FIRE AND THE ENDANGERED INDIANA BAT

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Abstract.—Fire and Indiana bats (*Myotis sodalis*) have coexisted for millennia in the central hardwoods region, yet past declines in populations of this endangered species, and the imperative of fire use in oak silviculture and ecosystem conservation, call for an analysis of both the risks and opportunities associated with using fires on landscapes in which the bat occurs. In this paper, we explore the potential direct effects of prescribed fire and associated smoke on Indiana bats. We identify the immediate effects on bats, such as exposure to smoke and displacement, when individuals are in tree roosts (under exfoliating bark or in crevices) and hibernacula (caves and mines). Radio-tracked northern long-eared bats (*Myotis septentrionalis*), an Indiana bat surrogate, flushed shortly after prescribed fire ignition in the Daniel Boone National Forest (Kentucky) on a warm spring day, confirming previously reported observations. We also consider the longer-term effects on bats of the habitat changes caused by fire use. Finally, we review National Forest Plans and ask how the available science supports their standards and guidelines. Efforts to manage Indiana bats are based on limited monitoring of the effects of habitat manipulations and a body of research that is deficient in key areas, providing a poor basis on which to either practice adaptive management or counter restrictions on growing-season burning.

INTRODUCTION

The Indiana bat (*Myotis sodalis*) is a rather small (6 to 9 g), aerially feeding (insectivorous), tree-roosting, and migratory bat with a summer distribution that encompasses much of the Midwest, and portions of New England and the south-central states (Harvey et al. 1999, U.S. Fish and Wildlife Service [USFWS] 2007a). Tree roosting occurs under exfoliating bark and in crevices in dead trees (snags) and live trees. First reproduction for healthy females occurs in their first year and females can give birth to a single pup each year for 14 to 15 years (Humphrey et al. 1977, Humphrey et al. 1977). Pregnant females and females with young aggregate in maternity colonies of tens to hundreds of individuals. The bat's distribution is believed to be associated with the prevalence of limestone caves in the eastern United States (Menzel et al. 2001). Today, hibernacula include both caves and mines.

The species was listed as endangered on March 11, 1967, after winter populations declined significantly at the majority of known hibernacula (USFWS 2007a). Early recovery efforts focused on protection and rehabilitation of hibernacula, yet declines in populations of the species continued with an estimated 350,000 individuals remaining as of the 1997 census. Through the period of declines, losses in southerly hibernacula have been partially offset by increases in northerly hibernacula (Clawson 2002). Trends since 2001 have been upward, and 2007 population estimates reached approximately 468,000 (USFWS 2008). On the negative side, mortality of Indiana bats associated with white-nose syndrome in the Northeast over the winter of 2007-2008 has been confirmed (USFWS 2009c).

Indiana bat foraging and roosting habitat includes forested areas outside of hibernacula used during the period of transition out of hibernation (staging), areas used during the warmer months of the year (summer habitat), and, again, areas outside of hibernacula used during the breeding period before hibernation (swarming). Indiana bats either stay close to hibernacula during the summer or migrate, with a maximum known migration distance of 520 km (Gardner and Cook 2002). Males and females have different roosting requirements during the summer; female Indiana bats form maternity colonies that use collections of snags and live roosts (Humphrey et al. 1977, Kurta et al. 1993, Callahan et al. 1997, Britzke et al. 2003, 2006). During the swarming period, bats breed and must gain weight rapidly to prepare for hibernation (USFWS 2007a).

Implementing the widely advocated prescription for controlled burns to restore and maintain oak ecosystems (see papers in Dickinson 2006, Yaussy et al. 2008), the U.S. Forest Service (USFS) is carrying out prescribed fire treatments on oak forests, including those that occur within the distributional limits of the Indiana bat (e.g., Alexander et al. 2006, Lyons et al. 2006). For example, on the Daniel Boone National Forest, plans call for burning upwards of 22,700 ha/year within the next decade (Mann 2006). Use of growing-season burning as a silvicultural and ecological restoration tool in mixed-oak forests has been proposed and causes concern about increased risks to bats from the direct effects of smoke, yet holds promise for improving bat habitat. Growing-season burning is an emerging issue for which scientific information is needed on attendant risks and opportunities for bats.

Widespread use of fire might have both direct (short-term) and indirect effects on bats. Direct effects include displacement, injury, and mortality. During fires, roosting bats may be exposed to heat from flames and the smoke plume. In addition, elevated concentrations of the products of combustion (e.g., carbon monoxide and irritants) occur over burn units and through the canopy. Exposure depends not only on fire behavior but also on roost characteristics, bat behavior, whether the bats are in torpor (a diurnal hibernation-like state, marked by a temporary decline in body temperature and metabolic rate), and bat gender and age. Risks from heat and gases probably would be greatest for nonreproductive bats in torpor, particularly if they are roosting near the ground or on dry landscape positions where smoke exposures are likely to be greatest. Reproductive female bats also use torpor though they appear to do so during conditions that would often not be conducive to burning. Arousal of bats from exposure to smoke in hibernacula is a concern relative to dormant-season burning. Bats arouse from hibernation periodically as a normal course of affairs, possibly because of the need to rehydrate, but each arousal is energetically equivalent to many days of hibernation (e.g., approximately 60 days for little brown bats [*M. lucifugus*] in the laboratory), and extra arousals from smoke exposure or other causes are a serious concern (Thomas et al. 1990, USFWS 2007a).

