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Roost tree selection by northern myotis (*Myotis septentrionalis*) maternity colonies following prescribed fire in a Central Appalachian Mountains hardwood forest

Joshua B. Johnson [a,*], John W. Edwards [a], W. Mark Ford [b], J. Edward Gates [c]

[a] *West Virginia University, Division of Forestry and Natural Resources, Box 6125, Morgantown, WV 26506, USA*
[b] *US Army Engineer Research and Development Center, CEERD-EE-E, 3909 Halls Ferry Road, Vicksburg, Mississippi, MS 39180, USA*
[c] *University of Maryland Center for Environmental Science, Appalachian Laboratory, 301 Braddock Road, Frostburg, MD 21532, USA*

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ABSTRACT

Following decades of fire suppression in eastern forests, prescribed fire as a tool to restore or enhance oak (*Quercus* spp.)-dominated communities is gaining widespread acceptance in the Appalachian Mountains and elsewhere. However, the interactions of fire with biotic components such as wildlife that might be impacted by prescribed fire are poorly documented. For tree-roosting bats, fire can enhance roosting habitat by creating snags and increasing solar radiation at existing roosts. In 2007 and 2008, we examined roost selection of forest-interior dwelling northern myotis (*Myotis septentrionalis*) maternity colonies in stands treated with prescribed fire (hereafter, fire) and in unburned (hereafter, control) stands on the Fernow Experimental Forest, West Virginia. Using radio telemetry, we tracked 36 female northern myotis to 69 roost trees; 25 in the fire treatment and 44 in the control treatment. Using logistic regression and an information-theoretic model selection approach, we determined that within the fire treatment, northern myotis maternity colonies were more likely to use cavity trees that were smaller in diameter, higher in crown class, and located in stands with lower basal area, gentler slopes, and higher percentage of fire-killed stems than random trees. Moreover, roosts often were surrounded by trees that were in the upper crown classes. In the control treatment, northern myotis were more likely to roost nearer the tops of larger diameter cavity trees in early stages of decay that were surrounded by decaying trees in the upper crown classes than random trees. Roost trees in the fire treatment were associated with larger overall canopy gaps than roost trees within the control treatment. Regardless of treatment, northern myotis maternity colonies roosted in black locust (*Robinia pseudoacacia*) in greater proportion than its availability. Ambient temperatures recorded at a subset of roost trees in fire and control treatments indicated that daily minimum temperatures were similar, but daily mean and maximum temperatures were higher in the fire treatments, possibly due to larger canopy gaps created by the senescence and decay of the surrounding fire-killed overstory trees. Northern myotis roost-switching frequency, distance between successive roosts, and duration of individual roost tree use were similar between the fire and control treatments, suggesting similar roost tree availability despite a significantly higher proportion of potential roost trees in the fire treatment. Northern myotis readily exploited alterations to forest structure created by the reintroduction of fire, which accelerated snag creation and enlarged existing or created new canopy gaps, but it remains to be determined if these conditions translate into increased recruitment and survivorship.

1. Introduction

Over the past decade, numerous studies investigating the interactions of bat roosting and foraging ecology with forest management practices have been conducted in forested landscapes of the eastern United States (Miller et al., 2003). Results therein suggest that in the eastern United States, some level of forest harvesting is tolerated by bats, and may even increase foraging opportunities for certain species by reducing structural clutter, provided that adequate numbers of roost trees are retained (Owen et al., 2002, 2004; Ford et al., 2005; Perry and Thill, 2007). The reintroduction of prescribed fire as an intermediate or periodic disturbance agent into forest management options may impact roost tree selection by bats through changes in spatial and temporal roost availability, and in the structure of the forest, but its impacts remain largely unexamined (Brose et al., 2001; Boyles and Aubrey, 2006). Limited knowledge of the effects of prescribed fire on availability of roost trees and selection by bats impairs

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[*] Corresponding author. Tel.: +1 304 293 2941; fax: +1 304 293 2441.
E-mail address: j-johnson3@juno.com (J.B. Johnson).

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conservation and management decisions regarding bat use of roost trees.

Throughout the Appalachian Mountains and Central Hardwoods forest regions, insufficient retention and/or regeneration of hard-mast producing species such as oaks (*Quercus* spp.) and hickories (*Carya* spp.) in managed and unmanaged forest stands are a major concern of forest and wildlife managers. This failure to adequately maintain oak has been attributed in part to fire suppression and uneven-aged management practices that favor shade-tolerant tree species such as maples (*Acer* spp.) (Clark, 1993; Schuler and Fajvan, 1999; Brose et al., 2001; Schuler, 2004; Nowacki and Abrams, 2008). Oak retention and regeneration can benefit from a combination of prescribed fire and forest canopy thinning by selected removal, girdling, or herbicide of competitors, to augment oak seedling initiation and survival through reduced competition and increased canopy openness (Miller, 1993; Brose et al., 1999, 2001). These methods potentially could result in a net increase in snag abundance that in turn could favor snag-dependent wildlife species, including bats (Brose et al., 2001; Hallett et al., 2001; Albrecht and McCarthy, 2006; Boyles and Aubrey, 2006). Prescribed fire is within the management prescriptions for many wildlife species (Kepler et al., 1996; Brennan et al., 1998; Tucker et al., 2004; Blake, 2005; Thatcher et al., 2006); however, using prescribed fire to create suitable roost conditions, in either live trees or snags, for bats is a largely unexplored, but a potentially valuable area of research (Leput, 2004; Boyles and Aubrey, 2006; Loeb and Waldrop, 2008). Based on observational data, both Carter (2006) and Keyser and Ford (2006) hypothesized that periodic fire as a forest disturbance may have historically created a shifting mosaic of suitable roosting habitat for the disturbance-related endangered Indiana myotis (*Myotis sodalis*) in upland forests of the eastern United States. The heterogeneous patches of forest that remain after a fire event can be attributed to differing fire intensity within a burned area (Turner et al., 1994). Although fire may reduce the longevity or utility of individual roost trees in terms of bat use, it also kills or scars other trees, creating suitable roosting structures in the form of loose bark and cavities (Smith and Sutherland, 1999; Russell et al., 2006). Moreover, fire-killed trees leave gaps in the forest canopy, increasing the amount of solar radiation reaching the subcanopy, i.e., lower tree limbs and boles, where bats roost (Menzel et al., 2001). Increased solar radiation may be a preferred characteristic of bat roost sites, as warmer temperatures facilitate more rapid development of neonates (Sedgeley, 2001; Boyles and Aubrey, 2006; Lausen and Barclay, 2006). However, loss of foliage from fire-killed trees could reduce the roosting opportunities for foliage-roosting bats, including the hoary bat (*Lasiurus cinereus*) and eastern red bat (*L. borealis*). Forest management practices attempting to increase the oak component in forest communities may inadvertently be a proactive bat habitat enhancement technique that increases the number of suitable roost trees for cavity- and exfoliating bark-roosting bats (Boyles and Aubrey, 2006; Keyser and Ford, 2006).

