Available online at www.sciencedirect.com
SCIENCE DIRECT®
Forest Ecology and Management 222 (2006) 108–115
Forest Ecology and Management
www.elsevier.com/locate/foreco

Managing forests with prescribed fire: Implications for a cavity-dwelling bat species

Justin G. Boyles [a], Doug P. Aubrey [b,*]

[a] Department of Ecology and Organismal Biology, Indiana State University, Terre Haute, 47809, USA
[b] USDA Forest Service, Savannah River, P.O. Box 700, New Ellenton, SC 29809, USA

Received 1 June 2005; received in revised form 27 September 2005; accepted 30 September 2005

Abstract

Prescribed burning is used as a restoration and management technique in many deciduous forests of eastern North America. The effects of fire have been studied on habitat selection of many vertebrate species, but no studies have reported the effect of fire on bat roosting habitat. Fire initially leads to an influx of dead and dying trees, an increase of light availability, and a decrease of canopy and sub-canopy tree density. These characteristics are beneficial to many forest-dwelling vertebrates including cavity-roosting bats. We evaluated evening bat (*Nycticeius humeralis*) roost-site selection at the stand-scale in order to determine roosting preferences as they relate to prescribed burning. Standard radiotelemetry techniques were used to locate evening bat roost trees. Canopy light penetration and overstory tree density were measured in both burned and unburned forests. Sixty-three trees used as roosts by both male and female evening bats were located during both the summer and winter and all 63 roosts were located in the burned portion of the study area. Canopy light penetration was higher and canopy tree density was lower in the burned forest than unburned forest. An increase in light availability may release bats from one of the constraints suggested for many forest-dwelling bat species in roost tree selection—sun-exposure. This should increase the abundance of trees with characteristics suitable for roosting and may allow bats to roost throughout the interior of the forest as opposed to only on forest edges, thereby allowing bats to roost closer to foraging grounds and possibly lessening predation rates. Lower tree density may allow for ease of flight within the forest as well as more efficient locating of roost trees. In addition, there were a significantly higher proportion of dead trees, which evening bats commonly use as roost trees, in burned forests compared to unburned forests. Prescribed burning appears to initially lead to creation or restoration of favorable cavity-dwelling bat habitat and its continual implementation perpetuates an open sub-canopy. Therefore, we suggest that prescribed burning may be a suitable tool for management of roosting habitat for cavity-roosting bats.

Keywords: Fire ecology; Forest restoration; *Nycticeius humeralis*; Oak-hickory forest; Prescribed burning; Roost selection

1. Introduction

Fire is critical in regulating and maintaining many forest ecosystems (Huddle and Pallardy, 1996; van Lear, 2002). In particular, much of the western portion of North America's eastern deciduous forest is thought to have been shaped and maintained through fires set by Native Americans prior to European settlement (Cottam, 1949; Ladd, 1991; Pyne, 1982). Prescribed burning has been shown to alter many characteristics of forest habitat potentially affecting forest-dwelling bats including tree mortality, which increases available trees commonly used by wildlife (Huddle and Pallardy, 1996; Arthur et al., 1998; Hartman and Heumann, 2003; Aubrey, 2004); pathogen susceptibility, which expedites cavity formation (Burns, 1955; Paulsell, 1957; Smith and Sutherland, 2001); and canopy light penetration (Anderson and Brown, 1986; McCarty, 1998; Aubrey, 2004), which is known to affect roost suitability (Kurta et al., 1993; Brigham et al., 1997).

Many forests are managed for timber harvest by the use of mechanical thinning or clear-cutting. Prescribed fire differs from these management techniques because fire is generally used to maintain or restore natural forest ecosystems and reduce understory competition, while other silvicultural methods are predominately used to maximize harvest yield and quality. When first implemented, prescribed burning decreases overstory tree density and basal area (Anderson and Brown, 1986; Peterson and Reich, 2001). Following this initial fire with frequent burns generally reduces fuel accumulation and subsequent burns are

* Corresponding author. Tel.: +1 803 725 1758; fax: +1 803 725 0311.
E-mail address: daubrey@fs.fed.us (D.P. Aubrey).

0378-1127/$ – see front matter
doi:10.1016/j.foreco.2005.09.024

therefore relatively cool and somewhat non-uniform (Ladd, 1991). However many fire-sensitive seedlings and saplings are generally eliminated or prevented from regenerating (Lorimer, 1985; Ladd, 1991; Moser et al., 1996; Brose and van Lear, 1997; Barnes and van Lear, 1998). Fire-tolerant trees remain as overstory dominants and canopy recruitment coincides with periods of decreased burn frequency or intensity (Crow et al., 1994). For example, oaks possess thick bark which insulates them from heat associated with burning and are capable of rapid compartmentalization when damaged by fire which inhibits fungal infection and makes mature individuals relatively tolerant of fire (Lorimer, 1985; Abrams, 1985; Crow, 1988; Stearns, 1991; Smith and Sutherland, 1999; Peterson and Reich, 2001). Much of the western portion of the eastern deciduous forest is believed to have resembled the structure and composition of a woodland (i.e. moderate to low canopy coverage) more than a forest (i.e. high canopy coverage) prior to European settlement, which is largely attributed to fire (Cottam, 1949; Curtis, 1959; Nuzzo, 1986; Ladd, 1991). Therefore, managing forests with prescribed fire reintroduces a historic disturbance process that other silvicultural techniques lack, and may provide a more heterogeneous habitat for wildlife that is similar to forested areas prior to wide-spread fire suppression by European settlers. Furthermore, prescribed burning has become increasingly common over the past few decades, as land managers have seen the effects of fire suppression. Specifically, fire has been most commonly reintroduced to systems where conservation of biodiversity and restoration of historic ecosystem processes are paramount.

