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RESPONSE OF NORTHERN BATS (*MYOTIS SEPTENTRIONALIS*) TO PRESCRIBED FIRES IN EASTERN KENTUCKY FORESTS

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Prescribed fire is becoming a common management tool for restoring forests of North America; however, effects of prescribed fire on forest-dwelling bats remain unclear. During 2006 and 2007, we monitored prey availability, diet, foraging behavior, and roost selection of adult female northern bats (*Myotis septentrionalis*) before and after 2 prescribed fires in dissected terrain of the Red River Gorge on the Daniel Boone National Forest in eastern Kentucky. Size of home ranges and core areas did not vary between bats radiotracked before and after fires. Bats foraged more often in the vicinity of pine stands than hardwood or mixed stands, and along ridges and midslopes than lower slopes, regardless of burn condition. Home ranges were closer to burned habitats following fires than to unburned habitats. Abundance of coleopterans, dipterans, and all insects combined captured in blacklight traps increased following prescribed fires. Fecal samples of bats demonstrated lepidopterans, coleopterans, and dipterans to be the 3 most important groups of insect prey, with consumption of dipterans increasing after burning. Bats chose roosts that were taller in height and in earlier stages of decay than random snags, and after prescribed fires chose roosts in trees with a greater number of cavities and a higher percentage of bark coverage. More roosts were observed in burned habitats (74.3%; $n = 26$) after fires than in unburned habitats (25.7%; $n = 9$). The results of this work suggest that northern bats are tolerant to prescribed fire on the landscape pattern and scale observed in this study. Northern bats responded to habitat alterations resulting from prescribed fires through shifts in the location of foraging areas as bats tracked changes in insect availability, and through shifts in the selection of roost trees by occupying trees and snags possessing more potential roosting microsites.

Key words: diet, fire ecology, foraging habitat, habitat selection, home range, insect communities, *Myotis septentrionalis*, northern bats, prescribed fire, roost selection

Fire alters composition, structure, and functioning of forests (Fulé et al. 1997; Moritz 1997; Mushinsky and Gibson 1991). Fire is known to modify habitat conditions for birds (Finch et al. 1997) and mammals (Keyser and Ford 2006); however, data on the effects of fire on habitats of forest-dwelling bats and on the behavioral responses of bats to fire remain limited (Carter et al. 2002). Fire in winter is known to disturb red bats (*Lasiurus borealis*) roosting in litter on the forest floor (Moorman et al. 1999; Saugey et al. 1989), and growing-season fires likely disrupt red bats presumably due to effects of smoke and heat reaching where these bats roost (Rodrigue et al. 2001). Fire can produce but also destroy standing snags that are suitable for bark- and cavity-roosting bats (Carter et al. 2002). A study of snag production and loss associated with prescribed fires in western North American forests demonstrated losses of up to 20% of the standing snags, whereas few new snags were created (Randall-Parker and Miller 2002). Nevertheless, examination of data on roosting behavior of evening bats (*Nycticeius humeralis*) in deciduous forests in Missouri suggests extensive use of snags in stands treated with prescribed fires (Boyles and Aubrey 2006). Vulnerability of bark- and cavity-roosting bats to heat and smoke during fires is unknown, although a simulation study using models of roosting structures demonstrated smoke concentrations inside roosts to be comparable to that of ambient levels (Guelta and Balbach 2005). Activity by bats in response to prescribed fires in pine (*Pinus*) forests in South Carolina did not differ across 2 growing seasons among stands treated with prescribed burns, stands thinned and burned, and control stands (Loeb and Waldrop 2008). However, there are no published data on

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foraging behavior of bats in response to fires or on the effects of fire on the prey base of bats (Carter et al. 2002; Loeb and Waldrop 2008).

Historically, fire played a significant role in the ecology of forests in eastern North America by creating disturbance regimes that altered forest species composition and structure (Brose et al. 2001; Delcourt and Delcourt 1998; Waldrop et al. 1992). The use of prescribed fire is increasing in eastern forests to produce stand conditions typical of those believed to exist before fire suppression (Brose et al. 1999; Hutchinson et al. 2005; Van Lear et al. 2000; Waldrop et al. 1992), to control populations of insect pests (Martin and Mitchell 1980; Miller 1979; Mitchell 1990), and to reduce fuel loads that may contribute to wildfires (Fettig et al. 2007; McCullough et al. 1998; Van Lear et al. 2004).

Declines in insect abundance can be substantial in the hours immediately following fire (Paquin and Coderre 1997; Siemann et al. 1997); however, long-term numeric responses are more variable (Swengel 2001). Orthopterans and coleopterans increase in abundance following fires (Galley and Flowers 1998; Pippin and Nichols 1996; Reed 1997), potentially a positive outcome for bats. Some moths are attracted to fires causing direct mortality, which suggests that the seasonality of fires relative to the timing of insect life stages is an important consideration when examining the effects of fire on nocturnal lepidopterans (Gerson and Kelsey 1997; Miller 1979). In general, examination of data demonstrates that composition of insect communities remains altered for up to 16 years following fires (Buddle et al. 2006; Moretti et al. 2006; Warren et al. 1987). Therefore, data on bat responses to insect communities altered by prescribed fire are needed to determine the implications of prescribed fire in forested areas occupied by bats.

The northern bat (*Myotis septentrionalis*) is ubiquitous in eastern North American forests (Broders and Forbes 2004; Carter and Feldhamer 2005; Lacki and Schwierjohann 2001; Menzel et al. 2002), so it is a good model to assess the use of prescribed fire. Northern bats form maternity colonies in dead and living trees during the summer (Carter and Feldhamer 2005; Foster and Kurta 1999), and forage in areas close to roosts (Henderson and Broders 2008).

The northern bat is a gleaner, that is, it captures prey directly from the surface of objects, and uses echolocation calls that enable it to successfully catch moths (Faure et al. 1993). The northern bat also is hypothesized to use aerial-hawking to capture prey (Ratcliffe and Dawson 2003; Whitaker 2004), because the diet of these bats consists of numerous other arthropod groups typical of bats that are generalist feeders (Brack and Whitaker 2001; Griffith and Gates 1985; Whitaker 2004). Two insect groups commonly eaten by northern bats, coleopterans and dipterans, exhibit population-level increases with changes in available resources resulting from fire, smoke, and freshly burned wood, with the latter used for oviposition sites (Frost 1984; Gerson and Kelsey 1997; Miller 1979; Reed 1997; Warren et al. 1987). This suggests that abundance of some prey of northern bats may increase following fire. We tested the response of adult female northern bats to prescribed fire by comparing diet, foraging behavior, habitat selection, and roosting behavior of bats before and after prescribed fires on the Daniel Boone National Forest, Kentucky. We evaluated these data in relation to habitat available and abundance of nocturnal insects before and after fires.

MATERIALS AND METHODS

Study area.—The study took place in the Red River Gorge Geological Area, Daniel Boone National Forest, Kentucky (37°51′N, 83°39′W). The forest community and topography are typical of the Cumberland Plateau physiographic region in eastern Kentucky. The area was covered in 2nd-growth forest, comprised mainly of mixed mesophytic tree species including American beech (*Fagus grandifolia*), cucumber magnolia (*Magnolia acuminata*), oaks (*Quercus*), maples (*Acer*), tulip poplar (*Liriodendron tulipifera*), white ash (*Fraxinus americana*), eastern hemlock (*Tsuga canadensis*), and various pines and other conifers (Jones 2005). The terrain is characterized by dissected valleys, steep slopes, cliffs, and rocky outcrops, with elevations ranging from 200 to 365 m above sea level (McGrain 1983). The climate is moderate with average temperatures ranging from 16.6°C to 22.9°C from May to August and an average annual precipitation of 101 cm; rainfall events are common in all months except for August and September.