Northern myotis (northern long-eared bat; *Myotis septentrionalis*) is one of the most common bat species in eastern North America, particularly in the Appalachian Mountains, and is a forest-roosting and foraging obligate species in most areas (Barbour and Davis, 1969; Caceres and Barclay, 2000; Ford et al., 2005; Chapman, 2007). Females form maternity colonies of <100 individuals, roosting in cavities in snags or under exfoliating bark of live or dead trees (Sasse and Pekins, 1996; Foster and Kurta, 1999; Menzel et al., 2002a; Owen et al., 2002). Although many hardwood tree species are used as roost trees, research in the Central Appalachian Mountains has shown that male and female northern myotis selectively roost in black locust (*Robinia pseudoacacia*), a rot-resistant, long-lasting species that remains suitable as a roost for many years, thereby promoting philopatry (Lewis, 1995; Menzel et al., 2002a; Owen et al., 2002; Ford et al., 2006b; Kahler and Anderson, 2006). However, the temporal aspect of forest disturbances, including fire, and its association with snag dynamics and bat-roost selection remains to be investigated. Although northern myotis maternity roost trees are found in relatively closed-canopy forests, forest manipulation in the form of snag creation, thinning, or patch clearcutting that promotes recruitment of black locust into the subsequent stand, may be tolerated by and augment roosting conditions for northern myotis in the long-term (Sasse and Pekins, 1996; Foster and Kurta, 1999; Cryan et al., 2001; Menzel et al., 2002a; Carter and Feldhamer, 2005; Ford et al., 2006b; Perry and Thill, 2007). The conditions, e.g., decay stage, of trees immediately surrounding roost trees, as well as the presence of canopy gaps, also are factors in selection by northern myotis (Cryan et al., 2001; Menzel et al., 2002a; Carter and Feldhamer, 2005; Perry and Thill, 2007; Perry et al., 2007). For northern myotis, the use of prescribed fire to promote oak in forest stands can create snags or modify stand structure, improving existing roost availability or conditions in the near-term, as well as inadvertently promote the establishment of species such as black locust. Whether prescribed fire enhances roost habitat in the longer-term, remains speculative (Leput, 2004; Boyles and Aubrey, 2006). Moreover, it is unclear if northern myotis maternity roost tree availability is a resource that is lacking, and if so can possibly be remedied through proactive forest management strategies, including prescribed fire. Roost tree availability in disturbed and undisturbed forests can be evaluated by examining the roost tree switching behavior of bats (Chaverri et al., 2007).

Whether or not the availability of roost trees, i.e., their frequency of occurrence or distance between trees, has an influence on roost-switching behavior such as frequency or distance between roosts has not been well quantified, particularly for bat species of eastern North America (Wilkinson, 1985; Crampton and Barclay, 1998; O'Donnell and Sedgeley, 1999; Kunz and Lumsden, 2003). Extrinsic and intrinsic factors that influence roost-switching are speculative, but undoubtedly include reduced predation risks, parasite loads, distance to foraging areas, or more favorable roost microenvironment (Wilkinson, 1985; Lewis, 1995; O'Donnell and Sedgeley, 1999; Kunz and Lumsden, 2003). Non-random selection of roosts, roost-switching frequency and distance traveled between successive roosts are indicators of roost availability (Sedgeley and O'Donnell, 1999; Chaverri et al., 2007). Throughout much of their range, female northern myotis typically switch roost trees every 1–5 days and may travel up to ~2 km between successive roost trees, but roosts are commonly clustered in small (<20 ha) areas (Foster and Kurta, 1999; Menzel et al., 2002a; Carter and Feldhamer, 2005; Broders et al., 2006; Perry and Thill, 2007). How these facets of northern myotis natural history change in forests subjected to prescribed fire is unknown.

The primary objective of our study was to compare roost selection of northern myotis maternity colonies in forest stands subjected to prescribed fire (hereafter, fire) and in unburned (hereafter, control) stands in the Central Appalachian Mountains by analyzing physical characteristics of roost trees and potential roost trees. We predicted that northern myotis would select roost trees within forest gaps created by prescribed fires. Secondarily, we also examined roost abundance and availability by comparing frequency of roost switching and distances traveled between successive roosts located in fire and control treatments. We predicted that roost-switching frequency would be higher and distances travelled shorter in forest stands subjected to prescribed fire.

2. Methods

2.1. Study area

We conducted our research at the Fernow Experimental Forest (FEF) in Tucker County, West Virginia (Fig. 1). The FEF is a 1900 ha

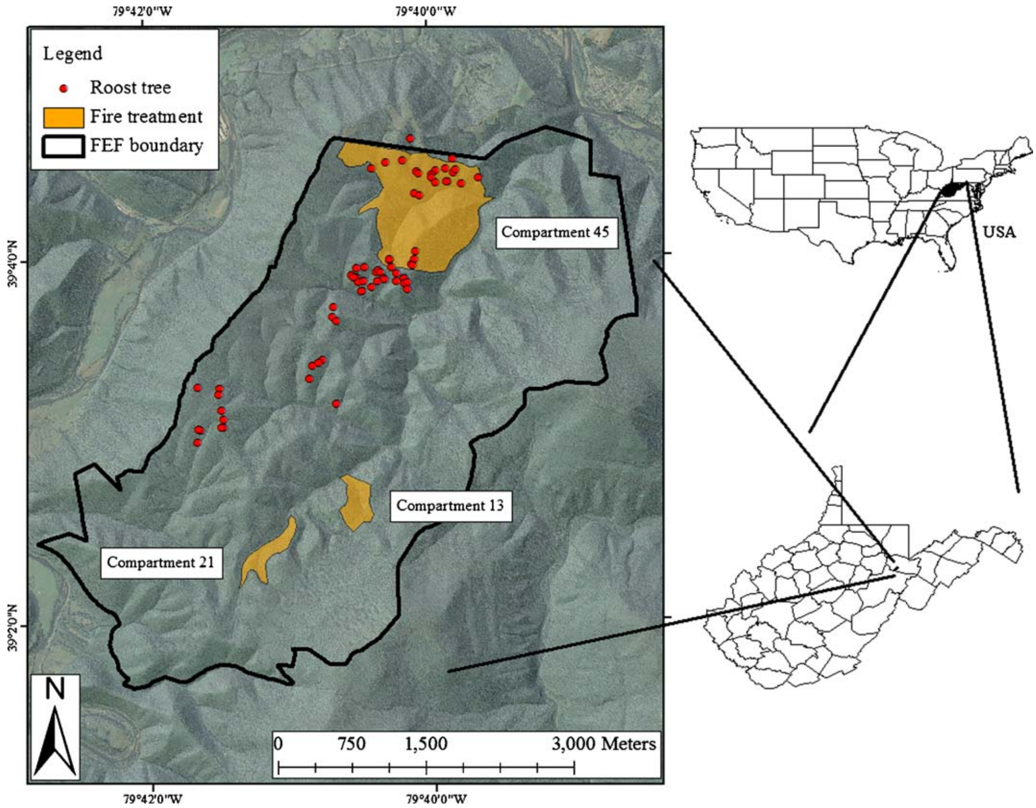

Fig. 1. Northern myotis maternity roost tree locations within fire and control treatments on the Fernow Experimental Forest, Tucker County, West Virginia, 2007 and 2008.