Numerous studies have focused on vertebrates in forests maintained by prescribed burning (e.g. reptiles, McLeod and Gates, 1998; small mammals, Simon et al., 2002; amphibians, Schurbon and Fauth, 2003; birds, Blake, 2005). However, to our knowledge, there are no studies reporting habitat selection of tree-dwelling bats in burned forests, although the need for such studies has been suggested (Menzel et al., 2001b; Carter et al., 2002). Furthermore, the effects of forest management on roosting habitat of bats are not clear and it has been suggested that wildfires and prescribed burning may have detrimental (Chambers et al., 2002) or beneficial (Carter et al., 2002) impacts on bats. For some bat species, such as the eastern red bat (*Lasiurus borealis*), fire may pose a direct threat to survival as early spring burns remove litter where occasional winter roosting occurs and can potentially scorch hibernating individuals (Moorman et al., 1999; Rodrigue et al., 2001). Bats roosting in snags (standing dead trees) are also susceptible to direct disturbance from fire if roost trees ignite (Rodrigue et al., 2001), but this is probably not a major cause of mortality unless the roost burns quickly and the bat is in deep torpor (Carter et al., 2002). Availability of suitable roosts likely influences habitat selection (Kunz, 1982) and roosting sites are thought to be of critical importance to conservation of many bat species (Fenton, 1997). Fire generally removes understory saplings and may lead to the creation of suitable roost trees for cavity-roosting bats. Fire may also remove standing snags if fuel loading is high. However, fuel should not accumulate directly under a snag when burning is frequent so snags should persist under these circumstances. As fire increases the heterogeneity of forest structure and composition (Fule et al., 2004), there should be an increase in the diversity of available roosting habitat.

Previous studies have focused on activity (Humes et al., 1999; Patriquin and Barclay, 2003; Tibbels and Kurta, 2003; Mazurek and Zielinski, 2004), demographic parameters (Miller, 2003), and roosting preference (Campbell et al., 1996; Menzel et al., 2002; Elmore et al., 2004) of bats in heavily managed forests, but have not examined fire-based management. With the exception of a few anecdotal reports of *L. borealis* being driven from their leaf litter hibernacula during winter burns (Moorman et al., 1999; Rodrigue et al., 2001), there is little empirical data about how fire affects forest-dwelling bats.

The objective of this study was to determine evening bat (*Nycticeius humeralis*) roost-site selection at the stand-scale in a forest heavily managed by fire and to understand those characteristics of the forest that may influence roost tree selection. The evening bat is a locally abundant cavity-dwelling bat species found throughout much of the southeastern United States, but it may be declining in parts of its range (Whitaker et al., 2002; Whitaker and Gummer, 2003). Evening bats are known to roost in large numbers in man-made structures (Watkins, 1969; Watkins and Shump, 1981; Bain and Humphrey, 1986; Wilkinson, 1992) and tree cavities (Wilkinson, 1992; Bowles et al., 1996; Menzel et al., 1999, 2001a; Boyles et al., 2003; Boyles and Robbins, in press). Evening bats roost mainly in cavities in trees of various stages of decay (Bowles et al., 1996; Boyles and Robbins, in press), but relatively little is known about the formation or microclimate of the roosts. During the summer, evening bats roost mainly in large dead trees, but during the winter, live trees are commonly used (Boyles and Robbins, in press). They have a short wingspan and high wing loading so it has been predicted that they are not highly maneuverable relative to other bat species (Norberg and Rayner, 1987). Due to relatively inefficient flight, this species may avoid long foraging trips (Norberg and Rayner, 1987) and it has been suggested that evening bats forage close to their roosting areas (Duchamp et al., 2004). Evening bats feed heavily on coleopterans, homopterans, and hemipterans (Whitaker, 2004). As with other tree roosting bat species, they spend over half of its time each day in roosts (Brigham et al., 1997), so conserving roosts is important in managing this species. Evening bats are commonly referred to as migratory in middle latitudes (Jones et al., 1967; Humphrey and Cope, 1968; Watkins, 1969; Wilkinson, 1992; Sparks et al., 1999; Geluso et al., 2004), but it appears that the population discussed herein is largely non-migratory (Boyles et al., 2003; Boyles and Robbins, in press) so roost trees refer to trees used throughout the year.

It was predicted that evening bats would prefer roosting in burned forests because of an increase in the density of dead and dying trees, an increase in light penetration and an overall decrease in overstory and understory tree density. These characteristics should benefit forest-dwelling bats and promote use of burned forests as roosting habitat. This study compliments previous work (Boyles and Robbins, in press), which reports the characteristics of roost trees and the surrounding habitat used by this population of evening bats during both the summer and winter. The results presented herein focus on roost selection at the forest stand-level.

2. Methods

2.1. Study area

We conducted this research on the Drury Conservation Area (DCA) in Taney County, Missouri (UTM 40.47.000N, 4.93.000E). DCA is a 1200 ha area located in extreme southwestern Missouri in the Ozark Mountains Region and is bordered on two sides by Bull Shoals Lake. It is actively managed by the Missouri Department of Conservation, which has implemented prescribed burning on approximately 55% of the potential area available for roosting habitat in an attempt to restore historic glades and oak-hickory woodlands and reduce red cedar (*Juniperus virginiana*) concentrations. Burning was initiated in 1999 after nearly 50 years of fire suppression and the area was then burned on a biennial schedule. All burning was conducted in March or April. The initial 1999 burn was probably more intense than subsequent burns because of accumulated fuels; therefore more overstory tree mortality may have occurred during or as a result of the initial burn (Aubrey, 2004).