The study area was organized into 3 experimental units. Two units, Powder Mill and Bear Waller, were exposed to independent prescribed burns, whereas the 3rd unit remained unburned. The burn units were selected in collaboration with United States Forest Service personnel to meet both research and management needs. The burn units were within 0.53 km of each other, separated by a single ridgeline. Neither burn unit had a history of prescribed burning; however, there are reports of ‘‘numerous fires having burned’’ within the original Cumberland purchase area before 1930 (Collins 1975:195). The ignition pattern for both burn units consisted of firing ridgelines and burn-unit boundaries with a drip torch and allowing the fire to burn down the slope. This produced a mosaic of burned habitats mixed with unburned habitats, especially where moisture conditions were higher. The Powder Mill burn occurred on 10 April 2007 and covered 435 ha, with 53.8% of the area burned. The Bear Waller burn occurred on 30 April 2007 and covered 185 ha, with 54.1% of the area burned. Flame height during both burns ranged from 0.2 to 2.5 m, but was typically <1 m. General fire behavior was similar for both burns. Fire spread over most of the ridges and upper slopes, whereas much of the lower slopes and drainages remained unburned as did some areas below cliffs. In 2007, we added a 3rd study unit, that is, unburned unit, which was approximately 2,400 ha in size, due to the spatial arrangement and number of roosts discovered in this area during preburn sampling. This unit bordered the southwestern edge of the 2 burned units.

Capture and tracking of bats.—We captured bats from 14 June to 20 July 2006 and 22 April to 9 September 2007 using nylon mist nets (Avinet Inc., Dryden, New York) of varying lengths. Nets were placed over deep pools in drainages, and upland wildlife ponds in the interior of burned and unburned units. We recorded sex, reproductive condition, body mass, and forearm length of each northern bat captured. We affixed 0.36- or 0.42-g transmitters (LB-2N; Holohil Systems Ltd., Carp, Ontario, Canada) to 18 adult female northern bats between the shoulder blades using Skinbond adhesive cement (Smith and Nephew United, Largo, Florida). Transmitter mass ranged from 3.9% to 8.0% of bat body mass. All protocols followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

We tracked bats daily while foraging and to roost trees using TRX-1000S receivers and 3-element yagi antennas (Wildlife Materials Inc., Murphysboro, Illinois). Tracking of bats continued until the transmitter battery failed or the transmitter was shed. Bats were followed for an average of 6.33 days ± 0.46 *SE*. Nighttime telemetry began each night after bats left their roosts and continued until at least midnight, terminating when all tracked bats night-roosted. Two or 3 observers were stationed at high-elevation locations and their position recorded with a global positioning system. Contact among observers was maintained using handheld radios permitting simultaneous azimuths to be obtained, because the direction of bat positions was sustained by each observer up to the moment that bearings were requested from the data-recording station. This permitted azimuths to be recorded at 3- to 5-min intervals. When a 3rd observer was used, the 3rd tracking station helped in identifying signal bounce and ensuring correct crosses. Further, vehicles were used to shift among tracking stations, depending on the landscape position of bats, to facilitate detection and tracking of bats and, when a 3rd observer was available, ensure that bats were in the areas determined from the intersection of azimuths. An approach similar to ours was successfully used by Johnson et al. (2007) in radiotracking long-legged myotis (*Myotis volans*) in Idaho. We tracked individuals in alternating 30-min time periods and, on most nights, tracked ≤ 3 bats. This sampling scheme likely resulted in some autocorrelation in the foraging data (White and Garrott 1990), possibly resulting in underestimates of the actual home-range and core-area sizes used by bats. Regardless, because our purpose was to evaluate spatial use parameters of bats before and after experimental treatment, we suggest that autocorrelation likely affected pre- and postburn foraging data sets similarly, and, thus, did not influence outcomes of the experimental design.

Home range and characterization of foraging habitat.—We used triangulation to determine the locations of radiotagged bats during nightly foraging (White and Garrott 1990). We entered azimuths into the Locate 3.19 program to determine exact crossings in order to estimate bat locations (Nams 2006). We used 2 azimuths to determine each bat location. Other studies have shown that the use of >2 azimuths does not necessarily increase accuracy or precision (Nams and Boutin 1991). We used ArcGIS version 9.2 (ESRI, Redlands, California) to calculate 95% home ranges and 50% core-area estimates using Hawth's Tools extension version 3.27 (Beyer 2004). We generated pre- and postburn estimates of home-range and core-area sizes of bats captured and radiotagged on the burn units for which we had >20 locations. We compared the size of home ranges and core areas before and after prescribed burns using Kruskal–Wallis tests (Hollander and Wolfe 1973).

We analyzed habitat use with the Euclidian distance method (Conner and Plowman 2001; Conner et al. 2003). This method compares distances of animal locations and random locations to each habitat type. We performed 2nd-order (location of home ranges relative to habitat types on the landscape—sensu Johnson 1980), and 3rd-order (use of habitat types within a home range) habitat analyses. We extended each burn-unit boundary outward by the maximum distance a bat moved in a single night within its burn unit, 1.3 km and 0.7 km for the Powder Mill and Bear Waller burn units, respectively. We merged the extended burn units to create an area for use in distance analyses totaling 2,670 ha. We combined bats into preburn and postburn groupings to assess the effects of burning on use of foraging habitat.

We evaluated 4 habitat variables using 2nd- and 3rd-order analyses. Habitat variables were aspect, stand type, slope position, and whether areas had burned or not burned during prescribed fires. We derived data for aspect from digital elevation models based on geographic information system coverage available from the Kentucky Geospatial Data Clearinghouse Web site (http://kygeonet.ky.gov/). We defined slope aspects as north (315°–45°), east (45°–135°), south (135°–225°), and west (225°–315°) facing. We obtained data on stand availability in the study area from the United States Forest Service, and categorized stands into 4 types. We defined pine and hardwood stands as having $\geq 70\%$ of the dominant and codominant basal area as pine or hardwoods, respectively. We defined pine–hardwood and hardwood–pine stands as having 51–69% of the dominant and codominant basal areas as pine or hardwoods, respectively. We used a geographic information system to create slope position classes using the Topographic Position Index extension version 1.2 (Jenness 2006). We based the classification system used for defining the slope position index on the 6-Class scheme (Jenness 2006). We classified location as ridge, midslope, and lower slope. United States Forest Service personnel delineated burned area coverage on a topographic map and we digitized the areas burned into a geographic information system. Analysis of distance data for burn condition (i.e., burned versus unburned) was restricted to the postburn bat grouping.

We measured distances of observed and random (expected) locations to available habitat types in a geographic information system using the Nearest Features 3.8b extension (Jenness 2004). To determine 2nd-order habitat selection, we generated 5,000 random points within the study area and calculated the minimum distances to each available habitat type. For 3rd-order habitat selection, we generated 1,000 random points within each bat's 95% home range and calculated the minimum distances to each available habitat type. Under the null hypothesis, habitat use should be occurring at random and the ratio of bat locations to random distances should equal 1.0 (Conner and Plowman 2001). We analyzed distance ratios to available habitat types using multivariate analysis of variance (MANOVA). When MANOVAs were significant, we used *t*-tests to rank habitat types in order of closest to farthest from bat locations or home ranges (Conner and Plowman 2001; Conner et al. 2003).