experimental forest managed by the U.S. Forest Service, Northern Research Station, and is located in the Unglaciated Allegheny Mountains subsection of the Appalachian Plateau Physiographic Province (Kochenderfer et al., 2007). Elevations range from 530 to 1100 m. Elklick Run, a 2.4-km fourth-order stream, roughly bisects FEF east to west. Approximately 5.5 km of dendritic intermittent and permanent streams feed into Elklick Run and incise the steep slopes and plateau-like ridgetops, providing all possible slope aspects (Madarish et al., 2002). Mean annual precipitation at FEF is 145.8 cm, ranging from 9.7 cm in October to 14.4 cm in June. Mean annual temperature is 9.2 °C, ranging from −18.0 °C in January to 20.6 °C in July (Kochenderfer, 2006). Vegetation at the FEF is a mosaic of second- and third-growth, mixed-mesophytic and northern hardwood forest that has been managed by even (patch clearcut,)- and uneven (single-tree selection)-aged silviculture since the mid-20th century, or has been left undisturbed following initial harvesting in the Elklick watershed from 1903 to 1911 (Schuler and Fajvan, 1999). Although American chestnut (*Castanea dentata*) and oak species, such as northern red oak (*Q. rubra*), historically dominated the forest overstory, the chestnut blight (*Cryphonectria parasitica*) and subsequent lack of intense disturbance, including fire and clearcutting, since the mid-20th century has allowed forest composition to shift toward shade-tolerant tree species, such as maples and American beech (*Fagus grandifolia*) (Schuler and Fajvan, 1999; Schuler, 2004). Prescribed fire has recently been used to promote oak regeneration in the forest that is currently dominated by sugar maple (*A. saccharum*), red maple (*A. rubrum*), yellow-poplar (*Liriodendron tulipifera*), black cherry (*Prunus serotina*), American beech, sweet birch (*Betula lenta*), and basswood (*Tilia americana*) (Schuler, 2004). In April or May (depending on management compartment) 2007 and 2008, prescribed fire treatments were conducted in management compartments 45 (121 ha), 13 (13 ha), and 21 (12 ha) on FEF (Fig. 1). The three management compartments were burned for 1 day during each treatment using a strip head fire technique, ignited with hand-held drip torches after fire-blackened perimeters were established. Actual flame heights and combustion varied from dying out to >3.5 m high in some spots, due to variability in leaf litter, slope, and aspect. Additionally, 48, 20-m radius plots were randomly located in each of the three management compartments, and all overstory or midstory trees, other than oak or hickory, were herbicided or girdled (Schuler, USDA Forest Service, personal communication).

From spring through autumn, the bat community at FEF is comprised of northern myotis, little brown myotis (*M. lucifugus*), big brown bats (*Eptesicus fuscus*), eastern pipistrelle (*Pipistrellus subflavus*), eastern red bats, silver-haired bats (*Lasionycteris noctivagans*), and hoary bats (Owen et al., 2004; Ford et al., 2005). A small number of male Indiana myotis and Virginia big-eared bats (*Corynorhinus townsendii virginianus*) that hibernate in Big Springs Cave in the central portion of the FEF remained in the area during summer (Ford et al., 2002).

2.2. Radio telemetry

To capture bats, we erected mist nets (Avinet, Inc., Dryden, New York) over stream corridors, small pools, skidder trails, and service roads from May to August 2007 and 2008. Mist netting sites were located within the fire treatment and control treatment. We considered the control treatment to be any area outside the three management compartments where prescribed fires were used. Mist netting was conducted <5 h following sunset, unless prevented by periods of rain, wind ≥20 kph, or temperatures <10 °C as these conditions can influence bat activity levels (Erickson and West, 2002). For each captured bat, we determined species, sex, age, weight, forearm length, and reproductive condition (Menzel et al., 2002b). We used Skin Bond® (Smith and Nephew, Largo, Florida) surgical cement to affix a 0.35-g radio transmitter (Model LB-2N; Holohil Systems Ltd., Carp, Ontario, Canada) between the scapulae of captured female northern myotis. Bat capture and handling protocols were approved by the Animal Care and Use Committee of West Virginia University (Protocol Number No. 08-0504) and followed the guidelines of the American Society of Mammalogists (ACUC, 1998). We used a radio receiver and 3-element Yagi antenna (Wildlife Materials, Inc., Murphysboro, IL) to locate roost trees. To record roost tree locations within 10 m of their true geographic location, we used a Garmin GPSmap 60CSx global positioning unit.

2.3. Habitat variables

In ArcMap (Version 9.2, Environmental Systems Research Institute, Redlands, California), we used the Zonal Statistics tool in Spatial Analyst to determine the elevation of each roost tree and the median elevation of watersheds where each roost tree was located. Watersheds were delineated from a 3-m resolution digital elevation model with the watershed tool in Spatial Analyst using a 45-ha minimum threshold. We used a 1-sample median test to determine if roost trees were randomly located along the elevation gradient (Conover, 1999).