Indirect effects of fire on bats arise from fire-induced habitat change. Fire use is generally advocated as a way of improving bat habitat, through snag production, creation of more open stands preferred for foraging, and increased insect abundance and diversity (e.g., USDA FS 2003, USFWS 2007a). Fire, alone or in combination with thinning, may affect bat roost availability. Fires both create and destroy snags, with unknown long-term effects in eastern hardwood forests. Fires would be expected to reduce insect prey abundances in the short run, but their long-term effects on prey abundances are unknown.

Krusac and Mighton (2002) estimate that 5.5 million ha of lands managed by the USFS occur within the distributional limits of the Indiana bat, though not all forests contain summer habitat. The discovery in 1994 of a reproductive female bat on the Daniel Boone National Forest galvanized search and discovery of more reproductive females on other forests and, by way of the Endangered Species Act (1973), formal consultation between Forests and the USFWS. Since 1994, most National Forests within the range have revised their forest plans, including standards and guidelines intended to maintain and improve bat habitat and reduce risk to bats from management activities such as fire. State and private lands, which, combined, represent the majority of forest area in the East, presumably offer important habitat for bats, but little information is available on their importance for Indiana bats. Coordination efforts between state and private land managers and the USFWS have just begun.

Identifying the factors that have caused both the historical declines in Indiana bat populations, as well as recent increases, is central to recovery efforts (e.g., Caughley and Gunn 1995, USFWS 2007a). Authors have identified hydric habitats in the Midwest as core habitat supporting more robust maternity colonies than those that occur in upland forests, yet these habitats are severely diminished by conversion to agriculture and other land uses (e.g., Carter 2005). Research in the forested Appalachians has shown that foraging bats use riparian habitats more heavily than they use such upland sites as undisturbed stands and stands impacted by an array of forestry practices (Owen et al. 2004, Ford et al. 2005). Toxic effects of agricultural and other pesticides have potential, but unproven, negative consequences for bats (USFWS 2007a). The hibernation phase continues to be of concern because of bats' exacting microclimatic requirements; changes in hibernation patterns, perhaps owing to climate change; responses to ongoing cave disturbance; and, most recently, succumbing to white-nose syndrome during hibernation. Research and monitoring should continue to focus on the effects of bottomland hardwood habitat loss, pesticide toxicology, and hibernation problems on Indiana bat populations in order to identify the most effective management actions.

While hydric and riparian habitats are crucial to Indiana bats' life cycle, upland habitats are also used by Indiana bats for roosting and foraging during swarming, staging, and maternity periods. Furthermore, upland habitats are connected ecologically and hydrologically with riparian and hydric habitats. Because of the bat's endangered status, considerable efforts, including forest burning, are being made on Federal lands to maintain and improve summer habitat for Indiana bats, yet it is not possible to say whether these efforts are leading to gains in Indiana bat populations and, if so, why. Given low rates of upland burning relative to historical levels, it is worth considering whether fire suppression has a role in bat population declines and whether seasonal restrictions on burning are counterproductive. In this paper, as the data permit, we focus on the direct and indirect effects of fire on Indiana bats in upland mixed-oak habitats. We first report results of a field study on behavior of an Indiana bat surrogate species during and in the days after a prescribed fire and the results of a literature survey of Indiana bat roost characteristics and roosting behavior. Then, we discuss potential short-term effects of upland fires on bats and the longer-term effects of fire on bat habitat (see also Carter et al. 2002). Finally, we examine National Forest Plan standards and guidelines with relevance to fire management and adaptive management of Indiana bats.

OBSERVATIONS ON NORTHERN LONG-EARED BAT RESPONSE TO FIRES

The objectives of the following study were to document short-term behavioral response of tree-roosting bats to a prescribed fire. Longer-term responses will be reported in a forthcoming paper. Because no Indiana bats were captured as a part of this study, we chose the northern long-eared bat (*M. septentrionalis*) as a surrogate for the Indiana bat. The Indiana bat and the northern long-eared bat overlap in distribution, are similar in body mass and wing morphology, and form maternity colonies in live trees and snags during summer months (Foster and Kurta 1999, Carter and Feldhamer 2005, Lacki et al. 2008).