Approximately 60% of DCA is dominated by oak-hickory forest with the remainder of the area being glades, wildlife food plots, ponds, and riparian areas (Missouri Department of Conservation, 1991). Elevation ranges from 185 to 335 m on DCA. Several gravel roads facilitate access to the interior of much of the forest and one large gravel road serves as the firebreak between burned and unburned portions of the forest. The canopy of the area consists almost entirely of deciduous trees from the white and red oak groups (*Quercus* spp.), hickories (*Carya* spp.), elms (*Ulmus* spp.), and ashes (*Fraxinus* spp.).

2.2. Location of roosting sites

Bats were captured from March 2003 to March 2004 using mist nets (Avinet, Dryden, NY, USA) of various lengths (6, 9, 12, or 18 m) placed across ponds or forest roads. The majority of netting sites were on the gravel road that acts as a firebreak between the burned and unburned forest, but one pond and two roads in the burned forest and one pond and one creek bed in the unburned forest were also netted. Approximately 55% of the available roosting area for evening bats was located in an area treated with prescribed fire. Thus, if evening bats were roosting at random, we would expect 55% of roost trees to be located in burned forest and 45% of roost trees to be located in unburned forest. Twenty-three evening bats were fitted with radio-transmitters (0.52 g; Model LB-2N, Holohil, Carp, Canada) by clipping fur to the skin in the interscapular region and affixing the transmitter with surgical adhesive (Skin Bond, Smith and Nephew Inc., Largo, FL, USA). The range of weights of bats fitted with transmitters was 7.5–13.5 g; therefore the transmitter represented 3.9–6.9% of the individual's body mass.

Each bat's roost tree was located every day following attachment of the transmitter and tracking was discontinued when the transmitter expired, was shed by the bat, or the bat remained outside of the study area for more than 5 days. This study was conducted year-round so roost trees include those used during both summer and winter by males and females in all reproductive classes (pregnant, lactating, post-lactating, and non-reproductive). All animal handling methods follow guidelines of the American Society of Mammalogists (Animal Care and Use Committee, 1998).

2.3. Canopy light penetration sampling

Leaf area index (LAI) was used as a measure of canopy light penetration to determine if three biennial prescribed burns had resulted in a more open canopy. LAI is an estimate of the ratio of overstory leaf area relative to ground area. A LAI of 0 indicates complete canopy light penetration whereas a LAI of 12 indicates no canopy light penetration (Hyer and Goetz, 2004). Here we define canopy light penetration (CLP) as: $12 - \text{LAI}$.

Two blocks each containing three transects in burned and unburned forests were monitored throughout the 2003 growing season. Unburned and burned forests were adjacent to one another with a gravel road acting as a fire buffer between them. LAI was obtained indirectly at each transect using an AccuPAR PAR-80 light interception device (Decagon Devices Inc., Pullman, WA, USA). Individual light measurements were collected 1.2 m above ground-level at five randomly spaced points along each transect. These five measurements were then averaged to calculate one LAI value, and therefore, one CLP value for each transect per sample period. Measurements were collected monthly throughout the 2003 growing season (April through September). The majority of canopy trees were deciduous species; thus, CLP was high in both burned and unburned forests during winter and was not measured from October through March.

2.4. Tree density

Canopy tree density was estimated in 0.05 ha circular plots centered on 25 randomly selected trees in each of the burn treatments. A random number generator was used to select UTM coordinates for the trees. Coordinates were located using a GPS unit (eTrex, Garmin International Inc., Olathe, Kansas) and selected the tree nearest that point to serve as the center of the plot. All trees in the plot greater than 10 cm diameter at breast height (dbh) were considered overstory trees and were counted and classified as either live or dead.

2.5. Statistical analysis

A binomial probability distribution was used to determine if bats roosted at random or at a proportion different from what would be expected given the amount of burned and unburned forest available. The effect of prescribed fire on CLP was assessed using a multi-factorial analysis of variance (ANOVA). The experiment was a nested block design with repeated measures. Month (April–September) and habitat (burned forest and unburned forest) were treated as fixed factors. Block ($n = 2$) and transect ($n = 12$) were treated as random factors, with transect nested under treatment. Mean separations were performed using a post hoc Tukey test. Tree density was analyzed using a t-test. In addition to absolute densities, the arcsine of the proportion of dead trees compared to total trees was calculated and analyzed using a t-test (Zar, 1984). All statistical analyses were conducted in Minitab 14. Alpha is 0.05 for all analyses.

3. Results

3.1. Roost tree location

Sixty-three roost trees were used by 23 (11 females and 12 males) evening bats from 9 March 2003 to 31 March 2004. All 63 roost trees were located in the portion of the area that was subjected to prescribed burning, although many of the bats were captured on the road that serves as the break between burned and unburned forest or within 200 m of that road. Bats roosted in the burned forest exclusively and significantly more often than expected if they selected burned or unburned forest randomly ($P < 0.001$). In addition, nearly all the trees used as roosts were located more than 50 m from any forest edge (62 of 63). The one exception was a large white oak *Quercus alba* (L.) used by a male evening bat in October that was located at the forest edge less than 50 m from where that individual was captured. This tree was not used the first day after capture; it was used on the second and fourth days, so it appears that this tree was actively selected and was not used in response to stress caused by handling.