We measured characteristics of each roost tree, the four trees (>10 cm dbh) nearest to the roost tree, and the site at which the roost tree was located. For each roost tree, we determined tree species, diameter (cm) at breast height with a diameter (dbh) tape (DBHR), decay class (Cline et al., 1980; i.e., 1 = live, 2 = declining, 3 = recent dead, 4 = loose bark, 5 = no bark, 6 = broken top, 7 = broken bole; DECAYR), crown class (Nyland, 1996; i.e., 1 = suppressed, 2 = intermediate, 3 = codominant, 4 = dominant; CROWNR), tree height (m) with a hypsometer (HEIGHT), roost height when known (ROOSTHGHT), visual estimate of percent bark remaining on the tree (BARK), and roost type (cavity = 1, bark = 0; ROOSTTYPE). For each of four trees nearest to the roost tree, we determined tree species, diameter (cm) at breast height (DBHN), distance (m) to the roost tree (DISTN), decay class (DECAYN), and crown class (CROWNN), all of which were averaged for the four trees. We photographed the forest canopy at each roost tree with a Nikon Coolpix 8400 camera and FC-E9 fisheye lens (Melville, New York) mounted to a self-leveling mount and tripod (Regent Instruments, Inc., Canada). We used WinScanopy and XLSCanopy software (Regent Instruments, Inc., Canada) to analyze each canopy photograph. This software allowed us to analyze the percent canopy gap within the hemispherical photograph of the canopy as a whole (TOTALGAP), as a 45° wedge off the horizon (HORIZGAP), as a 90° wedge centered on the midpoint (OVERHEADGAP), and as a 90° wedge each centered on the north, east, south, and west aspects (NORTHGAP, EASTGAP, SOUTHGAP, WESTGAP, respectively). We recorded aspect (ASPECT) with a compass, percent slope (SLOPE) with a clinometer at the plot (11.3 m radius centered on the roost tree), and stand basal area with a 20 factor prism (m^2/ha; BASAL). At each roost tree in the fire treatment, we also estimated the percent (0%, 25%, 50%, 75%, or 100%) of understory (UNDERSTORY) and midstory (MIDSTORY) trees that were killed by fire. Within fire and control treatments, we located potential roost trees at random coordinates generated with ArcMap. We attempted to sample the same number of random trees as we accumulated roost trees. Potential roost trees were identified as any tree (>10 cm diameter at breast height) that contained either a cavity or exfoliating bark that possibly could be used by a northern myotis maternity colony as described by Owen et al. (2002). We measured the same variables at the potential roost trees as we did at the actual roost trees (Appendix A). Temperature (° C) was measured at a random sample of roost trees located in fire and control treatments with StowAway® Tidbit® (Onset Computer Corp., Pocasset, Massachusetts) data loggers that recorded ambient temperature every minute for 1-week periods from mid-June through mid-July. Data loggers were affixed to the south side of tree boles.

2.4. Statistical analysis

To select models that best predicted tree use within and between treatments, we used an information-theoretic approach (Burnham and Anderson, 2002) within logistic regression analyses (Proc Logistic; SAS Institute Inc., 2004). Individual models were developed on the basis of prior research indicating that characteristics of individual roost trees, as well as the condition of immediately surrounding trees and site are selected by northern myotis (Menzel et al., 2002a; Carter and Feldhamer, 2005). Also, the size of the canopy gap over northern myotis roost trees appears to be a factor in northern myotis roost selection (Cryan et al., 2001; Menzel et al., 2002a; Carter and Feldhamer, 2005; Perry and Thill, 2007; Perry et al., 2007). We aggregated appropriate variables in candidate models to represent characteristics of the roost tree (ROOSTTREE), roost tree and 4 nearest surrounding trees (TREECLUSTER), immediate and surrounding forest canopy gap (GAP), physical characteristics of the surrounding site (SITE), and a global model that contained all variables (GLOBAL) (Appendix A). We used logistic regression analysis to conduct three contrasts: (1) we predicted roost tree use, i.e., roost tree = 1, potential roost tree = 0, within the fire treatment; (2) we predicted roost tree use within the control treatment, i.e., roost tree = 1, potential roost tree = 0; and (3) we predicted roost tree use between the fire treatment and control treatment, i.e., fire treatment = 1, control treatment = 0. Before conducting logistic analyses, we arcsine-transformed all percentage data and examined all variable pairs for correlation. We removed a member of a variable pair before subsequent analyses if their Spearman's rank (Proc Corr, SAS Institute Inc., 2004) correlation coefficient was ≥ 0.60. We removed the variable that either was correlated with several other variables or potentially would be more difficult to replicate or implement when using the model to manage for northern myotis roost trees (e.g., we would retain crown class, which is a relative measure, and discard actual height of roost trees, which will vary among areas). We used AIC_c for small sample sizes to determine the best approximating candidate model. Candidate models separated by ≤ 2 AIC_c were considered to be competing models. We used Akaike weights, w_{AIC_c}, to indicate the probability that a particular model was the best approximating model in the candidate set. Naglekerke's max-rescaled R^2 was used to evaluate global model fit (Burnham and Anderson, 2002).

We determined if northern myotis maternity colonies selectively roosted in particular tree species of a unique structure by recording diameter, crown class, presence of cavity or exfoliating bark, and decay class of all trees >10 cm within 20 m × 100 m belt transects located near known northern myotis roost trees in fire and control treatments (Menzel et al., 2002a; Owen et al., 2002). Our protocol for determining characteristics of trees within transects was identical to those used for the northern myotis maternity colony roost trees. We used a Fisher's exact test (Proc Freq, SAS Institute Inc., 2004) to determine if northern myotis maternity colonies selectively roosted in tree species relative to their availability, and to compare roost tree availability, i.e., number of roost trees, within fire and control treatments. We compared the structure (diameter, crown class, and decay class) of available roost trees in fire and control treatments with a Wilcoxon test (Proc Npar1way, SAS Institute Inc., 2004).

Lastly, we used a Wilcoxon test to compare the frequency that northern myotis switched roosts, measured as the number of consecutive days spent in a roost tree and total number of roost trees used per bat, between fire and control treatments. We used a

Kruskall–Wallis (Proc Npar1way, SAS Institute Inc., 2004) test to compare distances (m) between consecutive roosts in the fire treatment, in the control treatment, and both directions of between-treatment movements. We used a sign test (Proc Univariate; SAS Institute Inc., 2004) to compare minimum, mean, and maximum daily temperatures recorded at roost trees.

3. Results

During 2007, we mist netted 5 nights within the fire treatment, capturing 17 bats, including 15 northern myotis and 2 big brown bats. We radio-tagged 3 reproductive female northern myotis and located 8 roost trees; 5 were within the fire treatment and 3 were located in the control treatment (Fig. 1). During 2008, we mist netted 27 nights, capturing 130 bats representing 8 species, including 107 northern myotis, 9 little brown myotis, 7 big brown bats, 3 eastern pipistrelles, 1 Virginia big-eared bat, 1 Indiana myotis, 1 silver-haired bat, and 1 eastern red bat. We radio-tagged 33 female northern myotis and located 65 roost trees, 25 of which were within the fire treatment (Fig. 1). Although there were plots within the fire treatment where trees were subjected to girdling or herbicide, none of the roost trees were located within these plots. Of roost trees located in the control treatment ($n = 40$), 17 were located in other specific management compartments, including 6 roost trees within stands subjected to 2–3% financial maturity harvest with stand entries occurring every 10 years, and 11 roost trees in silvicultural control compartments that were last harvested before 1960. The remaining roost trees were located in unmanaged portions of the FEF not currently dedicated to any manipulative research, and presumably relatively undisturbed since initial logging on the FEF. Four roost trees recorded in 2007 were reused in 2008, 3 of which were located in the fire treatment. All roost trees were located at elevations ranging from 626–860 m (median = 743 m) and were more frequently located at higher elevations within their respective watersheds ($z = 5.538$, $P < 0.001$).