Methods

Study Area and Burn Unit

The Bear Waller unit is located in Red River Gorge Geological Area, Daniel Boone National Forest, Kentucky (37° 51'N, 83° 39'W). The terrain of the region is characterized by dissected valleys, steep ridges, cliffs, and rocky outcrops, with elevations ranging from 200-365 m (McGrain 1983). The forest community is typical of the Cumberland Plateau physiographic region in eastern Kentucky. Forest composition is primarily mixed mesophytic species,including several oaks (*Quercus* spp.), American beech (*Fagus grandifolia*), cucumber magnolia (*Magnolia acuminata*), maples (*Acer* spp.), tulip tree (*Liriodendron tulipifera*), white ash (*Fraxinus americana*), eastern hemlock (*Tsuga canadensis*), and several pine species (Jones 2005). 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.

The burn unit encompassed approximately 185 ha of uneven terrain and supported second-growth forest at the time of the burn event. A prominent ridgeline traverses the unit, where a storm blow-down occurred in the recent past. Thus, much of the ridgeline was overgrown with thick stands of greenbrier (*Smilax rotundifolia*) and red maple (*A. rubrum*) prior to burning. Two wildlife ponds are located in the immediate area, one of which is situated directly within the burn unit and is surrounded by a closed canopy of upland hardwoods. This pond served as the focal point for capturing bats. The burn unit was selected in collaboration with U.S. Forest Service personnel to meet both research and management needs. The burn unit had no history of management with prescribed fire; however, reports exist of "numerous fires having burned" within the original Cumberland purchase unit prior to 1930 (Collins 1975). An 8-ha wildland fire was documented near the center of the burn unit on Oct. 30, 1994.

The experimental burn occurred on April 30, 2007 and was conducted by Daniel Boone National Forest, Cumberland Ranger District staff. The ignition pattern consisted of igniting ridgelines with a drip torch and allowing the fire to back down slopes. Flame heights ranged from 0.2 to 2 m, but were typically <1 m. At the time of burn, new seasonal vegetative growth was abundant in the under- and overstory. Scattered smoldering and mid- and lower-slope flaming on the day after the burn produced low-level smoke exposures on ridges (see below); thus, the burn can be considered an early growing-season burn. Scattered snags and downed woody debris were found smoldering on the unit as late as May 9, 2007. For smoke monitoring, carbon monoxide sensors (Sixth Sense, Inc. Eco-Sense 2e electrochemical sensors with a custom electronics signal conditioning board) were placed at 2.4 and 6.1 m above ground on towers at three ridge locations within the burn unit.

Bat Capture and Tracking

We captured bats from April 22 to April 29, 2007 using nylon mist nets (Avinet Inc., Dryden, NY) of varying widths. Nets were placed over the wildlife pond at the interior of the burn unit. We recorded gender, reproductive condition, body mass, and forearm length of each captured bat. Our netting effort in the surrounding area in summer 2006, along with 2007, resulted in no Indiana bat captures, so we chose to use the northern long-eared bat as a surrogate.

We fitted five adult northern long-eared bats (four females and one male) with 0.36 to 0.42 g transmitters (LB-2N, Holohil Systems Ltd., Carp, ONT) between the shoulder blades using Skinbon® adhesive cement (Smith and Nephew United, Largo, FL). We held bats with transmitters for 20 to 30 min to allow the adhesive to form a secure bond between transmitters and the dorsal surface of bats. Before release, we observed bats to ensure normal behavior and, thus, the safety of the animals, and to verify that transmitters were working properly. Transmitter load was 5.8 to 8 percent of the bats' body mass.

We tracked radiotagged bats to roost trees each day with TRX-1000S receivers and three-element yagi antennas (Wildlife Materials Inc., Murphysboro, IL). Tracking continued until a transmitter battery failed or the transmitter was shed by the bat. Transmitters lasted for approximately 8 to 10 days and we report behavior up to 7 days post-burn in this paper. We determined coordinates for each roost tree using a geographic positioning system (GPS). For each roost tree we recorded species, whether the tree was alive or dead, height of the tree (m), and diameter of the tree (cm). When possible, we measured height of the roost (m), noted whether the roost was beneath a plate of bark or inside a crevice or cavity, and counted the number of bats exiting the roost on the night it was first discovered.

On the day of the prescribed burn, we located roost trees of each radiotagged bat prior to ignition at 1620 EST. Afterwards, two crew members were outfitted with receivers and stationed near roost trees known to be occupied by two of the radiotagged bats. A USFS Safety Officer monitored fire and smoke conditions near the telemetry crew to ensure a safety zone and an exit route. For safety reasons, the telemetry crew was required to work close to each other; thus, behavior of only two bats was monitored during the burn. Monitoring consisted of recording time of emergence, when bats were roosting or in flight, flight patterns, time spent in flight, and any other observations deemed pertinent. We monitored behavior of these bats until 1930 EST, at which time the general roosting positions of all five radiotagged bats was determined. On the day of the burn, we could not identify the specific roost trees of all bats prior to their exiting for nightly foraging because of time constraints and inaccessibility to habitats due to fire; however, by determining general roosting areas after the burn, we were able to confirm whether individual bats relocated during the fire.