3.2. Canopy light penetration

Both the main effects of treatment ($P < 0.001$) and month ($P < 0.001$) as well as their interaction ($P < 0.001$) significantly affected CLP. Maximum leaf expansion occurred in May for the burned forest and July in the unburned forest. Averaged over the 6-month sample period, canopy light penetration was significantly greater in burned forest as compared to unburned forest ($P < 0.001$). CLP was high in both the burned and unburned forests in April (Fig. 1). Pairwise comparisons suggest that there was no difference in canopy light penetration between burned and unburned forests in April or May but differences were significant throughout the rest of the growing season (June–September, $P < 0.05$ in all comparisons). As expected, measurements collected prior to leaf expansion (April) suggest that there was no difference in CLP between the burned and unburned forests; therefore, there was likely no difference in light availability between the treatments during the winter.

3.3. Tree density

Mean overstory tree density per hectare was significantly higher in unburned forest (612.0 ± 25.0) relative to burned forest (513.6 ± 24.2; $t = 2.83$, $P = 0.007$) and live tree density was significantly higher in unburned forest (576.0 ± 24.6) than burned forest (468.0 ± 24.1; $t = 3.13$, $P = 0.003$). The density of dead trees was not significantly different between the burned (45.6 ± 7.3) and unburned forests (36.0 ± 4.3; $t = 1.14$, $P = 0.263$). However, the proportion of dead trees compared to total trees was significantly higher in burned forest (0.092 ± 0.014) relative to unburned forest (0.060 ± 0.007; $t = 2.08$, $P = 0.045$).

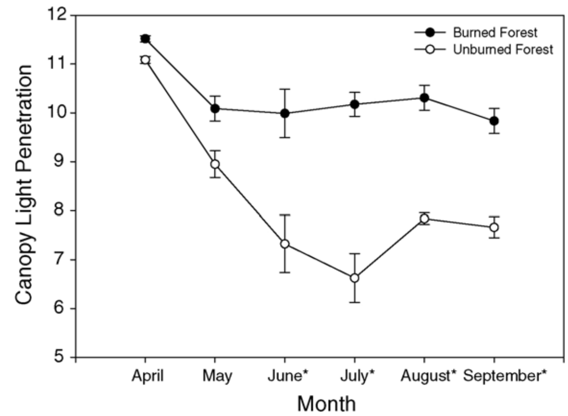

Fig. 1. Seasonal trends (mean ± S.E.) in canopy light penetration (CLP) calculated as 12 − leaf area index in burned and unburned forest on Drury Conservation Area, Taney County, Missouri during the 2003 growing season. CLP, as defined herein, is measured on a scale of 0–12, with 12 indicating complete light penetration and 0 indicating no light penetration. All measurements were collected mid-month. Asterisks indicate significant differences (at alpha = 0.05) between burned and unburned forests in each month.

4. Discussion

In our study area, evening bats showed a strong preference for forests managed with prescribed fires. Although there are no data on roost tree selection by evening bats before prescribed burning was initiated, it is likely that the forest characteristics were similar between what are now burned and unburned forests (Aubrey, 2004). All roost trees used by both males and females throughout the year were in the burned portion of the study area. For at least a few years after the initial burn, prescribed fire enhances roosting habitat for evening bats in several ways. First, burning increases the abundance of dead trees in some forests (Burns, 1955; Paulsell, 1957; Huddle and Pallardy, 1996; Peterson and Reich, 2001; Fule et al., 2004) and therefore increases the number of tree cavities formed by decay. We did not directly test the effect of fire on overstory tree mortality; however, dead trees were found in higher densities and at significantly higher proportions in the burned forest. Initial burns with high fuel accumulation can result in the formation of dead trees (Paulsell, 1957; Scowcroft, 1966; Anderson and Brown, 1986; White, 1986; Peterson and Reich, 2001) and leads to a forest with a large number of trees in various stages of decay. Ambient temperatures vary widely during the winter in southwestern Missouri so a large number of trees in varying stages of decay may provide sufficient options for evening bats to meet thermoregulatory needs simply by roost-switching. It has also been suggested that fire-scars allow entry for fungal pathogens, which can lead to heartrot and possibly mortality, which should promote cavity formation (Smith and Sutherland, 2001; Parsons et al., 2003). This population of evening bats is known to roost in trees in all decay stages (Boyles and Robbins, in press) and frequent burning should increase options for roost tree selection.

Second, CLP is significantly higher in burned forest than the unburned forest during the growing season. Although evening bats are not known to preferentially roost on forest edges, many tree-dwelling bats are thought to select roost trees that receive high levels of sun-exposure during the summer months (Kurta et al., 1993); therefore, trees selected as roosts are commonly taller than the canopy (Vonhof and Barclay, 1996; Britzke et al., 2003), near forest edges (Grindal, 1999) or areas with an open canopy (Menzel et al., 2001a). High light exposure is known to improve roost suitability (Kurta et al., 1993; Brigham et al., 1997) so high light penetration into the interior forest will allow bats to roost in trees that would not receive adequate sun-exposure to facilitate thermoregulation in unburned forests. The ability to roost in interior forest trees that would not receive adequate sun-exposure in unburned forest may yield many benefits for evening bats. For example, the opportunity to use interior forest trees as roosts increases the availability of suitable roost trees in the habitat relative to populations that are forced to roost near forest edges or openings. This increase in suitable roost trees may allow bats to roost closer to their preferred foraging area and therefore reduce commuting distance and energy expenditure. Predation by meso-carnivores (Sparks et al., 2003) should also be lessened because the roosting sites are not concentrated in small forest patches or along forest edges, which may be easily found by and accessible to predators. An abundance of suitable roost trees may also facilitate frequent roost switching, which in turn may lessen ecto-parasite loads (Lewis, 1995).