Spearman's rank correlation coefficients exceeded 0.60 for 6 variable pairs within the control treatment contrast, 9 variable pairs within the fire treatment contrast, and 17 variable pairs in the fire treatment versus control treatment contrast (Table 1). Within the fire treatment, the TREECLUSTER, ROOSTTREE, and SITE candidate models were competing ($\Delta \mathrm{AIC}_c < 1.31$; Table 2). However, all variables in the ROOSTTREE model were included in the TREECLUSTER model. Model-averaged variables indicated that northern myotis maternity colonies were more likely to use cavity trees rather than trees with exfoliating bark, that were smaller in diameter but were higher in crown class than random trees, and that were closely surrounded by trees that also were higher in crown class than surrounding random trees (Table 3). The SITE model indicated that northern myotis maternity colonies were more likely to roost in trees located within stands with lower basal area, gentler slope, and higher percentage of fire-killed stems than sites where random trees were located (Table 3). Within the control treatment, the TREECLUSTER and ROOSTTREE models were competing ($\Delta \mathrm{AIC}_c = 1.72$; Table 2). Again, all variables in the ROOSTTREE model were included in the TREECLUSTER model, and indicated that northern myotis were more likely to roost nearer the tops of larger, both in diameter and height, cavity trees in early stages of decay that were surrounded by decaying trees that were higher in crown class (Table 3). The GAP model best explained differences in northern myotis maternity colony roost tree selection between fire and control treatments (Table 2). Roost trees in the fire treatment were associated with larger overall canopy gaps than roost trees in the control treatment (Table 3).

Within the six belt transects in the fire treatment ($n = 3$) and control treatment ($n = 3$), we tallied 391 trees of 19 species and 369 trees of 23 species, respectively. Northern myotis maternity colonies roosted disproportionately more often in black locust trees and disproportionately less often in oaks and maples than expected in fire and control treatments (Table 4). Availability of roost types (cavity or exfoliating bark) was disproportionately higher in the fire treatment (Table 5). Available roost trees were smaller in diameter and lower in the canopy, i.e., crown class, but were similar in decay class in the fire treatment than in the control treatment. The majority (68%) of roost trees in the fire treatment and half of roost trees in the control treatment were either of intermediate or suppressed crown class. The majority of roost trees were of decay class ≥4 in the fire treatment (60%) and control treatment (62%). Only 2 and 4 live trees were used in the fire treatment and control treatment, respectively.

At 44 randomly selected roost trees, daily minimum temperatures were similar ($M = -2.0$, $P = 0.618$) between the fire ($n = 15$, mean = 14.26 °C, SE = 0.46) and control treatments ($n = 29$, mean = 14.36 °C, SE = 0.45). However, daily mean temperatures differed ($M = -11.5$, $P < 0.001$) between fire (mean = 19.58 °C, SE = 0.43) and control treatments (mean = 19.03 °C, SE = 0.44). Daily maximum temperatures also differed ($M = -7.5$, $P = 0.020$)

Table 1

Spearman's rank correlation coefficients ($\rho > 0.60$) for variable pairs in three models predicting *Myotis septentrionalis* roost tree use at the Fernow Experimental Forest, West Virginia, 2007 and 2008. Variables in bold were retained in models.

Fire tree use (vs. fire potential tree use)		Control tree use (vs. control potential tree use)		Fire tree use (vs. control tree use)	
Variable pair	ρ	Variable pair	ρ	Variable pair	ρ
TOTALGAP, HORIZGAP	0.906	**CROWNR**, HEIGHT	0.852	SOUTHGAP, HORIZGAP	0.891
TOTALGAP, SOUTHGAP	0.830	**TOTALGAP**, HORIZGAP	0.767	**TOTALGAP**, HORIZGAP	0.837
CROWNR, HEIGHT	0.757	**BARK**, DECAYR	−0.713	**CROWNR**, HEIGHT	0.835
TOTALGAP, WESTGAP	0.757	DECAYR, HEIGHT	−0.622	ROOSTHGHT, HEIGHT	0.716
DECAYR, BARK	−0.729	**TOTALGAP**, WESTGAP	0.613	**TOTALGAP**, SOUTHGAP	0.697
WESTGAP, HORIZGAP	0.709	**CROWNR**, DECAYR	−0.604	**DECAYR**, BARK	−0.687
CROWNR, ROOSTHGHT	0.656			**CROWNR**, ROOSTHGHT	0.662
SOUTHGAP, HORIZGAP	0.655			**TOTALGAP**, WESTGAP	0.639
OVERHEADGAP, MIDSTORY	0.652			**DECAYR**, HEIGHT	−0.617
HEIGHT, ROOSTHGHT	0.652				
OVERHEADGAP, SOUTHGAP	0.648				
OVERHEADGAP, WESTGAP	0.639				
DECAYN, MIDSTORY	0.635				
UNDERSTORY, MIDSTORY	0.627				
SOUTHGAP, WESTGAP	0.625				
DBHR, HEIGHT	0.607				
CROWNN, DBHN	0.606				

Table 2

Logistic regression analysis and model selection using Akaike Information Criteria (AIC_c) difference with correction for small sample sizes (ΔAIC_c), number of parameters in model (K), and model weight (w_{AIC_c}) for *Myotis septentrionalis* maternity colony roost tree use at the Fernow Experimental Forest, West Virginia, 2007 and 2008. All candidate models (GLOBAL) are included for comparison and are not necessarily among the best models.

Response variable	R^2 (Naglekerke's max-rescaled)	K	AIC_c	Δ AIC_c	w_{AIC_c}	Model
Fire tree use (vs. fire potential tree use)	0.19	6	69.01	0.00	0.416	SITE
	0.35	15	69.81	0.80	0.279	ROOSTTREE
	0.52	18	70.32	1.31	0.216	TREECLUSTER
	0.20	6	72.08	3.07	0.090	GAP
	0.74	18	82.81	13.80	0.000	GLOBAL
Control tree use (vs. control potential tree use)	0.33	14	111.17	0.00	0.695	TREECLUSTER
	0.16	10	112.89	1.72	0.294	ROOSTTREE
	0.22	7	120.73	9.56	0.008	GAP
	0.52	22	121.04	9.86	0.007	GLOBAL
	0.02	5	130.61	19.44	0.000	SITE
Fire tree use (vs. control tree use)	0.68	6	53.97	0.00	1.000	GAP
	0.81	26	83.84	29.87	0.000	GLOBAL
	0.25	5	85.17	31.19	0.000	SITE
	0.16	15	96.04	42.06	0.000	ROOSTTREE
	0.31	19	99.67	45.70	0.000	TREECLUSTER

between fire (mean = 32.16 °C, SE = 0.75) and control treatments (mean = 30.83 °C, SE = 1.11).