Table 1.—Sex, reproductive class, body mass, and spatial data for northern long-eared bats radiotracked on and adjacent to the April 30, 2007, Bear Waller burn on the Daniel Boone National Forest, KY

Sex/ ID no.	Female reproductive class	Body mass (g)	Home range size (ha[a])	Pre-burn % locations (# locations)		Post-burn % locations (# locations)	
				on unit	off unit	on unit	off unit
Female (B5)	nonreproductive	5.25	64.9	100 (32)	0 (0)	75 (30)	25 (10)
Female (B9)	nonreproductive	5.25	59.1	no data[b]	no data	100 (24)	0 (0)
Female (B10)	nonreproductive	6.0	-[c]	no data	no data	no data	no data
Female (B11)	Pregnant	7.25	57.5	no data[a]	no data	23 (11)	77 (37)
Male (B7)	-	5.75	56.8	86 (32)	14 (5)	100 (45)	0 (0)

[a]Conversion to acres: 1 ha = 2.47 ac.

[b]Bats B9 and B11 were captured the night prior to the burn, so no pre-burn foraging data are available.

[c]Bat B10 was not located during nightly foraging in the vicinity of the burn unit.

Home Range and Habitat Use

We used triangulation to determine location of radiotagged bats during nightly foraging. Triangulation began after bats left their respective roosts and continued until at least midnight each night. Two to three crew members were stationed at high elevation locations and recorded their position with a GPS. Simultaneous azimuths were taken and estimated foraging locations were derived by means of triangulation (White and Garrott 1990). We recorded azimuths at 3 to 5 min intervals and communicated via hand-held radios. We tracked individual bats in alternating 30-min time periods. Foraging data were collected on nights before and after the burn. We did not collect foraging data on the first night after ignition as a safety precaution.

We entered telemetry station locations and azimuths into the Locate 3.19 program to determine bat locations (Nams 2006). In all cases, two azimuths were used to determine a bat location. Studies with other animal species have shown that use of >2 azimuths does not necessarily increase accuracy or precision when radiotracking (Nams and Boutin 1991). We limited home range calculations to bats with ≥ 30 locations, although 50 locations are considered to be optimal (Seaman et al. 1999). We used ArcGIS version 9.2 (ESRI, Redlands, CA) to calculate 95-percent home ranges using Hawth's Tools extension version 3.27 (Beyer 2004). We generated pre- and post-burn estimates of home range size for bats where data were sufficient. We evaluated use of the burn unit by bats while foraging relative to timing of the burn. We compared percentage of radiolocations on the burn unit to those off the burn unit before and after the burn and across radiotagged bats using a chi square test of homogeneity (Daniel 1974).

Results

Response of Northern Long-Eared Bats to Fire

Northern long-eared bats demonstrated an average home range of 59.6 ± 1.84 (SE) ha, with a male B7 possessing the smallest home range (Table 1). One female B10 was not recorded after the night of tagging and release. We had sufficient data to derive home range estimates for two bats pre- and post-burn. Female B5 demonstrated a home range of 41.4 ha pre-burn, which increased to 74.7 ha following the burn. In turn, male B7 possessed a home range of 60.9 ha before the burn, which declined to 46.1 ha post-burn.

Use of foraging habitat was significantly different among bats ($\chi^2 = 157$, df = 9, $p < 0.005$). Female B5 and male B7 spent the majority of time foraging over the burn unit, both pre- and post-burn (Table 1). Female B9, not tagged until just before the burn, foraged exclusively over the burn unit following the burn. Only female B11, the lone pregnant female that we tracked, foraged more often off the burn unit than over the burn unit after the burn was completed.

Northern long-eared bats were tracked to nine roost trees of four species, the majority of which were oaks (Table 2). Of these, 77.8 percent were live trees with

Table 2.—Description of roosts of northern long-eared bats located on the Bear Waller burn unit on the Daniel Boone National Forest, KY

Species	Live vs. dead	Roost type (m)	Roost height size	Estimated colony (cm)	Tree diameter (m)	Tree height
Quercus prinus	live	cavity	17.7	29	30.4	22.6
	live	-[a]	-	1	57.1	27.4
	live	crevice	22.9	29	53.5	29.0
Q. coccinea	live	-	-	6	37.3	24.7
	live	-	-	1	49.5	24.4
Q. alba	live	bark	7.6	1	36.5	32.0
Acer rubrum	live	-	-	1	24.3	21.3
Unknown[b]	dead	cavity	7.6	39	18.1	8.5
	dead	crevice	10.4	18	38.8	12.2

[a]Specific roost location could not be identified.
[b]Snags were in an advanced stage of decay, preventing species identification.

bats roosting in cavities and crevices and beneath bark. Diameter of roost trees averaged 38.4 ± 4.37 cm and ranged from 18.1 to 57.1 cm. Height of roost trees averaged 24.3 ± 1.86 m and ranged from 12.2 to 32.0 m. Height of roosts aboveground averaged 13.4 ± 2.96 m and ranged from 7.6 to 22.9 m. Maximum size of maternity colonies varied from 1 to 39 bats, with an average of 15.5 ± 5.41 bats. The lone roost recorded for male B7 was a white oak and he was the only bat observed exiting the tree.