Finally, prescribed burning may improve foraging habitat, thereby encouraging bats to roost in the vicinity. High fire frequency of low to moderate intensity prevents the regeneration of a sapling layer if preceded by a high intensity fire that removes this layer (Peterson and Reich, 2001). Exclusion of this stratum will reduce obstructions and make navigation easier in burned forest compared to unburned forest (Boyles and Robbins, in press). Evening bats forage in open areas and wooded habitats (Duchamp et al., 2004) and it has been noted that activity is higher for some bat communities in thinned forest compared to unthinned forest (Humes et al., 1999). It has been predicted that evening bats are not highly maneuverable and have relatively inefficient flight (Norberg and Rayner, 1987). This may prohibit evening bats from roosting in unburned areas because of dense understory that would make straight flight difficult. Other studies have also noted a preference for roosting in areas with a more open understory (Castleberry et al., 2005). Previous work has suggested that evening bats forage close to their roosting areas (Duchamp et al., 2004); therefore roost selection in burned forest may simply be an artifact of selection of burned habitat for foraging. In addition, the major food source of evening bats, coleopterans (Whitaker, 2004), have been found at both higher abundances and greater species richness in burned forests than unburned forests (Saint-Germain et al., 2004). Although it is difficult to distinguish if roosting habitat or foraging habitat is more important in observed habitat selection, anecdotally there does appear to be a close association between the two in this population of evening bats.

It is unlikely that any one of these reasons alone can adequately explain the preferential habitat selection seen in evening bats. Combinations of any or all of these broad forest characteristics may contribute to suitable habitat for this species and each may be of fluctuating importance throughout the year. For example, the difference in light penetration between burned and unburned forest is probably only important during the summer months. Because of the deciduous nature of the majority of the trees in southwestern Missouri, the difference in light penetration between burned and unburned forest will be lessened during the winter. Therefore, it is likely that evening bats roosted exclusively on the burned portion of the area during the winter because of prey availability, lessened clutter, or simple roost fidelity. However, it should be noted that many tree-dwelling bat species in the eastern United States only roost in trees during the summer months, so this may be inconsequential in reference to those species.

5. Conclusions

Prescribed burning has the potential to provide habitat for evening bats and possibly other species and should be taken into consideration when constructing management plans for these species. Fire may initially increase both the quantity and quality of roosting habitat for evening bats by creating an influx of dead and dying trees as well as facilitating disease and decay in live trees. This study deals only with the first 6 years following the initial burn, and long-term effects of burning may not be as beneficial to evening bats. For example, frequent burning may lead to a decline in roost trees by felling suitable snags and creating a canopy of fire-tolerant species that are not generally killed by fire (Curtis, 1959; Pyne, 1982; Crow, 1988; Ladd, 1991). However, anecdotal evidence suggests that snags persist through these low intensity burns, possibly because leaf litter fails to accumulate underneath a snag (personal observation). The same type of anecdotal evidence exists in southeastern long-leaf pine systems where biennial fire leaves snags intact because of reduced fuel accumulation near the base of the tree (S. Castleberry, University of Georgia, personal communication). To our knowledge, no studies have addressed the fate or residence time for snags suitable for roosting in a frequently burned system. Fire frequency should not remain a static part of management strategy. If biennial burns are continued, eventually the only trees left in the canopy will be fire-tolerant. It is necessary to withhold fire from areas to allow a sufficient fuel source to accumulate, which will allow for high-intensity fires that can cause canopy tree mortality and create snags. However, benefits of managing with prescribed fire may surpass those of mechanical thinning techniques because of the random and delayed mortality imposed on canopy trees (Loomis, 1974). Furthermore, prescribed burning is a more cost-effective management tool than mechanical methods (Wade and Lunsford, 1988; Dubois et al., 1999).

This study demonstrates the preference of evening bats to periodically burned forest, but fire can also be beneficial to other bat species that utilize trees as roosts. For example, the Indiana bat (*Myotis sodalis*), listed as federally endangered in the United States, is known to use a large number of dead and dying trees as roosts because these trees often offer the exfoliating bark that this species uses as a roost-site (Kurta et al., 1993). Through mortality and damage to bark, fire will increase the abundance of trees with exfoliating bark (Burns, 1955; Paulsell, 1957; Smith and Sutherland, 1999) and thereby increase available roosting habitat for species such as the Indiana bat. Other bat species could benefit from fire as a management tool and it should be investigated in other regions with other bat species.

Fire does have the potential to negatively affect forest-dwelling bat habitat. For species that preferentially roost in trees in late stages of decay, frequent fire may destroy roost trees before they become suitable for roosting. Frequent fire may also cause the loss of winter habitat for litter-roosting species such as *L. borealis* (Moorman et al., 1999; Boyles et al., 2003) by continually removing accumulated leaf litter from the forest floor. Long-term studies are necessary to understand the patterns and processes of snag residence time in a periodically burned forest. Resource managers should consider the different habitat needs and life history traits of both tree-dwelling and litter-roosting bats when creating management plans. Furthermore, forests respond differently according to the season when burning occurs. For example, summer burns have been shown to cause increased overstory tree mortality relative to burns conducted in other seasons (van Lear and Waldrop, 1991; Brose and van Lear, 1997). Fires in this season would therefore benefit tree-dwelling species as well as allow leaf litter to accumulate in fall benefiting litter-roosting species. More research examining the effect of burn frequency and season of burning on a variety of taxa is necessary to properly manage forests for biodiversity.