Characteristics of roost trees.—For all roost trees and random snags we recorded geographic position and tree or stand characteristics in a tree-centered 20-m-radius plot. We identified tree species, decay class (Hunter 1990), and estimated the number of cavity openings. We measured diameter at breast height (DBH; cm), tree height (m), and canopy height (m), and visually estimated canopy cover (%), bark coverage (%), and exfoliating bark coverage (%). We counted the number of snags and live trees $\geq$16 cm DBH within 20 m of the focal tree. At roost trees we estimated roost height (m) and diameter at roost height (cm) and compared these values for roosts selected before and after the burn using *t*-tests. We determined roost position as above, below, or within the canopy, and the roost structure as crevice, cavity, or bark. We counted the number of bats exiting a roost the night after it was 1st discovered and sporadically thereafter when logistics permitted. For all roost trees and random snags found after burning, we estimated the percentage of the 20-m plot that burned and recorded char (i.e., fire scar) height on the tree (m).

We sampled random snags by taking a random azimuth and locating the 1st suitable snag that was between 40 and 100 m from the roost tree. If none was found, we randomly selected new azimuths until a random snag was located. We chose 40 m as the minimum distance to ensure no overlap in circular plots between random snags and roost trees, and chose random snags to ensure no overlap of circular plots among random snags. A suitable random snag had to have a decay class of 3–7 (Hunter 1990), and a minimum diameter of 16 cm based on the mean diameter for roost trees of northern bats recorded elsewhere in Kentucky (Lacki and Schwierjohann 2001). We compared tree and stand characteristics using Kruskal–Wallis tests (Hollander and Wolfe 1973) between roosts and random snags measured preburn, and between roosts and random snags measured postburn.

Insect sampling and food habits.—In 2006 and 2007, we sampled insect communities with blacklight traps (Universal Light Trap; Bioquip Products, Gardena, California). Blacklight traps preferentially attract lepidopterans and are a commonly used trap type for assessing insect abundance (Lacki et al. 2007a). Regardless, traps are effective in elucidating patterns as long as only relative comparisons (e.g., preburn versus postburn) of prey taxa are made. We activated blacklights within 1 h of sunset and operated the traps until sunrise. Insects captured were killed with ethyl acetate. We established 4 trap locations in each of the 2 burn units; 2 traps were positioned on north-facing (mesic) slopes and 2 on south-facing (xeric) slopes. Trap sites ranged from 294 to 387 m in elevation and were situated on slopes ranging from 18% to 40%. We sampled all trap locations within a burn unit on the same nights, and trapping occurred at 10-day intervals. This scheme resulted in 68% of trap nights occurring during radiotracking sessions, with the remainder occurring before or after tracking sessions. Trapping of insects took place from 10 July to 25 September 2006 (preburn sampling) and from 22 April to 1 October 2007 (postburn sampling). We identified insects that were $\geq$10 mm in size to the ordinal level. Smaller insects were often in too poor a condition to identify to order.

We analyzed responses of the insect community using 2-factor analyses of variance (ANOVAs), with the main effects being aspect and burn condition (preburn versus postburn). Response variables included abundance of all insects combined (i.e., number of individuals $\geq$10 mm in size), and abundance of Lepidoptera, abundance of Coleoptera, and abundance of Diptera because these groups are known to be eaten by northern bats (Faure et al. 1993; Whitaker 1972, 2004). We tested homogeneity of variance using a variance ratio *F*-max test, with ANOVAs based on log-transformed values when variances were heterogeneous to ensure that data were homoscedastic (Sokal and Rohlf 1969).

Fecal samples collected from bats captured and radiotagged were frozen until analysis. Pellets were dissected following Whitaker (1988) and prey remains identified to order. In our identification of insects the order Hemiptera included the suborder Auchenorrhyncha, previously recognized as the order Homoptera (Triplehorn and Johnson 2005). We determined the frequency of occurrence of prey items (i.e., present or not present in a pellet) and also estimated percent volume of prey items in pellets from each bat to the nearest 5%. Up to 3 pellets from each bat were dissected and values were averaged across pellets to determine the percent values for each prey item for each bat (Lacki et al. 2007b). Percent volume of insect orders in pellets of bats radiotracked before the burn were compared to values for bats radiotracked after the burn using Kruskal–Wallis tests (Hollander and Wolfe 1973).

RESULTS

In 2006 and 2007, we captured and radiotagged pregnant females ($n = 6$) from 29 April until 10 June, lactating females ($n = 3$) in mid-June (19–22 June), postlactating females ($n = 2$) from 20 July to 2 September, and nonreproductive females ($n = 7$) in early spring from 22 to 29 April and in late summer from 6 to 8 August. Body mass of female northern bats, irrespective of reproductive condition, averaged 6.6 g ± 0.25 *SE*.

Maternity colonies began forming as early as 29 April and persisted through 26 June. Large colonies (i.e., >15 bats exiting a roost) were recorded at 18 different trees with the largest exit counts of 56 and 52 observed on 15 June and 26

Table 1.—Second- and 3rd-order habitat use by stand type, slope position, and burn condition for female northern bats (*Myotis septentrionalis*) on the Daniel Boone National Forest, Kentucky, in 2006 and 2007. Habitats are ranked from closest to farthest from bat locations. Only comparisons where differences were found are shown. Within rows, different letters (A, B, C) indicate habitats that differ significantly ($P < 0.1$) from each other in their distances from bat locations.

	Closest			Farthest
Stand type				
Preburn, 3rd order	Pine^{A}	Hardwood^{A,B}	Hardwood–pine^{A,B}	Pine–hardwood^{B}
Postburn, 2nd order	Pine^{A}	Pine–hardwood^{A,B}	Hardwood^{B,C}	Hardwood–pine^{C}
Slope position				
Preburn, 2nd order	Midslope^{A}	Ridge^{A}		Lower slope^{B}
Postburn, 2nd order	Midslope^{A}	Ridge^{B}		Lower slope^{C}
Burn condition				
Postburn, 2nd order	Burned^{A}			Unburned^{B}

May 2007, respectively. Both roosts with the largest exit counts were in tall (>25 m in height) and large (>45 cm DBH) tulip poplar snags. Bats used multiple roosts (3.8 roosts per bat ± 0.42 *SE*) and switched roosts frequently, as demonstrated by a pregnant female (B 11), which over 6 nights used 3 different roosts holding 18–39 bats.

Foraging behavior.—Mean home-range size of female northern bats was no larger after burning (72.3 ha ± 6.2 *SE*; $n = 9$ bats) than before (60.2 ± 14.1 ha; $n = 5$ bats; Kruskal–Wallis = 0.54, $P = 0.46$). The largest home range recorded was 172 ha for a pregnant female captured on 10 June 2007, and the smallest was 18.6 ha for a postlactating female captured on 20 July 2006. Mean core-area size was no larger after burning (13.5 ± 0.8 ha) than before (11.4 ± 6.1 ha; Kruskal–Wallis = 0.36, $P = 0.55$).