Day of the burn. We were able to locate roost trees for four bats immediately before the burn; however, the roost tree of the remaining bat was known to be within the burn unit. The male and female bats we tracked during ignition operations and the main burning period (B7 and B9) displayed similar behavior. The ignition line ran within 20 m of roost trees of each bat, and both bats exited their roosts within 10 min of ignition near their respective roosts (between 1640 and 1650 EST). The two observers, one monitoring each bat, were approximately 30 m from the respective roost tree. Ambient temperature was approximately 31 °C (88 °F). Both bats flew for about 45 min after initially leaving their roosts, then roosted for about 1 hr. They cycled through periods of flight and roosting during the burn.

Because of burning conditions and safety constraints, we could not determine whether bats returned to their pre-fire roosts, but they did return to the vicinity. Both bats continued with an alternating flying and roosting pattern until sunset, when they emerged to forage. The time the bats spent roosting increased as the day progressed. While in flight, bats concentrated their activity over habitat that the fire had not yet reached, such as upland drainages that were slow to burn. Moreover, both bats were originally roosting on the north side of the burn unit near the ignition line; however, they chose to fly in the area opposite of the ignition line where the backing fire and smoke had not yet reached. We assume that bats were attempting to limit their exposure to conditions created by fire. At no point did they fly outside of their typical home range area, nor did they travel far from the burn itself. Although no behavioral data were collected for the remaining radiotagged bats, these bats behaved similarly to the bats that were monitored, all having switched roosts at some point during the fire. A roost tree that had been used by female B5 before the fire fell after its base was weakened by smoldering combustion; all other roosts remained standing. All bats were located within the burn unit following the burn.

Days 1 and 2 after the burn. Fire was still spreading in some areas of the burn unit the day after the burn and smoke was present on the unit and in adjacent forest. Peak carbon monoxide (CO) concentrations of 50-190 parts per million (ppm) were measured at 2.4 m aboveground at three stations on the second day compared with concentrations of 350 to ≥400 PPM during burning the first day (CO sensors saturated at 400 PPM on one of three stations). Concentrations of CO during the night after ignition approached background. Two sensors at 6.1 m failed so only 2.4 m data are provided as an indication of relative smoke concentrations during the second day. All five bats roosted near the core of the burn unit on the day after the burn. That night we observed very few insects flying within the burned area. We observed male B7 foraging farther away from where he had been typically foraging, moving down-slope, and closer to the burn unit boundary near areas that had not burned. Female B5 foraged normally for the first hour after emergence then altered her foraging behavior from previous nights by foraging in areas where she had not been recorded. She covered a considerable distance, sometimes leaving the range of detection. She returned to her usual foraging/roosting area at 0200 hr. It rained all day the second day following the burn and no data were collected.

Days 3-7 after the burn. It rained sporadically throughout day 3. Logs and stumps remained burning, with continued smoke production and haze. Flying insects were scarce. Female B10 shed her transmitter, and no signal was received on male B7. Although Female B5 was found roosting away from the burn site, we could not find the roost tree. That evening, she exited her roost and was tracked for about 30 min before we lost her signal. She was not recorded again that evening. Steady rain fell during days 4 and 5 after the burn and no tracking was attempted.

Despite the rain, some downed logs remained smoldering on day 6. Flying insects were more prevalent. No signal was received from female B5, but she returned on the evening of day 7 and foraged in the burn unit and surrounding habitats. Male B7 was observed foraging downslope near the burn unit boundary on the evenings of both days 6 and 7. From our observations, overall foraging behavior of all four remaining radiotagged bats during the evenings of days 6 and 7 appeared to return to pre-burn norms in terms of emergence time, length of foraging bouts, and use of the burn unit and adjacent habitats.

INDIANA BAT ROOSTING CHARACTERISTICS

We review studies which report information on roost trees in order to better quantify what constitutes a quality roost and to assess bat risk during fires relative to the aboveground height at which they roost.

Literature Review Methods

We used data available in published studies on summer habitat of the Indiana bat to examine frequency distributions of roost tree diameter and height and the height of roosting sites above ground (sources are provided in Lacki et al. 2008). We combined data from all habitats across the range of the Indiana bat, though lack of data prevented us from comparing maternity and other roosts and roosting behavior by gender. We evaluated predictive capability of roost characteristics by developing regression models of roost height as a function of tree diameter and tree height using mean values per published study and, where available, for individual roost trees (SAS Institute, Inc., Cary, NC, 2003).

