous studies stated above, richness and abundance of herbivorous flying and foliar insects has long been associated with plant species richness (Hartley and others 2007, Knopps and others 1999, Murdoch and others 1972) because many insect species forage on the foliage, pollen, or nectar of specific plant species. Fires may produce more lush plant growth, and postburn vegetation may be attractive to recolonizing insects (Swengel 2001), although size and heterogeneity of burns likely affect the ability of flying insects to recolonize burned areas. In eastern oak forests, the herbaceous layer harbors the majority of plant species richness, and burning typically increases community diversity and abundance of herbaceous plants (Hutchinson 2006). Consequently, one would expect short-term reductions in insects due to mortality from fire and a temporary reduction in understory foliage, followed by subsequent increases in flying and foliar insects from enhanced abundance and diversity of herbaceous plants later.

Results of studies examining burning and abundance of flying insects often give conflicting results. In grasslands, studies that collected flying insects suggest that recently burned sites produce more flying insects than nonburned sites (Hansen 1986, Nagel 1973), although burning may reduce abundance of ground-dwelling insects (Buffington 1967, Bulan and Barrett 1971, Seastedt 1984, Warren and others 1987). Studies suggest that fires may cause a short-term decrease of 95 percent in soil macroarthropods immediately after fire (Paquin and Coderre 1997), which could ultimately affect volant species because many volant species have a larval or pupae stage that is resident in litter or soil. Nevertheless, studies in other regions suggest many flying insects are resilient to burning and recover quickly because of their mobility, whereas ground- and litter-dwelling insects have low resilience

to fire (Lamotte 1975, Moretti and others 2006). In California chaparral, insect abundance peaked the first year after fire, likely because of an influx of generalist species that took advantage of the lush vegetation in the postburn area, but abundance declined the second and third years after burning (Force 1981).

In oak-dominated forests of the eastern United States, thinning or other reductions in basal area likely has more of an effect on herbaceous plant growth than burning alone. In eastern oak forests, combinations of thinning and burning along with mechanical understory shrub control may produce substantially more flying insects than forest stands that are burned but not thinned or in unburned stands (Campbell and others 2007). In oak savannas, abundance of flying insects may be low the year of fire but quickly rebounds in subsequent years after burning (Siemann and others 1997). However, Lacki and others (2009b) found a 34 percent increase in nocturnal insects used by bats in burned areas during the first year following spring burns in Kentucky. Thus, fire in eastern oak forests may or may not cause a short-term decrease in abundance of flying insects, but may ultimately increase overall abundance.

Fires may also have indirect effects on insect production. For example, in riparian areas, fires may increase nutrient delivery into streams and reduce canopy cover, which may increase water temperatures, all leading to increased productivity (Minshall and others 1997, Spencer and Hauer 1991). Increases in emerging insects may result from this increased productivity (Malison and Baxter 2010, Minshall 2003), providing more food resources for bats. Malison and Baxter (2010) found streams in high severity burned areas had substantially greater insect emergence than streams in low severity burns or unburned areas, and bat activity in severe burn areas was substantially greater.

Moths are one of the most important insect groups in the diets of many eastern bats, and some bats are moth specialists, including the big-eared bats (*Corynorhinus* spp.) (Burford and Lacki 1995b, Hurst and Lacki 1997, Leslie and Clark 2002). Although most larval caterpillars of moths feed on vegetation (many are agricultural pests), adults either use nectar sources such as herbaceous flowers or do not feed as adults. Consequently, abundant and diverse herbaceous vegetation likely produces more food sources for those adults that feed. Restored woodlands subjected to periodic burning may produce substantially more nectar sources than mature unmanaged forests (Rudolph and others 2006). In forests, caterpillars of most moth species feed on woody plants such as oaks (Summerville and Crist 2002). Furthermore, early seral clearcut stands may be dominated by moth species whose caterpillars feed on tree species such as *Prunus* spp. and herbaceous vegetation, whereas mature forests may be dominated by species whose caterpillars feed on oaks, hickories, acorns, fungi, and lichens (Summerville and Crist 2002). Therefore, abundance and diversity of woody plants may be more important to moths than abundance and diversity of herbaceous vegetation in the understory.

Studies of moths in the eastern oak region have compared abundance and diversity of moths among forest age classes and pasture monocultures (Burford and others 1999, Dodd and others 2008, Summerville and Crist 2002), but relatively few studies have examined effects of burning on moth abundance. Lacki and others (2009b) found a 22 percent increase in moth abundance the first year after burning in Kentucky, although the difference was not significant. In frequently burned pine woodlands of Arkansas, Thill and others (2004) found moth abundance was generally greater in forests managed using frequent fire compared to unburned controls, except for the first couple of months immediately following the burn.

FOREST DIVERSITY AND BATS

During landscape-level burns, differences in forest density and topography often result in a mosaic of burned and unburned areas that provide different levels of clutter and density of snags. For example, riparian areas (greenbelts, streamside management zones, or riparian zones) are often not subject to harvest or thinning and often burn less intensely than the surrounding forest due to greater shading and moister litter conditions. These buffers often provide greater densities of trees, more cluttered habitats, and more small trees and small snags than the surrounding forest landscape. Individual bat species may use these areas more or less than their availability. For example, Perry and others (2007b) found that within thinned and burned stands, less than 2 percent of Seminole bat roosts were in unthinned greenbelts, whereas most (90 percent) roosts of tri-colored bats were in greenbelts. Furthermore, Loeb and Waldrop (2008) found activity of big brown bats greater in thinned stands than unthinned controls, whereas activity of tri-colored bats did not differ among treatments. Thus, heterogeneous habitats created by various levels of thinning and burning intensity may provide a range of roosting and foraging habitats for a varied bat community.

CONCLUSIONS

Fire is increasingly being used in oak forests to promote oak regeneration, improve wildlife habitat, and reduce hazardous fuel loads. Although recent research has begun to shed light on the relationships among fire, bats, and bat habitat, these interactions are not yet understood. These interactions offer substantial opportunities for expanded research. Studies suggest burning may have positive, negative, or no effect on various aspects of bat ecology, but effects may vary among bat species, time of the year, fire frequency, ambient temperatures, and intensity of burns. In general, burning appears to improve habitat by creating snags and opening up habitats for foraging and roosting. Fire may also help create heterogeneous landscapes that provide a variety of habitats for

multiple species. Abundance of bat food (insects) may also respond positively to fire. Direct effects of fire on bats during the burning process are still uncertain but may vary considerably due to timing and intensity of burns and the species of bat considered. Nevertheless, bats likely adapted to this disturbance over the millennia in areas such as the eastern oak region where fire has played a central role in the formation and maintenance of these forests.

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