Roost-switching frequency by northern myotis was similar ($P = 0.403$) between the fire treatment (mean = 1.43 days, SE = 0.155, switched every 1–6 days) and control treatment (mean = 1.32 days, SE = 0.091, switched every 1–5 days). In the fire treatment, northern myotis used 1–7 (mean = 2.35, SE = 0.402) roost trees for the duration of transmitter retention (mean = 4.36 days, SE = 0.560, range = 2–8). In the control treatment, northern myotis used 1–7 (mean = 3.04, SE = 0.340) roost trees for the duration of transmitter retention (mean = 5.00 days, SE = 0.507, range = 1–9). Distances between consecutive roost trees were similar ($P = 0.115$) among the fire treatment (mean = 152 m, SE = 21.3, $n = 18$, range = 16–314 m), control treatment (mean = 230 m, SE = 24.4, $n = 49$, range = 7–634 m), and between-treatment movements (fire to control treatment:

Table 3

Variables included in best approximating candidate models selected using Akaike Information Criteria (AIC_c) within logistic regression analysis predicting *Myotis septentrionalis* roost tree use at the Fernow Experimental Forest, West Virginia, 2007 and 2008.

Parameter	Estimate	SE	Wald χ^2	$P >$ Wald χ^2	Odds ratio	95% CI
Fire tree use (vs. fire potential tree use)						
ROOSTTREE + TREECLUSTER + SITE[a,b]						
Intercept	12.180	10.249	1.413	0.235		
DBHR	−0.171	0.086	4.020	0.045	0.84	0.71–0.99
DECAYR	0.432	0.390	1.229	0.277	1.54	0.72–3.31
CROWNR	1.454	0.888	2.684	0.101	4.28	0.75–24.37
ROOSTTYPE	3.095	1.899	2.655	0.103	22.09	0.53–913.98
DISTN	−1.772	0.809	4.801	0.028	0.17	0.04–0.83
DECAYN	−0.339	1.093	0.096	0.756	0.71	0.08–6.07
CROWNN	0.775	1.732	0.200	0.655	2.17	0.07–64.72
ASPECT	−0.020	0.013	2.404	0.121	0.98	0.96–1.01
SLOPE[c]	−0.106	0.057	3.525	0.061	0.90	0.81–1.01
BASAL	−0.033	0.016	4.462	0.035	0.97	0.94–0.99
UNDERSTORY[c]	0.025	0.022	1.282	0.258	1.03	0.98–1.07
Control tree use (vs. control potential tree use)						
TREECLUSTER[d]						
Intercept	−6.970	2.806	6.170	0.013		
DBHR	0.019	0.023	0.711	0.399	1.02	0.98–1.07
ROOSTHGHT	0.147	0.088	2.802	0.094	1.16	0.98–1.38
BARK	−0.016	0.010	2.720	0.099	0.98	0.97–1.00
CROWNR	0.071	0.483	0.022	0.883	1.07	0.42–2.77
ROOSTTYPE	1.755	0.685	6.573	0.010	5.78	1.51–22.12
DISTN	0.178	0.331	0.288	0.591	1.19	0.63–2.28
DBHN	−0.117	0.063	0.711	0.399	0.89	0.79–1.01
DECAYN	1.121	0.419	7.147	0.008	3.07	1.35–6.98
CROWNN	2.201	0.957	5.291	0.021	9.04	1.39–58.95
Fire tree use (vs. control tree use)						
GAP[e]						
Intercept	−9.766	3.121	9.795	0.002		
TOTALGAP[c]	59.497	26.087	5.202	0.023	>999.99	>999.99–>999.99
NORTHGAP[c]	11.995	12.459	0.927	0.336	>999.99	<0.01–>999.99
EASTGAP[c]	28.928	12.141	5.677	0.018	>999.99	169.43–>999.99
OVERHEADGAP[c]	−4.789	6.560	0.533	0.465	0.01	<0.01–>999.99

[a] Hosmer–Lemeshow $\chi 2 = 2.397$, $P = 0.935$; concordance = 92.6%.

[b] Model-averaged statistics presented.

[c] Analyses performed on arcsine-transformed data.

[d] Hosmer–Lemeshow $\chi 2 = 13.851$, $P = 0.086$; concordance = 80.3%.

[e] Hosmer–Lemeshow $\chi 2 = 10.056$, $P = 0.261$; concordance = 92.9%.

Table 4

Tree species selected as roosts by *Myotis septentrionalis* maternity colonies within areas that were and were not subjected to prescribed fire on the Fernow Experimental Forest, West Virginia, 2007 and 2008.

Species	Fire treatment						Control treatment					
	Maternal roosts	%	Potential roosts	%	χ^2	*P*	Maternal roosts	%	Potential roosts	%	χ^2	*P*
Robinia pseudoacacia	13	52.0	10	4.3	62.99	<0.001	20	45.5	13	9.6	28.61	<0.001
Quercus spp.	2	8.0	64	27.6	4.54	0.004	8	18.2	57	41.9	8.11	<0.001
Acer spp.	3	12.0	63	27.2	2.72	0.022	7	15.9	38	27.9	2.57	0.032
Sassafras albidum	3	12.0	15	6.5	1.06	0.249	2	4.5	1	0.7	–	–
Oxydendrum arboreum	3	12.0	35	15.1	–	–	0	0.0	3	2.2	–	–
Prunus serotina	1	4.0	0	0.0	–	–	2	4.5	3	2.2	–	–
Carya spp.	0	0.0	2	0.9	–	–	1	2.3	0	0.0	–	–
Liriodendron tulipifera	0	0.0	3	1.3	–	–	1	2.3	0	0.0	–	–
Magnolia spp.	0	0.0	3	1.3	–	–	1	2.3	3	2.2	–	–
Unknown	0	0.0	0	0.0	–	–	2	4.5	3	2.2	–	–
Fagus grandifolia	0	0.0	26	11.2	–	–	0	0.0	4	2.9	–	–
Betula lenta	0	0.0	6	2.6	–	–	0	0.0	6	4.4	–	–
Amelanchier spp.	0	0.0	3	1.3	–	–	0	0.0	3	2.2	–	–
Others	0	0.0	2	0.9	–	–	0	0.0	2	1.5	–	–

Table 5

Characteristics of available roost trees in prescribed fire and control treatments on the Fernow Experimental Forest, Tucker County, West Virginia, 2008.