Results

Too few data were available for male roosts and roosts used by both males and females to allow any comparison with female-only roosts. Hereafter, we focus on female-only roosts (primary maternity and other roosts combined). Individual roost data demonstrated that roost trees selected by female Indiana bats exhibited a modal peak at 40-cm diameter (Fig. 1a). Bats used trees of a wide range of heights, with a mode at 25 m (Fig. 1b). Height at which Indiana bats roosted demonstrated a distribution that was skewed left, with the modal peak at 10 m (Fig. 1c). The studies that report individual roost information, and which provided data for Figures 1a-c, largely included bottomland hardwoods and trees in swamps and it is not clear how relevant these data are to uplands. To avoid habitat-related bias, mean heights at which bats roosted reported in studies from across the bat's range were averaged, providing a mean roosting height of 9.12 m (N=13 studies, SD=2.14, 95% CI 4.92 to 13.3 m). From the few studies in which roosting heights were reported (Fig. 1c), the mean roosting height was 8.03 m (N=18 studies, SD=3.27, 95% CI 1.62 to

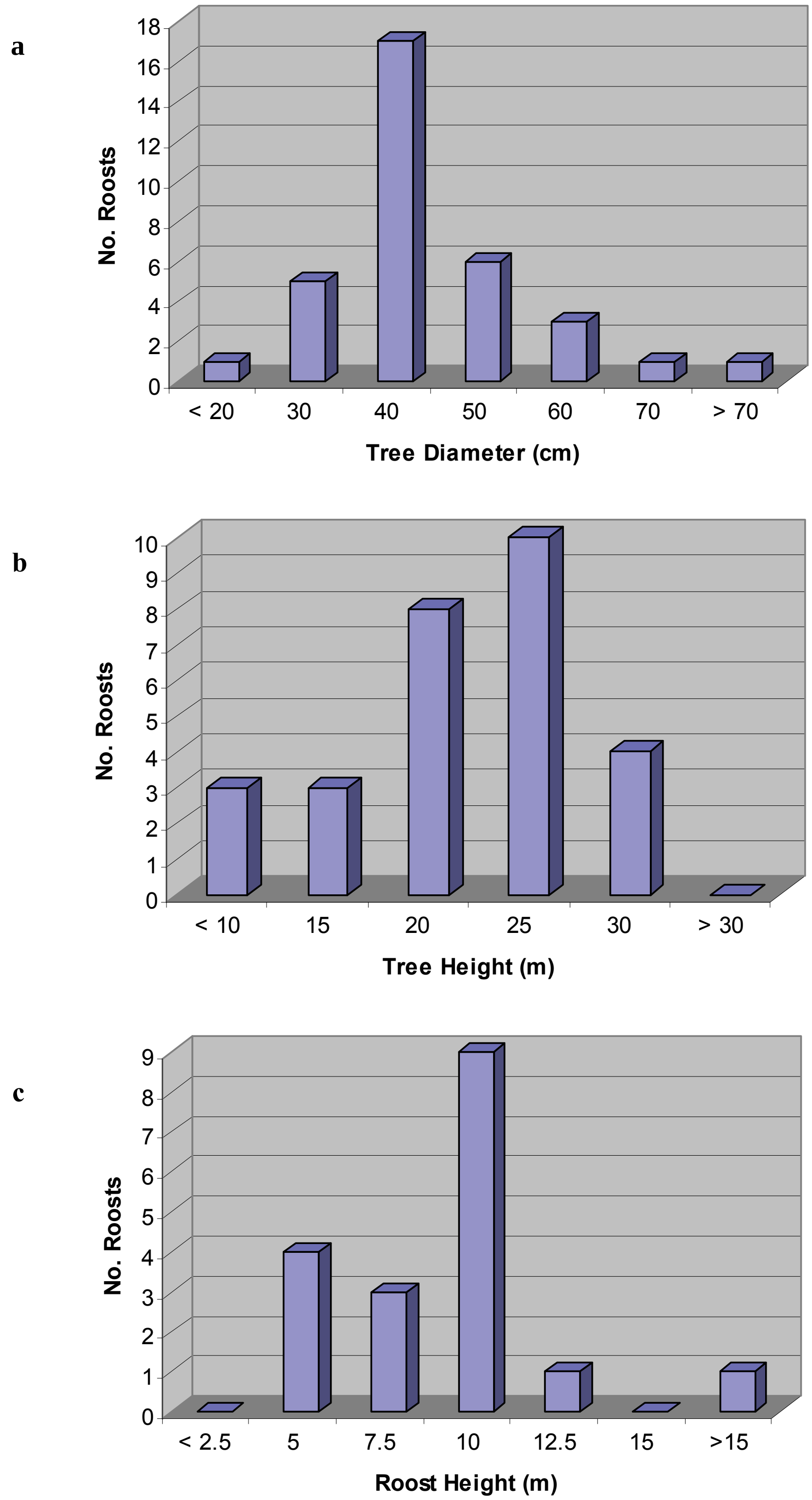

Figure 1.—Frequency distributions of female Indiana bat roost trees (maternity roosts and other) by (a) tree diameter, (b) tree height, and (c) roosting height aboveground. Sources for data are provided in Lacki et al. (2008).