Acknowledgements

Funding for this project was provided in part by the Missouri Department of Conservation, the City of Springfield, MO, Dickerson Park Zoo, and Southwest Missouri State University. We would like to thank L. Robbins and D.A. Wait for assisting in obtaining funding and providing equipment for this project. The Missouri Department of Conservation and the Bull Shoals Field Station provided vehicles, equipment, and access to their property. J. Timpone, M. Milam, B. Mormann, P. Brown, and many others assisted in capturing and tracking bats and conducting vegetation analysis. M. Milam, M. McKnight, M. Coleman, J. Orrock, and anonymous reviewers provided many helpful comments on earlier versions of this manuscript.

References

Abrams, M.D., 1985. Fire history of oak gallery forests in northeast Kansas tallgrass prairie. Am. Midl. Nat. 114, 188–191.

Anderson, R.C., Brown, L.E., 1986. Stability and instability in plant communities following fire. Am. J. Bot. 73, 364–368.

Animal Care and Use Committee, 1998. Guidelines for the capture, handling, and care of mammals as approved by The American Society of Mammalogists. J. Mamm. 79, 1416–1431.

Arthur, M.A., Paratley, R.D., Blakenship, B.A., 1998. Single and repeated fires affect survival and regeneration of woody and herbaceous species in an oak-pine forest. J. Torrey Bot. Soc. 125, 225–236.

Aubrey, D.A., 2004. Savanna restoration through prescribed fire: demographic and physiological responses of oak and hickory seedlings and saplings to a changing light environment. Master's Thesis, Southwest Missouri State University.

Bain, J.R., Humphrey, S.R., 1986. Social organization and biased primary sex ratio of the evening bat *Nycticeius humeralis*. Fla. Sci. 49, 22–31.

Barnes, T.A., van Lear, D.H., 1998. Prescribed fire effects on advanced regeneration in mixed hardwood stands. South. J. Appl. For. 22, 138–142.

Blake, J.G., 2005. Effects of prescribed burning on distribution and abundance of birds in a closed-canopy oak-dominated forest, Missouri, USA. Biol. Conserv. 121, 519–531.

Bowles, J.B., Howell, D., Van Zee, J.W., Wilson, G.M., 1996. Use of alternate roost trees by the evening bat, *Nycticeius humeralis*, in Iowa. In: Genoways, H.H., Baker, R.J. (Eds.), Contributions in Mammalogy: A Memorial Volume Honoring Dr. J. Knox Jones, Jr. Museum of Texas Tech University, Lubbock, Texas, pp. 217–224.

Boyles, J.G., Timpone, J.C., Robbins, L.W., 2003. Late-winter observations of red bats, *Lasiurus borealis*, and evening bats, *Nycticeius humeralis*, in Missouri. Bat Res. News 44, 59–61.

Boyles, J.G., Robbins, L.W. Characteristics of summer and winter roost trees used by evening bats (*Nycticeius humeralis*) in southwestern Missouri. Am. Midl. Nat., in press.

Brigham, R.M., Vonhof, M.J., Barclay, R.M.R., Gwilliam, J.C., 1997. Roosting behavior and roost-site preferences of forest-dwelling California bats (*Myotis californicus*). J. Mamm. 78, 1231–1239.

Britzke, E.R., Harvey, M.J., Loeb, S.C., 2003. Indiana bat, *Myotis sodalis*, maternity roosts in the southern United States. Southeast. Nat. 2, 235–242.

Brose, P.H., van Lear, D.H., 1997. Effects of seasonal prescribed fires on density of hardwood advanced regeneration in oak-dominated shelterwood stands. In: Proceedings of the 25th Annual Hardwood Symposium, "25 Years of Hardwood Silviculture: A Look Back and a Look Ahead", 7–10 May, 1997, Cashiers, NC. National Hardwood Lumber Association, Memphis, TN, pp. 139–146.

Burns, P.Y., 1955. Fire scars and decay in Missouri oaks. University of Missouri College of Agriculture, Agricultural Experiment Station Bulletin 642.

Campbell, L.A., Hallett, J.G., O'Connell, M.A., 1996. Conservation of bats in managed forests: use of roosts by *Lasionycteris noctivagans*. J. Mamm. 77, 976–984.

Carter, T.C., Ford, W.M., Menzel, M.A., 2002. Fire and bats in the Southeast and Mid-Atlantic: more questions than answers? In: Ford, W.M., Russell, K.R., Moorman, C.E. (Eds.), The Role of Fire for Nongame Wildlife Management and Community Restoration: Traditional Uses and New Directions. United States Department of Agriculture, General Technical Report NE-288. pp. 139–143.

Castleberry, S., Miles, A., Miller, D., Conner, L., 2005. Habitat ecology of bats at multiple scales in natural longleaf and intensively managed loblolly pine forests in Georgia. In: Abstract from 90th Annual Ecological Society of America Meeting, Montreal, Canada.

Chambers, C.L., Alm, V., Sider, M.S., Rabe, M.J., 2002. Use of artificial roosts by forest-dwelling bats in northern Arizona. Wildl. Soc. Bull. 30, 1085–1091.

Cottam, G., 1949. The phytosociology of an oak woods in south-western Wisconsin. Ecology 30, 271–287.

Crow, T.R., 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*): a review. Forest Sci. 34, 19–40.

Crow, T.R., Johnson, W.C., Adkisson, C.S., 1994. Fire and recruitment of *Quercus* in a postagricultural field. Am. Midl. Nat. 131, 84–97.

Curtis, J.T., 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison.

Dubois, M.R., Straka, T.J., Crim, S.D., Robinson, L.J., 1999. Costs and cost trends for forestry practices in the South. Forest Landowner 50, 28–32.