Variable	Fire treatment		Control treatment		*P*
	Mean	SE	Mean	SE	
Roost presence (%)[a,b]	59.3	–	36.9	–	<0.001
Cavity (%)[b]	41.1	–	32.5	–	0.027
Exfoliating bark (%)[b]	43.2	–	9.3	–	<0.001
DBH (cm)[c,d]	27.8	1.08	33.1	1.41	<0.001
Crown class[d,e]	2.1	0.06	2.3	0.08	0.007
Decay class[d,f]	2.3	0.06	2.4	0.12	0.362

[a] Includes cavity and exfoliating bark roost trees.

[b] Comparison made with Fisher's exact test.

[c] Diameter at beast height.

[d] Comparison made with Wilcoxon test.

[e] Crown class following Nyland (1996).

[f] Decay class following Cline et al. (1980).

mean = 294 m, SE = 64.1, $n = 8$, range = 136–684 m; control to fire treatment: mean = 249 m, SE = 29.0, $n = 5$, range = 166–341 m).

4. Discussion

Northern myotis responded favorably to prescribed fire by exploiting trees, mostly black locust, that were located in canopy gaps that were created by the senescence and decay of surrounding overstory trees. Northern myotis selection of black locust snags and large-diameter snags of other species as roost trees is typical of findings in the central Appalachian Mountains (Menzel et al., 2002a; Owen et al., 2002). The black locust snags used by northern myotis are a relict of past disturbances on the FEF in the early- to mid-1900s. Ford et al. (2006b) suggested that northern myotis selection of black locust snags as roost trees is a relatively recent phenomenon because historically, black locust was not a prevalent tree species in the Central Appalachian Mountains prior to the widespread harvesting that occurred regionally from the end of the 1800s into the 1920s (Abrams and McCay, 1996; Schuler and Fajvan, 1999). In the pre-settlement forest, northern myotis probably used cavities and exfoliating bark of large-diameter snags, such as American chestnut or sugar maple, located in canopy gaps created by the canopy die off of the roost tree itself or the senescence of surrounding overstory trees killed by natural disturbances such as ice and wind damage. Moreover, frequent fires (<25-year return interval) that were caused by lightning strikes or set by Native Americans not only perpetuated an oak-dominated forest, but also likely created periodic disturbances to the forest canopy that allowed shade-intermediate and intolerant species to become established in the understory during this gap phase in the forest growth cycle (Yamamoto, 1992; Schuler and Fajvan, 1999; Shumway et al., 2001). In the late 1800s and early 1900s, forest disturbances, including exploitative harvesting, frequent and often catastrophic fires, and chestnut blight, created conditions that favored shade-intermediate and intolerant tree species, such as black locust and oaks in the region (Boring et al., 1981; Abrams and McCay, 1996; Schuler and Fajvan, 1999; Shumway et al., 2001; Nowacki and Abrams, 2008). Fire-suppression efforts 15–30 years subsequent to the widespread harvesting through the present resulted in a gradual shift in forest species composition towards shade-tolerant species (Schuler and Fajvan, 1999; Hutchinson et al., 2008). Black locust trees that established in early 1900s as a result of forest disturbances were eventually overtopped by both shade-tolerant and intolerant species during the building phase of the forest growth cycle and remained in the forest as reliable, long-lasting snags that were used by bats for many consecutive years (Carey, 1983; Yamamoto, 1992; Lewis, 1995). During the mature phase of the forest growth cycle, forest species composition continued to shift toward more shade-tolerant species, such as maples, because of forest fire suppression and uneven-aged forest management practices (Clark, 1993; Brose et al., 2001; Schuler, 2004; Nowacki and Abrams, 2008). Within these mature forests, northern myotis maternity colonies roost in black locust snags and in the cavities or under the exfoliating bark of mature trees, of both shade-tolerant and intolerant species, and typically are associated with canopy gaps (Ford et al., 2002; Owen et al., 2002; this study). Indeed, northern myotis appear to be able to locate roosts in disturbed forests in various phases of the forest growth cycle.

The broader temporal aspect of fire and its association with forest and snag dynamics and bat roost selection has not been considered and remains to be investigated. In our study, the immediate impact of recent prescribed fires included the creation of potential northern myotis roosts by enhancing the exfoliation of bark in live and dead trees (mostly maples and American beech) and possibly made previously unsuitable roost trees suitable by increasing the amount of solar radiation reaching them. Despite the apparent abundance of available roost trees, we observed only one roost tree in the fire treatment that was attributable solely to the recent prescribed fires; a red maple that was fire-killed and had exfoliating bark as a result. All other roost trees in the fire treatment had cavities that were in existence prior to the fire treatment. Therefore, it is possible that northern myotis philopatry has continued despite prescribed fires, or that they have not had time to respond to the abundance of newly created roost trees. However, northern myotis on the FEF mostly roosted in cavities, possibly limiting the effectiveness of prescribed fire in creating newly available roosts in the short term, i.e., 1–2 years post-fire. Our fire treatment partially consumed the bases of some roost snags, undoubtedly shortening their useful duration as roosts. The senescence of fire-killed overstory trees allowed increased solar radiation to reach the subcanopy stratum, i.e., lower tree limbs and boles, of a greater number of trees, possibly providing more potential roosts through the improvement of microenvironmental conditions (Menzel et al., 2001; Boyles and Aubrey, 2006; Turbill and Geiser, 2008).

In the control treatment, northern myotis selected roost trees that were surrounded by decaying overstory trees. Clusters of decaying trees may provide alternate roosts and increased solar radiation to reach roost trees (Cryan et al., 2001; Perry and Thill, 2007; Perry et al., 2007). Roost trees located in some areas of the control treatment that had been subjected to light forest thinning is consistent with findings in the Ouachita Mountain region of Arkansas where northern myotis maternity colonies were observed roosting in thinned stands of mixed pine (*Pinus* spp.)-hardwoods (Perry et al., 2007). Prescribed fire may act as a surrogate to mechanical forest thinning or harvesting in that fire-killed mature trees, and consequent crown die off, allow increased solar radiation to reach roost trees. Indeed, the percentage of fire-killed stems surrounding roost trees was positively related to the canopy gap immediately over the roost trees ($\rho = 0.652$, OVERHEADGAP:MIDSTORY; Table 1). Additionally, canopy gaps in the fire treatment were associated with slightly higher maximum daily temperatures at roost trees and undoubtedly inside roost tree cavities. Higher roost temperatures could facilitate more rapid growth of developing juvenile bats (Sedgeley, 2001; Boyles and Aubrey, 2006; Lausen and Barclay, 2006; Turbill and Geiser, 2008). Roost temperatures can be influenced by the amount of canopy gap as well as by the location of the roost tree with respect to landform (Lacki and Schweirjohann, 2001). Similar to previous studies, northern myotis maternity colonies on the FEF selected roost trees that were located on upper slopes, presumably because of increased intensity and duration of solar radiation (Lacki and Schweirjohann, 2001; Broders and Forbes, 2004). The increased solar radiation in addition to the well-drained upper slopes where black locust is more likely to occur creates an ideal roosting situation for northern myotis (Clarkson, 1958).