Table 3.—Regression models predicting height of roosts aboveground for Indiana bats based on tree diameter (cm) and tree height (m). Models were developed using mean values per population, and data for individual roost trees where available. Published sources are from Lacki et al. (2008).

Form of data	Regression	R^2	F-value	P-value
Mean values per population	Roost height = 0.163(treediameter) + 2.75	0.27	4.15	0.07
	Roost height = 0.363(treeheight) + 1.77	0.33	5.47	0.04
Data for individual roost trees	Roost height = -0.04(treediameter) + 9.56	0.01	0.19	0.67
	Roost height = 0.135(treeheight) + 5.67	0.06	0.96	0.34

14.4 m). The lowest female roosting heights reported are 2 m (USFWS 2007b), 3.0 m (Belwood 2002), and 4.0 m (Butchkoski and Hassinger 2002).

From the few data that were available, male Indiana bat roost diameter averaged 34.0 cm (N=5, range 14-61 cm), tree height averaged 21.7 m (N=3), and roost height averaged 8.33 m (N=3). The diameter of combined male and female roosts averaged 33.2 cm (N=3) and there were no data for roost tree height and roosting height.

Regression models predicting the height aboveground of Indiana bat roosts demonstrated significant relationships with tree diameter and tree height when mean values per population were used for analysis (Table 3). Regressions based on these independent variables accounted for similar percentages of variation in roost height as indicated by R^2 values. These relationships did not hold up when data from the few studies where individual roost tree information was used for analysis, accounting for no more than 6 percent of the variation in height of roosts aboveground.

DISCUSSION

Short-term Effects of Fires on Tree-Roosting Bats

Smoke Effects in Summer Habitat

In prescribed surface fires, bats in roosts are exposed to gases and heat in the plume generated by the spreading fire. Exposures would depend on how high bats roost aboveground, bat physiological condition and flushing behavior, behavior of the fire (e.g., fuel consumption and fireline intensity), winds, terrain, and whether the canopy is leafless. If bats are in torpor or if flightless pups are present and too heavy to be carried, one can assume full exposure. Hot gases in the plume are mixed rapidly into the types of roosting sites (e.g., exfoliating bark, crevices) used by Indiana bats; these kinds of sites afford little protection (unpublished data, Guelta and Balbach 2005). Based on extrapolation from other species, incapacitation from carbon monoxide exposure would be expected if bats were exposed to ≥1000 PPM concentrations for 25 minutes or more and for shorter time periods if concentrations were higher (Spietel 1996). From our unpublished field data, incapacitating exposures are highly unlikely at any height above flames. Acting to reduce risk, irritants in smoke (e.g., acrolein, formaldehyde) cause an immediate reduction in breathing rate and depth (Chang et al. 1981). Elevated CO_2 levels would cause the opposite effect, but only if exposures were longer than several minutes (Purser 2002). Low breathing rates during torpor (e.g., Morris et al. 1994) would also reduce bat exposures to harmful gases.

A greater risk for bats might be external (skin) burns, which are a function of gas temperatures, their flow velocity, and skin properties (e.g., Diller et al. 1991). Skin burns could be a significant risk for bats roosting close to the ground and for those roosting at average heights above fires of intensities on the high end expected from prescribed burns (unpublished data). An ongoing project is analyzing smoke production and transport across burn units and bat toxicology for a range of prescribed fire scenarios.

From available observations, it seems reasonable to assume that bats exposed to smoke would flush if they could. All four northern long-eared bats located by radio tracking before and after a fire changed roosts during the burning period. A male and female bat tracked during the fire flushed within 10 minutes of nearby ignition, suggesting that both females and males were able to emerge from roosting sites in sufficient time (<10 min) to avoid direct impacts from heat and smoke produced by this prescribed fire conducted on a warm day. Roosting heights and roost characteristics for these northern long-eared bats were similar to those reported for Indiana bats, though most roosts were live trees (compare Table 2 and Fig. 1; see Lacki et al. 2008). Observations from other fires confirm our findings on bat movement during fires, for instance Rodrigue et al. (2001) report flushing of a roosting *Myotis* bat. Red bats (*Lasiurus borealis*) are a particular concern because they hibernate in the leaf litter during cold weather and have been shown to flush, or attempt to flush, from in front of fires (Saugey et al. 1989, Moorman et al. 1999). Rodrigue et al. (2001) also observed two red bats leaving a burn unit during a fire. Female bats are able to carry their young for some time after birth, which may reduce vulnerability (Carter et al. 2002). A drawback of flushing from fires is that bats may experience increased predation risk (Carter et al. 2002).

Risk Associated with Torpor

Risk to bats should be, in part, dependent on whether they are in torpor at the time of the burn and whether they can perceive a fire and arouse. Red bats, a species that roosts or hibernates on the ground during cold periods in oak forests, where fire is frequent, were shown to arouse in the laboratory at a 5 °C ambient temperature within 10-40 min in response to a combination of the sound of fire and smoke exposure (Scesny 2006). Little brown bats' arousal at 5 °C body temperature occurred in an average of 44 min (Thomas et al. 1990). Arousal time in a small insectivorous marsupial was found to increase exponentially as body temperatures tracked declining ambient temperatures (Geiser 1986); presumably, a similar pattern holds for bats (Carter et al. 2002).