Female northern bats foraged closer to pine stands than pine–hardwood stands before burning (Wilks' lambda = 0.0007, *d.f.* = 4, 1, $P < 0.04$), and located their home ranges closer to pine stands than to hardwood or hardwood–pine stands (Wilks' lambda = 0.035, *d.f.* = 4, 5, $P < 0.001$; Table 1) after the burns. Home ranges of bats were closer to midslope positions than to lower slope positions before burning (Wilks' lambda = 0.049, *d.f.* = 3, 2, $P < 0.07$), and closer to midslope positions than to either ridge or lower slope positions after burning (Wilks' lambda = 0.044, *d.f.* = 3, 6, $P < 0.001$). Home ranges of bats were closer to burned than to unburned habitats after burning (Wilks' lambda = 0.042, *d.f.* = 2, 7, $P < 0.001$). There was no difference in use of aspects by bats either before or after burning.

Data on insect abundance (≥10 mm in size) showed increases for coleopterans, dipterans, and all insects combined following burning (Table 2). The abundance of moths did not change. Fecal pellet analysis showed that bats consumed members of 7 orders of insects, with lepidopterans, coleopterans, and dipterans being the 3 most important prey groups (Table 3). Percent frequency and percent volume of dipterans increased in the diet of female northern bats after burning. Percent volume of all other orders of insects did not change following burning, although hymenopertans were only found in pellets before burning and neuropterans only in pellets after burning.

Roosting behavior.—We tracked female northern bats to 54 tree roosts, with 29.6% located before burning and 70.4% after. Bats roosted in 11 species and 3 additional genera of trees including chestnut oak (*Quercus prinus*; $n = 13$), red maple (*Acer rubrum*; $n = 8$), hickories (*Carya*; $n = 7$), tulip poplar ($n = 6$), pines (*Pinus*; $n = 4$), scarlet oak (*Q. coccinea*; $n = 3$), white oak (*Q. alba*; $n = 3$), black oak (*Q. velutina*; $n = 3$), sassafras (*Sassafras albidum*; $n = 2$), and 1 each of elm (*Ulmus*), cucumber magnolia, black walnut (*Juglans nigra*), black gum (*Nyssa sylvatica*), and flowering dogwood (*Cornus florida*).

All but 2 roost trees were in hardwood stands, with 74.3% of roost trees located in burned habitats and 25.7% in unburned habitats following burning. Distribution of roost trees by aspect shifted after burning from predominantly south- and west-facing aspects to south- and east-facing aspects (Table 4). Roost trees were most often found on midslope and ridge positions regardless of burn condition. Fire burned 80% of the area on 67.6% of sample plots surrounding roost trees with charred surfaces reaching 14.6 m in height, with charring caused by smoldering combustion. Fire burned 80% of the area on 54.4% of sample plots surrounding random snags with char reaching 17.6 m. The structural integrity of 2 roosts trees appeared to have been compromised from extensive smoldering combustion.

Table 2.—Means ± *SE* for abundance of insects (≥10 mm in size) captured per trap night in blacklight traps before and after prescribed burning on the Daniel Boone National Forest, Kentucky, in 2006 and 2007. ANOVA test outcomes are included.

	All insects combined	Coleoptera	Lepidoptera	Diptera
Preburn ($n = 43$)	140 ± 14	8.0 ± 1.47	126 ± 13	1.0 ± 0.25
Postburn ($n = 84$)	188 ± 14	24.3 ± 3.24	154 ± 13	2.4 ± 0.34
F-statistic (*P*-value)	4.1 (0.04)	20.3 (0.001)	0.3 (0.6)	12.2 (0.001)

TABLE 3.—Mean percent volume ± *SE* and frequency of occurrence (%) of insect prey in fecal samples of northern bats (*Myotis septentrionalis*) radiotracked before ($n = 6$ bats) and after ($n = 8$ bats) prescribed burning on the Daniel Boone National Forest, Kentucky, in 2006 and 2007.

	Percent volume		Percent frequency	
Taxon	Preburn	Postburn	Preburn	Postburn
Coleoptera	27.8 ± 2.8	35.5 ± 8.6	100.0	100.0
Diptera[a]	1.4 ± 1.1	11.0 ± 3.6	50.0	100.0
Hemiptera	6.1 ± 3.5	5.6 ± 1.9	83.3	75.0
Hymenoptera	1.4 ± 1.4	0.0	16.7	0.0
Lepidoptera	62.6 ± 5.2	46.4 ± 8.3	100.0	100.0
Neuroptera	0.0	0.2 ± 0.2	0.0	12.5
Trichoptera	0.4 ± 0.4	0.2 ± 0.2	16.7	12.5
Other[b]	0.8 ± 0.6	1.0 ± 1.0	33.3	62.5

[a] Between burn conditions, average percent volume for Diptera is different in fecal samples of radiotracked bats at $P < 0.01$.

[b] Represents unidentified materials, hair, or vegetation.

Comparisons of roost trees with random snags before burning indicate that female northern bats selected trees that were in an earlier stage of decay and taller (Table 5). After burning, bats continued to select trees in earlier stages of decay than random snags, but also chose trees as roosts with a greater number of cavities and higher percentages of bark coverage and exfoliating bark coverage than random snags. We found no difference between stand characteristics measured around roost trees and random snags.

Roost height ($t = 0.45$, *d.f.* $= 28$, $P > 0.2$) and stem diameter at roost ($t = 0.54$, *d.f.* $= 28$, $P > 0.2$) were not different between roosting sites of female northern bats before and after burning (Table 6). The majority of roosts were situated below the canopy and none was found above the canopy. Only type of structure used for roosting changed after burning with an increased selection for cavities and fewer roosts located under bark. This is consistent with comparisons made with random snags that showed number of cavities to be associated with selection of roost trees following burning.

DISCUSSION

We found size of home ranges and core areas of female northern bats was unaffected by changes in habitat caused by prescribed fire, suggesting populations of insect prey likely remained available in proximity to roosting sites. The higher abundance of coleopterans, dipterans, and all insects combined captured in blacklight traps postfire compared to prefire conditions supports this contention, because the former 2 insect groups were the 2nd and 3rd most important prey of these bats. The importance of these 2 insect groups is consistent with data for other populations of northern bats (Griffith and Gates 1985; Whitaker 2004).

TABLE 4.—Percentage of tree roosts ($n = 51$) of female northern bats (*Myotis septentrionalis*) by aspect and slope position before and after prescribed burning on the Daniel Boone National Forest, Kentucky, in 2006 and 2007.

Habitat characteristic	Preburn	Postburn
Aspect		
North	13.0	17.0
East	6.0	23.0
South	43.0	51.0
West	38.0	9.0
Slope position		
Ridgetop	44.0	54.0
Midslope	50.0	40.0
Lower slope	6.0	6.0

The home-range sizes we measured for female northern bats are likely minimum estimates because we limited our radiotracking to the early evening foraging period. Northern bats use a biphasic activity pattern when foraging (Owen et al. 2003), so our approach omitted the predawn foraging period. However, we argue that this influence likely affected both preburn and postburn estimates equally. Foraging behavior of adult female bats also is known to vary by reproductive condition, with lactating females using habitats where they can drink more frequently (Adams and Hayes 2008) and foraging earlier and for longer periods than pregnant, postlactating, or nonreproductive females (Barclay 1989). We radiotracked only 3 lactating females, 2 in the preburn period and 1 postburn, so it is unlikely that differences associated with foraging behavior of lactating females affected the outcome of our analyses. Moreover, the mean home-range size of lactating females (93.6 ha ± 4.8 *SE*) was comparable to that of pregnant females (95.5 ± 21.9 ha) in our study, so the influence of radiotagged lactating females was likely not significant on preburn versus postburn estimates of home-range size.