Duchamp, J.E., Sparks, D.W., Whitaker Jr., J.O., 2004. Foraging-habitat selection by bats at an urban-rural interface: comparison between a successful and less successful species. Can. J. Zool. 82, 1157–1164.

Elmore, L.W., Miller, D.A., Vilella, F.J., 2004. Selection of diurnal roosts by red bats (*Lasiurus borealis*) in an intensively managed pine forest in Mississippi. Forest Ecol. Manage. 199, 11–20.

Fenton, M.B., 1997. Science and the conservation of bats. J. Mamm. 78, 1–14.

Fule, P.Z., Cocke, A.E., Heinlein, T.A., Covington, W.W., 2004. Effects of an intense prescribed forest fire: is it ecological restoration. Restor. Ecol. 12, 220–230.

Geluso, K.N., Benedict, R.A., Kock, F.L., 2004. Seasonal activity and reproduction in bats of east-central Nebraska. Trans. Nebraska Acad. Sci. 29, 33–44.

Grindal, S.D., 1999. Habitat use by bats, *Myotis* spp., in western Newfoundland. Can. Field-Nat. 113, 258–263.

Hartman, G.W., Heumann, B.H., 2003. Prescribed fire effects in the Ozarks of Missouri: the Chilton Creek project 1996–2001. In: Proceedings of the Second International Wildland Fire Ecology and Fire Management Congress, 16–22 November, 2003, Orlando, FL.

Huddle, J.A., Pallardy, S.G., 1996. Effects of long-term annual and prescribed burning on tree survival and growth in a Missouri Ozark oak-hickory forest. Forest Ecol. Manage. 82, 1–9.

Humes, M.L., Hayes, J.P., Collopy, M.W., 1999. Bat activity in thinned, unthinned, and old-growth forests in western Oregon. J. Wildl. Manage. 63, 553–561.

Humphrey, S.R., Cope, J.B., 1968. Records of migration of the evening bat *Nycticeius humeralis*. J. Mamm. 49, 329.

Hyer, E.J., Goetz, S.J., 2004. Comparison and sensitivity analysis of instruments and radiometric methods for LAI estimation: assessments from a boreal forest site. Agric. Forest Meteorol. 122, 157–174.

Jones Jr., J.K., Fleharty, E.D., Dunnigan, P.B., 1967. The distributional status of bats in Kansas. Misc. Publ. Mus. Nat. Hist. Univ. Kansas 46, 1–33.

Kunz, T.H., 1982. Roosting ecology of bats. In: Kunz, T.H. (Ed.), Ecology of Bats. Plenum Press, New York, pp. 1–55.

Kurta, A., King, D., Teramino, J.A., Stribley, J.M., Williams, K.J., 1993. Summer roosts of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. Am. Midl. Nat. 129, 132–138.

Ladd, D., 1991. Reexamination of the role of fire in Missouri oak woodlands. In: Buger, G.V., Ebinger, J.E., Wilhelm, G.S. (Eds.), Proceedings of the Oak Woods Management Workshop, Eastern Illinois University, Charleston, pp. 67–80.

Lewis, S.E., 1995. Roost fidelity of bats—a review. J. Mamm. 76, 481–496.

Loomis, R.M., 1974. Predicting the losses in sawtimber volume and quality from fires in oak hickory forests. USDA Forest Service Research Paper NC-104.

Lorimer, C.G., 1985. The role of fire in the perpetuation of oak forests. In: Johnson, J.E. (Ed.), Challenges in Oak Management and Utilization. Cooperative Extension Service, University of Wisconsin, Madison, pp. 8–25.

Mazurek, M.J., Zielinski, W.J., 2004. Individual legacy trees influence vertebrate wildlife diversity in commercial forests. Forest Ecol. Manage. 193, 321–334.

McCarty, K., 1998. Landscape-scale restoration in Missouri savannas and woodlands. Restor. Manage. Notes 16, 22–32.

McLeod, R.F., Gates, J.E., 1998. Response of herpetofaunal communities to forest cutting and burning at Chesapeake farms, Maryland. Am. Midl. Nat. 139, 164–177.

Menzel, M.A., Krishon, D.M., Carter, T.C., Laerm, J., 1999. Notes on tree roost characteristics of the northern yellow bat (*Lasiurus intermedius*), the Seminole bat (*L. seminolus*), the evening bat (*Nycticeius humeralis*), and the eastern pipistrelle (*Pipistrellus subflavus*) Fla. Sci. 62, 185–193.

Menzel, M.A., Carter, T.C., Ford, W.M., Chapman, B.R., 2001a. Tree roost characteristics of subadult and female adult evening bats (*Nycticeius humeralis*) in the upper coastal plain of South Carolina. Am. Midl. Nat. 145, 112–119.

Menzel, M.A., Menzel, J.M., Carter, T.C., Ford, W.M., Edwards, J.W., 2001b. Review of the forest habitat relationships of the Indiana bat (*Myotis sodalis*). United States Department of Agriculture General Technical Report NE-284.

Menzel, M.A., Owen, S.F., Ford, W.M., Edwards, J.W., Wood, P.B., Chapman, B.R., Miller, K.V., 2002. Roost tree selection by northern long-eared bat (*Myotis septentrionalis*) maternity colonies in an industrial forest of the central Appalachian mountains. Forest Ecol. Manage. 155, 107–114.

Miller, D.A., 2003. Species diversity, reproduction, and sex ratios of bats in managed pine forest landscapes of Mississippi. Southeast. Nat. 2, 59–72.

Missouri Department of Conservation, 1991. Natural features inventory of Drury-Mincy Wildlife Area.