Prescribed fires conducted during our study created canopy gaps, which, if large enough, will create conditions on the forest floor that allow shade-intolerant species, including black locust to regenerate (Miller et al., 1995; Hutchinson et al., 2008). Although prescribed fire is intended to augment oak regeneration, in the long-term, it also fosters the regeneration of black locust and other shade-intolerant species that northern myotis, as well as other cavity/bark roosting bat species, can utilize (Beck and Hooper, 1986; Miller et al., 1995). Further, trees surviving the fires may compartmentalize fire scars, which may eventually form cavities, i.e., potential roost sites, in the long-term (Smith and Sutherland, 1999).

Despite an apparent abundance of potential roost trees in our fire treatment, northern myotis did not switch roost trees more frequently than found in the control treatment. However, northern myotis in our study did switch roosts more frequently (mean = 1.35 days per roost) than reported previously, both within the Central Appalachian Mountains (Menzel et al., 2002a (mean = 5.3 days per roost); Owen et al., 2002 (mean = 3.0 days per roost)), as well as in other parts of their range (Foster and Kurta, 1999 (mean = 5.6 tracking days and 3.6 roost trees); Cryan et al., 2001 (mean = 3.25 days per roost); Carter and Feldhamer, 2005 (mean = 3.9 tracking days and 2.5 roost trees)). Moreover, distances traveled between consecutive roosts were similar between fire and control treatments in our study, but were less (mean = 217 m) than in studies from other parts of the range [(Foster and Kurta, 1999 (mean = 333 m); Cryan et al., 2001 (mean = 600 m); Broders et al., 2006 (mean = 457)]. It is unclear if the greater roost-switching frequency and lesser distances traveled between successive roosts observed in our study were attributable to a comparatively large number of available roost trees throughout the FEF, or if other factors such as predator avoidance or parasite loads dictated movement patterns (Sedgeley and O'Donnell, 1999). That roost-switching frequency and distances traveled between successive roost trees were similar between fire and control treatments suggest that prescribed fire may not have effectively increased the abundance of suitable snags in treatment areas. Rather, a saturation level of roost trees possibly had already been reached throughout the FEF, considering that northern myotis in our study switched roosts every 1.35 days on average. However, the requisite density of available roost trees for northern myotis remains unclear. Although northern myotis, a forest-interior species, may or may not have substantially benefitted (e.g., increased survivorship and recruitment) from prescribed fire or other forest disturbances such as light thinning, other bat species, including the endangered Indiana myotis, may benefit from additional snags and canopy disturbance introduced by prescribed fire (Carter, 2006; Keyser and Ford, 2006). Conversely, canopy disturbance can reduce the roosting opportunities for foliage-roosting bats, including the hoary bat and eastern red bat, but this remains to be determined.

5. Conclusions

The use of prescribed fire as a management tool to restore oak species to forests is amenable to roosting requirements of northern myotis maternity colonies in the Central Appalachian Mountains and may be even more favorable to disturbance-related bat species. The creation of canopy gaps not only produces favorable thermal conditions at roost sites in the short-term, but also promotes the regeneration of shade-intermediate and intolerant tree species that could provide future roosting habitat, while injuries to existing overstory trees create potential roost trees in the long-term. However, fire may accelerate the decline of existing roost trees, particularly of older snags. Although it is unclear if prescribed fire creates a net increase in roost tree density in the long-term, a spatial mosaic of prescribed fire of <25-year return intervals might provide a continuum of forest and roosting conditions throughout the landscape (Ford et al., 2006a; Loeb and O'Keefe, 2006). Lastly, from an overall wildlife management standpoint, prescribed fire fosters the development of a forest dominated by hard-mast-producing species, which benefit a wide variety of wildlife (Edwards et al., 1993; Schuler, 2004).

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Appendix A. Characteristics of roost trees used by *Myotis septentrionalis* maternity colonies and randomly located potential roost trees within areas that were and were not subjected to prescribed fire on the Fernow Experimental Forest, West Virginia, 2007 and 2008.

Variable	Fire treatment				Control treatment			
	Roost (*n* = 25)		Random (*n* = 25)		Roost (*n* = 44)		Random (*n* = 45)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
ROOSTTREE								
DBHR (cm)	24.33	3.23	29.89	3.14	30.91	2.64	29.65	2.03
DECAYR	3.96	0.28	4.24	0.41	3.95	0.25	3.89	0.27
CROWNR	2.04	0.18	1.72	0.16	2.63	0.13	2.09	0.13
HEIGHT (m)	13.97	1.30	11.59	1.00	16.28	1.19	15.04	1.07
ROOSTHGHT (m)	8.55	1.02	7.58	0.59	8.79	0.73	7.59	0.43
BARK (%)	69.52	6.48	59.20	6.58	55.95	4.95	59.89	5.20
ROOSTTYPE	0.96	0.04	0.76	0.09	0.81	0.06	0.62	0.07
GAP								
TOTALGAP (%)	17.56	1.90	12.54	0.67	9.36	0.19	8.62	0.25
NORTHGAP (%)	9.51	0.87	8.34	0.83	6.02	0.43	7.05	0.60
EASTGAP (%)	16.34	1.67	13.63	1.21	8.25	0.43	9.49	0.54
SOUTHGAP (%)	26.81	4.01	15.10	1.52	13.00	0.57	10.15	0.59
WESTGAP (%)	16.54	2.62	12.53	1.49	9.24	0.56	7.17	0.57
OVERHEADGAP (%)	35.59	4.16	23.01	1.57	24.09	0.90	22.44	1.10
HORIZGAP (%)	11.33	1.19	9.12	0.83	6.41	0.28	5.87	0.33
TREECLUSTER								
DISTN (m)	3.20	0.16	3.39	0.20	3.35	1.14	3.60	0.17
DBHN (cm)	24.69	1.40	26.93	1.37	26.81	1.04	27.78	1.22
DECAYN	2.14	0.19	1.83	0.17	1.77	0.15	1.43	0.10
CROWNN	2.40	0.08	2.21	0.09	2.29	0.08	2.27	0.07
SITE								
ASPECT (°)	153.28	38.51	139.01	52.97	169.89	41.46	132.45	47.29
SLOPE (%)	35.60	2.60	40.56	2.72	26.14	1.85	24.58	2.05
BASAL (sq. m./ha)	32.70	2.01	32.51	2.26	35.06	1.60	33.47	1.69
UNDERSTORY (%)	69.57	7.53	53.13	5.89	–	–	–	–
MIDSTORY (%)	43.48	6.89	20.83	4.17	–	–	–	–

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