The home-range sizes we estimated were small compared to those reported for bats elsewhere in North America (Lacki et al. 2007a), but comparable to those measured for other populations of northern bats (Broders et al. 2006; Owen et al. 2003). Northern bats radiotracked in a heavily fragmented, forest–agricultural landscape used foraging areas an order of magnitude smaller than we found (Henderson and Broders 2008). These authors suggested that the possible behavioral differences in use of available foraging space by northern bats were associated with the available local landscape resulting from forest fragmentation. Thus, northern bats likely exhibit

Table 5.—Means (*SE*) of tree- and stand-level habitat characteristics for roosts of female northern bats (*Myotis septentrionalis*) and random snags before and after prescribed burning on the Daniel Boone National Forest, Kentucky, in 2006 and 2007. Asterisks indicate that within burn condition, characteristic is different between roosts and random snags; * $P < 0.05$; ** $P < 0.01$.

	Preburn		Postburn	
Habitat characteristic	Roosts ($n = 16$)	Random ($n = 11$)	Roosts ($n = 35$)	Random ($n = 57$)
Decay class (1–9)	3.62 (0.4)*	5.27 (0.4)	2.43 (0.2)**	4.46 (0.2)
Tree diameter (cm)	44.2 (4.0)	41.6 (6.6)	34.6 (3.4)	32.0 (1.8)
Tree height (m)	20.6 (2.5)*	12.1 (2.1)	19.7 (1.4)	17.8 (1.0)
No. cavities (*n*)	1.44 (0.7)	1.27 (0.6)	1.54 (0.5)*	0.82 (0.2)
Bark coverage (%)	62.0 (9.0)	40.0 (10.2)	83.0 (4.4)**	46.0 (4.9)
Exfoliating bark coverage (%)	16.0 (4.0)	25.0 (6.0)	7.0 (2.4)*	13.0 (2.1)
Canopy height (m)	21.3 (1.5)	16.9 (1.2)	27.8 (0.8)	30.5 (1.2)
Canopy cover (%)	47.0 (5.0)	51.0 (7.2)	65.0 (4.4)	61.0 (3.0)
Snag density (stems/ha)	40.5 (6.7)	27.5 (8.7)	25.2 (3.1)	33.9 (5.2)
Live tree density (stems/ha)	363 (50)	280 (27)	272 (10)	252 (10)

plasticity in foraging behavior with the magnitude of movements being related to the local landscape structure.

The preference of northern bats for foraging at heavily forested midslope positions, regardless of burn condition, suggests these bats feed in and around closed canopies and are likely cluttered-adapted (Aldridge and Rautenbach 1987; Crome and Richards 1988; Norberg and Rayner 1987); however, we do not know the extent to which they may have foraged above the canopy. The extensive use of forested habitats for foraging by northern bats in other landscapes with varying amounts of fragmentation is consistent with our findings (Broders et al. 2006; Caire et al. 1979; Henderson and Broders 2008; LaVal et al. 1977; Owen et al. 2003). Nevertheless, we found northern bats also foraged in or near pine-dominated stands more often than hardwood-dominated stands, regardless of burn condition, and in burned habitats more than unburned habitats. We argue that within forests bats used microhabitats with less clutter as our observations indicated pine stands and burned habitats possessed less-cluttered canopies than hardwood stands and unburned habitats, respectively. The behavior we observed is not consistent with activity by assemblages of bats in southern pine forests, where the use of burned habitats was no different from activity levels recorded in unburned habitats (Loeb and Waldrop 2008). However, northern bats were not among the suite of species examined.

Table 6.—Characteristics of roosting sites of female northern bats (*Myotis septentrionalis*) before and after prescribed burning on the Daniel Boone National Forest, Kentucky, in 2006 and 2007. Data are presented as percent of total or as mean ± *SE*. Sample sizes reflect our inability at times to locate the specific roosting site of the bats on the tree or snag.

Roost characteristic	Preburn ($n = 6$)	Postburn ($n = 24$)
Roost height (m)	10.6 ± 3.6	9.1 ± 1.4
Diameter of stem at roost (cm)	20.3 ± 6.8	24.0 ± 3.0
Roost position		
Above canopy (%)	0.0	0.0
Within canopy (%)	33.3	20.8
Below canopy (%)	66.7	79.2
Roost structure		
Crevice (%)	16.7	17.4
Cavity (%)	33.3	60.9
Bark (%)	50.0	21.7

Northern bats use a wide range of tree species as roosts (e.g., Broders and Forbes 2004; Carter and Feldhamer 2005; Foster and Kurta 1999; Menzel et al. 2002), and the pattern we observed for adult females was no different, with ≥11 species of trees used as roosts. On occasion we had difficulty classifying the species of tree beyond genus due to the state of decay, so it is likely that more species of trees were actually used. The majority of roosts (92.6%) were in hardwood species and only 7.4% of roosts occurred in pines. This contrasts with other data for northern bats where shortleaf pine (*Pinus echinata*) was the species of tree used most frequently (Lacki and Schwierjohann 2001; Perry and Thill 2007). Our data may partly reflect the extensive damage to and loss of pine snags that resulted from burning. Regardless, northern bats can use both hardwoods (Foster and Kurta 1999; Menzel et al. 2002) and conifers as roosts (Broders and Forbes 2004; Carter and Feldhamer 2005). Examination of our data shows that females preferentially chose roost trees in burned compared to unburned habitats, similar to evening bats in Missouri, which used snags in burned stands more frequently than in unburned stands (Boyles and Aubrey 2006).

Regardless of burn condition, the roosts of female northern bats were situated on ridge and midslope positions but rarely in lower slope positions. This is consistent with roost use by northern bats elsewhere in eastern Kentucky, where the majority chose roosts in upper slope positions (Lacki and Schwierjohann 2001). The aspect of roosts changed from south- and west-facing aspects to south- and east-facing aspects, likely due to the extent of forested stands on east-facing aspects that were burned. We found female northern bats chose live trees, and snags in earlier stages of decay than random snags; a common trait of cavity-roosting bats (Barclay and Kurta 2007). This pattern also is consistent with studies showing that northern bats use live trees more frequently than syntopic populations of Indiana bats (*Myotis sodalis*), a species that also roosts beneath bark and inside crevices of trees and snags (Carter and Feldhamer 2005; Foster and Kurta 1999).

Before burning, female northern bats roosted in tall trees and snags, but after burning the condition of the bole (i.e., main stem) was more important in regards to the selection of trees and snags. Bats still used trees in an early decay class; however, postburn roost trees had a higher percent cover of bark compared to those randomly available on the landscape after fires. Although not statistically compared, postburn roost trees on average had higher bark coverage compared to preburn roost trees. Overall, female northern bats used bark, crevices, and cavities as roosting structures, but roosts were situated more often beneath bark before burning and inside cavities after burning. The use of cavities as roosting structures after burning is consistent with our result that postburn selection was based on bole condition (i.e., number of cavities and bark coverage).

The importance of bole surface for roost choice by northern bats following fire was unexpected and its significance needs to be addressed. We propose 2 hypotheses. First, stems possessing more cavities and a higher percentage of exfoliating bark provide a wider range of choices for roosting, which may provide longer-term roosting sites. Second, stems possessing more cavities and a higher percentage of exfoliating bark provide a greater density of roosting sites within a tree in case bats need to relocate on the same roost tree to avoid smoke and heat effects during fire. Dickinson et al. (2009) suggested that both female and male northern bats emerge from roosting sites during prescribed burns and avoid smoke and heat by temporarily relocating to alternate roosts away from the fire. This is not consistent with our 2nd hypothesis.