Moorman, C.E., Russell, K.R., Menzel, M.A., Lohr, S.M., Ellenberger, J.E., Van Lear, D.H., 1999. Bats roosting in deciduous leaf litter. Bat Res. News 40, 74–75.

Moser, W.K., Ducey, M.J., Ashton, P.M.S., 1996. Effects of fire intensity on competitive dynamics between red and black oaks and mountain laurel. North. J. Appl. For. 13, 119–123.

Norberg, U.M., Rayner, J.M.V., 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philos. Trans. R. Soc. London B: Biol. Sci. 316, 335–427.

Nuzzo, V., 1986. Extent and status of midwest oak savanna: presettlement and 1985. Nat. Areas J. 6, 6–36.

Parsons, S., Lewis, K.J., Psyllakis, J.M., 2003. Relationships between roosting habitat of bats and decay of aspen in the sub-boreal forests of British Columbia. Forest Ecol. Manage. 177, 559–570.

Patriquin, K.J., Barclay, R.M.R., 2003. Foraging by bats in cleared, thinned and unharvested boreal forest. J. Appl. Ecol. 40, 646–657.

Paulsell, L.K., 1957. Effects of burning on Ozark hardwood timberlands. University of Missouri College of Agriculture, Agricultural Experimental Station Bulletin 640.

Peterson, D.W., Reich, P.B., 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. Ecol. Appl. 11, 914–927.

Pyne, S.J., 1982. Fire in America. Princeton University Press, Princeton, NJ.

Rodrigue, J.L., Schuler, T.M., Menzel, M.A., 2001. Observations of bat activity during prescribed burning in West Virginia. Bat Res. News 42, 48–49.

Saint-Germain, M., Drapeau, P., Hebert, C., 2004. Comparison of coleoptera assemblages from a recently burned and unburned black spruce forests of northeastern North America. Biol. Conserv. 118, 583–592.

Schurbon, J.M., Fauth, J.E., 2003. Effects of prescribed burning on amphibian diversity in a southeastern U.S. National Forest. Conserv. Biol. 17, 1338–1349.

Scowcroft, P.G., 1966. The effects of fire on hardwood forests of the Missouri Ozarks. M.S. Thesis, University of Missouri Columbia, MO, pp. 126.

Simon, N.P.P., Stratton, C.B., Forbes, G.J., Schwab, F.E., 2002. Similarity of small mammal abundance in post-fire and clearcut forests. Forest Ecol. Manage. 165, 163–172.

Smith, K.T., Sutherland, E.K., 1999. Fire-scar formation and compartmentalization in oak. Can. J. Forest Res. 29, 166–171.

Smith, K.T., Sutherland, E.K., 2001. Terminology and biology of fire scars in selected central hardwoods. Tree-Ring Res. 57, 141–147.

Sparks, D.W., Choate, J.R., Winn, R.J., 1999. Observations on reproduction in three species of bats. Prairie Nat. 31, 245–248.

Sparks, D.W., Simmons, M.T., Gummer, C.L., Duchamp, J.E., 2003. Disturbance of roosting bats by woodpeckers and raccoons. Northeast. Nat. 10, 105–108.

Stearns, F., 1991. Oak woods: an overview. In: Buger, G.V., Ebinger, J.E., Wilhelm, G.S. (Eds.), Proceedings of the Oak Woods Management Workshop, Eastern Illinois University, Charleston, pp. 1–7.

Tibbels, A.E., Kurta, A., 2003. Bat activity is low in thinned and unthinned stands of red pine. Can. J. Forest Res. 33, 2436–2442.

van Lear, D.H., 2002. Upland oak ecology and management. In: Spetich, M.A. (Ed.), Upland Oak Ecology Symposium: History, Current Conditions, and Sustainability.

van Lear, D.H., Waldrop, T.A., 1991. Prescribed burning for regeneration. In: Duryea, M.L., Dougherty, P.M. (Eds.), Forest Regeneration Manual. Kluwer Academic Publishers, The Netherlands, pp. 235–250.

Vonhof, M.J., Barclay, R.M.R., 1996. Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. Can. J. Zool. 74, 1797–1805.

Wade, D.D., Lunsford, J.D. 1988. A guide for prescribed fire in southern forests. Revised Edition. United States Department of Agriculture, Forest Service, Technical Publication R8-TP 11, Southern Region. Atlanta, Georgia, pp. 56.

Watkins, L.C., 1969. Observations on the distribution and natural history of the evening bat (*Nycticeius humeralis*) in northwestern Missouri and adjacent Iowa. Trans. Kansas Acad. Sci. 72, 330–336.

Watkins, L.C., Shump Jr., K.A., 1981. Behavior of the evening bat *Nycticeius humeralis* at a nursery roost. Am. Midl. Nat. 105, 258–268.

Whitaker Jr., J.O., 2004. Prey selection in a temperate zone insectivorous bat community. J. Mamm. 85, 460–469.

Whitaker Jr., J.O., Gummer, S.L., 2003. Current status of the evening, *Nycticeius humeralis*, in Indiana. Proc. Indiana Acad. Sci. 112, 55–60.

Whitaker Jr., J.O., Brack Jr., V., Cope, J.B., 2002. Are bats in Indiana declining? Proc. Indiana Acad. Sci. 111, 95–106.

White, A.S., 1986. Prescribed burning for oak savanna restoration in central Minnesota. USDA Forest Service, North Central Forest Experiment Station; Research Paper NC-266.

Wilkinson, G.S., 1992. Information transfer at evening bat colonies. Anim. Behav. 44, 501–518.

Zar, J.H., 1984. Biostatistical Analysis, 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.