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

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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 (\textit{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.

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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
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 (Boyles 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 no canopy light penetration whereas a LAI of 12 indicates complete 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 \((612.0 \pm 25.0)\) relative to burned forest \((513.6 \pm 24.2; t = 2.83, P = 0.007)\) and live tree density was significantly higher in unburned forest \((576.0 \pm 24.6)\) than burned forest \((468.0 \pm 24.1; t = 3.13, P = 0.003)\). The density of dead trees was not significantly different between the burned \((45.6 \pm 7.3)\) and unburned forests \((36.0 \pm 4.3; t = 1.14, P = 0.263)\). However, the proportion of dead trees compared to total trees was significantly higher in burned forest \((0.092 \pm 0.014)\) relative to unburned forest \((0.060 \pm 0.007; t = 2.08, P = 0.045)\).

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 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 full 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.

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