The extent to which roosts are limiting in forested habitats remains unclear (Crampton and Barclay 1998; Kunz and Lumsden 2003). Although there is evidence for competition among syntopic species of tree-roosting bats (Boonman 2000; Lumsden et al. 2002), other authors conclude the opposite based on use of available roosting structures (Sedgeley and O'Donnell 1999). There are few quantitative estimates of suitable roosting trees for bats inhabiting forests in eastern North America. Based on data from roosts with >15 bats exiting, or large flyouts, we estimated 30.8 ha per large-flyout roost at the Bear Waller burn unit, 87 ha per large-flyout roost at the Powder Mill burn unit, and 343 ha per large-flyout roost at the unburned control. The latter estimate is likely biased upward given the lower sampling effort, meaning important roosts likely went undiscovered relative to the 2 burn units.

We believe female northern bats exhibit behaviors consistent with being fire-tolerant as they foraged and roosted extensively in burned habitats after prescribed burning. Moreover, the use of both live trees and snags as roosts (Carter and Feldhamer 2005; Foster and Kurta 1999; Lacki and Schwierjohann 2001; Perry and Thill 2007; this study), the range of roosting structures (Carter and Feldhamer 2005; Foster and Kurta 1999; Lacki and Schwierjohann 2001; Perry and Thill 2007; this study), and the ability to arouse and move during fires (Dickinson et al. 2009) is strong evidence that northern bats adjust to changed habitats resulting from fires.

The heavily forested regions of eastern Kentucky have a long history of burning, and although the majority of forested habitats burn infrequently, some autumn fires can be large and their impact is likely severe on the resources needed by forest-dwelling bats (Maingi and Henry 2007). Knowledge of fire history is reflected in the long-term plan of the Daniel Boone National Forest, Kentucky, to prescribe-burn approximately 22,700 ha per year in the next decade (Mann 2006). Although the consequences of this policy are unknown for the majority of species our results suggest that there will be no negative effects on populations of northern bats. We argue that the bats will likely benefit from the proposed burning program, but monitoring is recommended.

Trends in the use of prescribed fire in national forests in the eastern United States suggests that early growing season (i.e., spring) burns will increase in frequency and extent because of their utility in vegetation management (Dickinson et al. 2009). Formation of northern bat colonies occurred from 29 April, about the time of the Bear Waller burn, and extended to the last week in June. Thus, increased spring burning (Dickinson et al. 2009) has the potential to disturb bats during the period when maternity colonies of northern and other bark- and cavity-roosting bat species are being established. Bats are capable of exiting tree and ground roosts before they experience extensive exposure to heat and gases during fires (Dickinson et al. 2009; Rodrigue et al. 2001; Saugey et al. 1989); however, adult females are more likely to use daytime torpor following nights of poor foraging success due to rainfall events or cooler nighttime temperatures that lower prey abundance (Audet and Thomas 1997; Kurta 1991). These are conditions that can be typical of early spring weather patterns in eastern North America, although prescribed burning would not occur during wet periods. Moreover, peak burning conditions occur during the daytime when ambient temperatures are highest and arousal times of bats likely the shortest (Chruszcz and Barclay 2002; Ruczyński 2006), further reducing the risk of bats to prescribed fire. Growing-season burns have the potential to be detrimental to nonvolant young, because these bats are not capable of escaping. Because of concern for the endangered Indiana bat, however, there are no proposals on National Forests for burning during the lactation period where Indiana bats are known to be present (Dickinson et al. 2009); this region overlaps a large portion of the range of the northern bat and other bat species.

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LITERATURE CITED

ADAMS, R. A., AND M. A. HAYES. 2008. Water availability and successful lactation by bats as related to climate change in arid regions of western North America. Journal of Animal Ecology 77:1115–1121.

ALDRIDGE, H.D.J.N., AND I. L. RAUTENBACH. 1987. Morphology, echolocation, and resource partitioning in insectivorous bats. Journal of Animal Ecology 56:763–778.

AUDET, D., AND D. W. THOMAS. 1997. Facultative hypothermia as a thermoregulatory strategy in the phyllostomid bats *Carollia perspicillata* and *Sturnira lilium*. Journal of Comparative Physiology, B. Biochemical, Systemic, and Environmental Physiology 167:146–152.

BARCLAY, R. M. R. 1989. The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*. Behavioral Ecology and Sociobiology 24:31–37.

BARCLAY, R. M. R., AND A. KURTA. 2007. Ecology and behavior of bats roosting in tree cavities and under bark. Pp. 17–59 in Bats in forests: conservation and management (M. J. Lacki, J. P. Hayes, and A. Kurta, eds.). Johns Hopkins University Press, Baltimore, Maryland.

BEYER, H. L. 2004. Hawth's analysis tools for ArcGIS. http://www.spatialecology.com/htools. Accessed 7 January 2008.

BOONMAN, M. 2000. Roost selection by noctules (*Nyctalus noctula*) and Daubenton's bat (*Myotis daubentonii*). Journal of Zoology (London) 251:385–389.

BOYLES, J. G., AND D. P. AUBREY. 2006. Managing forests with prescribed fire: implications for a cavity-dwelling bat species. Forest Ecology and Management 222:108–115.

BRACK, V., JR., AND J. O. WHITAKER, JR. 2001. Foods of the northern myotis, *Myotis septentrionalis*, from Missouri and Indiana, with notes on foraging. Acta Chiropterologica 3:203–210.

BRODERS, H. G., AND G. J. FORBES. 2004. Interspecific and intersexual variation in roost-site selection of northern long-eared and little brown bats in the Greater Fundy National Park ecosystem. Journal of Wildlife Management 68:602–610.

BRODERS, H. G., G. J. FORBES, S. WOODLEY, AND I. D. THOMPSON. 2006. Range extent and stand selection for roosting and foraging in forest-dwelling northern long-eared bats and little brown bats in the Greater Fundy Ecosystem, New Brunswick. Journal of Wildlife Management 70:1174–1184.

BROSE, P. H., T. M. SCHULER, D. H. VAN LEAR, AND J. BERST. 2001. Bringing fire back: the changing regimes of the Appalachian mixed-oak forest. Journal of Forestry 99:30–35.

BROSE, P. H., D. H. VAN LEAR, AND P. D. KEYSER. 1999. A shelterwood-burn technique for regenerating productive upland oak sites in the piedmont region. Southern Journal of Applied Forestry 23:158–162.

BUDDLE, C. M., D. W. LANGOR, G. R. POHL, AND J. R. SPENCE. 2006. Arthropod responses to harvesting and wildfire: implications for emulation of natural disturbance in forest management. Biological Conservation 128:346–357.

CAIRE, W., R. K. LAVAL, M. L. LAVAL, AND R. CLAWSON. 1979. Notes on the ecology of *Myotis keenii* (Chiroptera, Vespertilionidae) in eastern Missouri. American Midland Naturalist 102:404–407.

CARTER, T. C., AND G. A. FELDHAMER. 2005. Roost-tree use by maternity colonies of Indiana bats and northern long-eared bats in southern Illinois. Forest Ecology and Management 219:259–268.

CARTER, T. C., W. M. FORD, AND M. A. MENZEL. 2002. Fire and bats in the southeast and mid-Atlantic: more questions than answers? Pp. 139–143 in The role of fire in nongame wildlife management and community restoration: traditional uses and new directions (W. M. Ford, K. R. Russell, and C. E. Moorman, eds.). United States Department of Agriculture Forest Service, Northeastern Research Station, Newtown Square, Pennsylvania, General Technical Report NE-288:1–145.

CHRUSZCZ, B. J., AND R. M. R. BARCLAY. 2002. Thermoregulatory ecology of a solitary bat, *Myotis evotis*, roosting in rock crevices. Functional Ecology 16:18–26.

COLLINS, R. F. 1975. A history of the Daniel Boone National Forest 1770–1970. United States Department of Agriculture Forest Service, Winchester, Kentucky.

CONNER, L. M., AND B. W. PLOWMAN. 2001. Using Euclidian distances to assess nonrandom habitat use. Pp. 275–290 in Radiotelemetry and animal populations (J. Millspaugh and J. Marzluff, eds.). Academic Press, San Diego, California.

CONNER, L. M., M. D. SMITH, AND L. W. BURGER. 2003. A comparison of distance-based and classification-based analyses of habitat use. Ecology 84:526–531.

CRAMPTON, L. H., AND R. M. R. BARCLAY. 1998. Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. Conservation Biology 12:1347–1358.

CROME, F. H. J., AND G. C. RICHARDS. 1988. Bats and gaps: microchiropteran community structure in a Queensland rain forest. Ecology 69:1960–1969.

DELCOURT, P. A., AND H. R. DELCOURT. 1998. The influence of prehistoric human-set fires on oak-chestnut forests in the southern Appalachians. Castanea 63:337–345.

DICKINSON, M. B., M. J. LACKI, AND D. R. COX. 2009. Fire and the endangered Indiana bat. In Fire in eastern oak forests conference (T. F. Hutchinson, ed.). Northern Research Station, United States Department of Agriculture General Technical Report. Newton Square, Pennsylvania. NRS-P-46:1–154.

FAURE, P. A., J. H. FULLARD, AND J. W. DAWSON. 1993. The gleaning attacks of the northern long-eared bat, *Myotis septentrionalis*, are relatively inaudible to moths. Journal of Experimental Biology 178:173–189.

FETTIG, C. J., ET AL. 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. Forest Ecology and Management 238:24–53.

FINCH, D. M., J. L. GANEY, W. YONG, R. T. KIMBALL, AND R. SALLABANKS. 1997. Effect and interactions of fire, logging, and grazing. Pp. 103–136 in Songbird ecology in southwestern ponderosa pine forests: a literature review (W. M. Block and D. M. Finch, eds.). United States Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, General Technical Report RM-GTR-292:1–152.

FOSTER, R. W., AND A. KURTA. 1999. Roosting ecology of the northern bat (*Myotis septentrionalis*) and comparisons with the endangered Indiana bat (*Myotis sodalis*). Journal of Mammalogy 80:659–672.

Frost, P. G. H. 1984. The responses and survival of organisms in fire-prone environments. Pp. 274–309 in Ecological effects of fire in South African ecosystems (P. deV. Booysen and N. M. Tainton, eds.). Springer-Verlag, Berlin, Germany.

Fulé, P. Z., W. W. Covington, and M. M. Moore. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. Ecological Applications 7:895–908.

Galley, K. E. M., and R. W. Flowers. 1998. Rediscovery of a springtail and a grasshopper in Florida. Florida Entomologist 81:544–546.

Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

Gerson, E. A., and R. G. Kelsey. 1997. Attraction and direct mortality of Pandora moths, *Coloradia pandora* (Lepidoptera: Saturniidae), by nocturnal fire. Forest Ecology and Management 98:71–75.

Griffith, L. A., and J. E. Gates. 1985. Food habits of cave-dwelling bats in the central Appalachians. Journal of Mammalogy 66:451–460.

Guelta, M., and H. E. Balbach. 2005. Modeling fog oil obscurant smoke penetration into simulated tortoise burrows and bat colony trees. United States Army Corps of Engineers, Engineer Research and Development Center, Washington, D.C., ERDC/TR-05-31:1–49.

Henderson, L. E., and H. G. Broders. 2008. Movements and resource selection of the northern long-eared myotis (*Myotis septentrionalis*) in a forest–agriculture landscape. Journal of Mammalogy 89:952–963.

Hollander, M., and D. A. Wolfe. 1973. Nonparametric statistical methods. John Wiley & Sons, New York.

Hunter, M. L., Jr. 1990. Wildlife, forests, and forestry: principles of managing forests for biological diversity. Prentice-Hall, Englewood Cliffs, New Jersey.

Hutchinson, T. F., R. E. J. Boerner, S. Sutherland, E. K. Sutherland, M. Ortt, and L. R. Iverson. 2005. Prescribed fire effects on the herbaceous layer of mixed-oak forests. Canadian Journal of Forest Research 35:877–890.

Jenness, J. 2004. Nearest Features (nearfeat.avx) extension for ArcView 3.x, v. 3.8b. Jenness Enterprises. http://www.jennessent.com/arcview/nearest_features.htm. Accessed 4 February 2008.

Jenness, J. 2006. Topographic Position Index (tpi_jen.avx) extension for ArcView 3.x, v. 1.2. Jenness Enterprises. http://www.jennessent.com/arcview/tpi.htm. Accessed 4 February 2008.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, J. S., M. J. Lacki, and M. D. Baker. 2007. Foraging ecology of long-legged myotis (*Myotis volans*) in north-central Idaho. Journal of Mammalogy 88:1261–1270.

Jones, R. L. 2005. Plant life of Kentucky: an illustrated guide to the vascular flora. University Press of Kentucky, Lexington.

Keyser, P. D., and W. M. Ford. 2006. Influence of fire on mammals in eastern oak forests. Pp. 180–190 in Fire in eastern oak forests: delivering science to land managers, proceedings of a conference (M. B. Dickinson, ed.). United States Department of Agriculture Northern Research Station, Newtown Square, Pennsylvania, General Technical Report NRS-P-1:1–303.

Kunz, T. H., and L. F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. Pp. 3–89 in Bat ecology (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.

Kurta, A. 1991. Torpor patterns in food deprived *Myotis lucifugus* (Chiroptera: Vespertilionidae) under simulated roost conditions. Canadian Journal of Zoology 69:255–257.

Lacki, M. J., S. K. Amelon, and M. D. Baker. 2007a. Foraging ecology of bats in forests. Pp. 83–127 in Bats in forests: conservation and management (M. J. Lacki, J. P. Hayes, and A. Kurta, eds.). Johns Hopkins University Press, Baltimore, Maryland.

Lacki, M. J., J. S. Johnson, L. E. Dodd, and M. D. Baker. 2007b. Prey consumption of insectivorous bats in coniferous forests of north-central Idaho. Northwest Science 81:199–205.

Lacki, M. J., and J. H. Schwierjohann. 2001. Day-roost characteristics of northern bats in mixed mesophytic forest. Journal of Wildlife Management 65:482–488.

LaVal, R. K., R. L. Clawson, M. L. LaVal, and W. Caire. 1977. Foraging behavior and nocturnal activity patterns of Missouri bats, with emphasis on the endangered species *Myotis grisescens* and *Myotis sodalis*. Journal of Mammalogy 58:592–599.

Loeb, S. C., and T. A. Waldrop. 2008. Bat activity in relation to fire and fire surrogate treatments in southern pine stands. Forest Ecology and Management 255:3185–3192.

Lumsden, L. F., A. F. Bennett, and J. E. Silins. 2002. Selection of roost sites by the lesser long-eared bat (*Nyctophilus geoffroyi*) and Gould's wattled bat (*Chalinolobus gouldii*) in south-eastern Australia. Journal of Zoology (London) 257:207–218.

Maingi, J. K., and M. C. Henry. 2007. Factors influencing wildfire occurrence and distribution in eastern Kentucky, USA. International Journal of Wildland Fire 16:23–33.

Mann, R. 2006. Growing a burning program: challenges and opportunities. Pp. 263–266 in Fire in eastern oak forests: delivering science to land managers (M. B. Dickinson, ed.). United States Department of Agriculture Northern Research Station, Newtown Square, Pennsylvania, General Technical Report NRS-P-1:1–303.

Martin, R. E., and R. Mitchell. 1980. Possible, potential, probable, and proven fire-insect interactions. Pp. 138–144 in Proceedings of the 1980 National Convention of the Society of American Foresters, Spokane, Washington. Society of American Foresters, Bethesda, Maryland.

McCullough, D. G., R. A. Werner, and D. Neumann. 1998. Fire and insects in northern boreal ecosystems of North America. Annual Review of Entomology 43:107–127.

McGrain, P. 1983. The geologic story of Kentucky. Kentucky Geological Survey, University of Kentucky, Lexington, Series XI, Special Publication 8:1–74.

Menzel, M. A., et al. 2002. Roost tree selection by northern long-eared bat (*Myotis septentrionalis*) maternity colonies in an industrial forest of the central Appalachian mountains. Forest Ecology and Management 155:107–114.

Miller, W. E. 1979. Fire as an insect management tool. Entomological Society of America Bulletin 25:137–140.

Mitchell, R. 1990. Effects of prescribed fire on insect pests. Pp. 111–116 in Natural and prescribed fire in Pacific Northwest forests (J. D. Walstad, S. R. Radosevich, and D. V. Sandberg, eds.). Oregon State University Press, Corvallis.

Moorman, C. E., K. R. Russell, S. M. Lohr, J. F. Ellenberger, and D. H. Van Lear. 1999. Bat roosting in deciduous leaf litter. Bat Research News 40:73–75.

Moretti, M., P. Duelli, and M. K. Obrist. 2006. Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests. Oecologia 149:312–327.

Moritz, M. A. 1997. Analyzing extreme disturbance events: fire in Los Padres National Forest. Ecological Applications 7:1252–1262.

Mushinsky, H. R., and D. J. Gibson. 1991. The influence of fire periodicity on habitat structure. Pp. 237–259 in Habitat structure: the physical arrangement of objects in space (S. S. Bell, E. D. McCoy, and H. R. Mushinsky, eds.). Chapman and Hall, London, United Kingdom.

Nams, V. O. 2006. Locate III user's guide. Pacer Computer Software, Tatamagouche, Nova Scotia, Canada.

Nams, V. O., and S. Boutin. 1991. What is wrong with error polygons? Journal of Wildlife Management 55:172–176.

Norberg, U. M., and J. M. V. Rayner. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London, B. Biological Sciences 316:335–427.

Owen, S. F., et al. 2003. Home-range size and habitat use by the northern myotis (*Myotis septentrionalis*). American Midland Naturalist 150:352–359.

Paquin, P., and D. Coderre. 1997. Deforestation and fire impacts on edaphic insect larvae and other macroarthropods. Environmental Entomology 26:21–30.

Perry, R. W., and R. E. Thill. 2007. Roost selection by male and female northern long-eared bats in a pine-dominated landscape. Forest Ecology and Management 247:220–226.

Pippin, W. F., and B. Nichols. 1996. Observations of arthropod populations following the La Mesa Fire of 1977. Pp. 161–165 in Fire effects in southwestern forests: proceedings of the second La Mesa Fire symposium (C. D. Allen, ed.). United States Department of Agriculture Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, General Technical Report RM-GTR-286:1–216.

Randall-Parker, T., and R. Miller. 2002. Effects of prescribed fire in ponderosa pine on key wildlife habitat components: preliminary results and a method for monitoring. Pp. 823–834 in Symposium on the ecology and management of dead wood in western forests. United States Department of Agriculture Forest Service, Reno, Nevada, General Technical Report PSW-GTR-181:1–949.

Ratcliffe, J. M., and J. W. Dawson. 2003. Behavioural flexibility: the little brown bat, *Myotis lucifugus*, and the northern long-eared bat, *M. septentrionalis*, both glean and hawk prey. Animal Behaviour 66:847–856.

Reed, C. C. 1997. Responses of prairie insects and other arthropods to prescription burns. Natural Areas Journal 17:380–385.

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

Ruczyński, I. 2006. Influence of temperature on maternity roost selection by noctule bats (*Nyctalus noctula*) and Leisler's bats (*N. leisleri*) in Białowieża Primeval Forest, Poland. Canadian Journal of Zoology 84:900–907.

Saugey, D. A., D. R. Heath, and G. A. Heidt. 1989. The bats of the Ouachita Mountains. Proceedings of the Arkansas Academy of Science 43:71–77.

Sedgeley, J. A., and C. F. J. O'Donnell. 1999. Factors influencing roost cavity selection by a temperate rainforest bat (*Chalinolobus tuberculatus*, Vespertilionidae) in New Zealand. Journal of Zoology (London) 249:437–446.

Siemann, E., J. Haarstad, and D. Tilman. 1997. Short-term and long-term effects of burning on oak savanna arthropods. American Midland Naturalist 137:349–361.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Co., San Francisco, California.

Swengel, A. B. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitats. Biodiversity and Conservation 10:1141–1169.

Triplehorn, C. A., and N. F. Johnson. 2005. Borrer and DeLong's introduction to the study of insects. 7th ed. Thomson Brooks/Cole, Belmont, California.

Van Lear, D. H., P. H. Brose, and P. D. Keyser. 2000. Using prescribed fire to regenerate oaks. Pp. 97–102 in Proceedings of the workshop on fire, people, and the central hardwood landscape (D. A. Yaussy, comp.). United States Department of Agriculture Forest Service, General Technical Report NE-299:1–159.

Van Lear, D. H., R. A. Harper, P. R. Kapeluck, and W. D. Carroll. 2004. History of Piedmont forests: implications for current pine management. Pp. 139–143 in Proceedings of the 12th biennial southern silvicultural research conference (K. F. Conner, ed.). United States Department of Agriculture Forest Service, Southern Research Station, Asheville, North Carolina, General Technical Report SRS-71:1–600.

Waldrop, T. A., D. L. White, and S. M. Jones. 1992. Fire regimes for pine–grassland communities in the southeastern United States. Forest Ecology and Management 47:195–210.

Warren, S. D., C. J. Scifres, and P. D. Teel. 1987. Response of grassland arthropods to burning: a review. Agriculture, Ecosystems and Environment 19:105–130.

Whitaker, J. O., Jr. 1972. Food habits of bats from Indiana. Canadian Journal of Zoology 50:877–883.

Whitaker, J. O., Jr. 1988. Food habits analysis of insectivorous bats. Pp. 171–189 in Ecological and behavioral methods for the study of bats (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C.

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

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radiotracking data. Academic Press, San Diego, California.

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