Small mammals that use torpor often use energy available in their environment to passively maintain high body temperatures and facilitate rewarming (Hamilton and Barclay 1995, Lovegrove et al. 1999, Geiser and Drury 2003, Geiser et al. 2004). High solar exposure at Indiana bat maternity roosts aids in maintaining high body temperatures (USFWS 2007a). In contrast, male red bats in the Ouachita Mountains of Arkansas were found to prefer microsites with low solar exposure (north slopes and drainages) during hibernation in leaf litter, presumably because of the cooler and more constant temperatures they provided (Saugey et al. 1989).

It would be expected that pregnant or lactating female Indiana bats would use torpor less often than males and nonreproductive females because of a need to sustain high metabolic rates. Data from Kurta et al. (1996) demonstrated that adult female Indiana bats in Michigan sustained body temperatures of 35 °C for up to 12 hrs inside diurnal roosts and some bats sustained temperatures at that level for up to 6 consecutive days, suggesting that these individuals would be able to respond fairly quickly to an oncoming fire. On the other hand, studies on other species have demonstrated declines in body temperatures in reproductively active female bats after diet restriction, such as would happen after poor foraging success (Kurta 1991, Audet and Thomas 1997). Willis et al. (2006) demonstrated multi-day bouts of torpor in pregnant female bats during spring storms just prior to giving birth. Thus, at least periodically, maternity colonies may be at increased risk from fire because adult females may be in torpor. However, periods during which torpor is most likely would seem to coincide often with cool and/or wet periods and, thus, poor burning conditions.

Field studies found that male and nonreproductive female big brown bats (*Eptesicus fuscus*) select cooler roosts than reproductive females (Hamilton and Barclay 1995) and males enter torpor more regularly than reproductive females (Grinevitch et al. 1995). Given that male Indiana bats have a tendency to roost in smaller trees that are less exposed to solar radiation (Kurta 2005), we may assume that male Indiana bats also use torpor regularly. More data on roost microclimates and torpor dynamics for bats inside tree roosts and their relation to prescribed burn restrictions and prescriptions are needed to address issues of roost site selection and vulnerability of bats to prescribed fire (Boyles 2007).

Roost Characteristics

Roost characteristics, such as height above ground, snag condition, and landscape position, would also influence risk from fire. Because plumes radiate heat and mix rapidly with ambient air, the higher the roosting location on a snag or live tree, the lower the expected exposure to heat and gases, given similar fire behavior and ambient weather conditions. Our review of studies that provide Indiana bat roosting data (above, Lacki et al. 2008), particularly studies that compare roosts with random potential roosts (see Kurta 2005), support the expectation that reproductive and nonreproductive bats prefer larger than average, but otherwise suitable, roost trees. For fire effects, this preference is potentially important in that roosting locations in large trees tend to be higher above ground (Table 3, Kurta et al. 2002). Even though we found considerable variability in Indiana bat roost-tree height, data suggested that a minimum height of approximately 10 m is necessary before a live tree or snag is sufficiently tall to be desirable as even a secondary roost tree. Decay patterns of snags often lead to the loss of the top of the stem, reducing the height of the snag (Hunter 1990).

Fire Behavior

Smoke exposures determined by fire behavior are a realm over which the fire manager has substantial control through choice of burning conditions and firing methods. Fire managers are well versed in using ignition to influence fire behavior and fire effects on vegetation. In an ongoing fire-monitoring project on Appalachian landscapes, we documented the dramatic differences in heat and smoke release rates from ridge ignition (where the bulk of behavior is low-intensity backing spread) and a combination of helicopter ignition and strip head firing (where more high-intensity uphill runs occur). On flat ground, low heat release rates (where heat release rate is proportional to flame length and fireline intensity, kW/m) and the presence of wind will result in reduced exposures to high temperatures in plumes (Mercer and Weber 1994).

Terrain complicates exposures because of upslope flow of smoke and potential positive feedbacks between the plume and the fire. Smoke rising off burn units in a single plume core would be expected to cause increased gas and heat exposures in the canopy where the plume is centered relative to exposures resulting from smoke that is distributed among multiple plume cores (Achtemeier, this volume). In hilly landscapes, we would expect plume cores to be located along ridgelines above dry slopes and result in the greatest smoke exposures in those locations. We would expect lower exposures to daytime smoke at roosts at lower elevations and in landscape positions that provide topographic shading during the fire season (e.g., north-facing slopes during the winter and early spring).

Choice of burning weather and season are well-known methods of manipulating fire behavior and, thus, smoke exposures. Burning weather, of course, affects fuel moisture and winds, both key determinants of smoke production rates and transport. Evidence suggests that growing-season burns in mixed-oak forests are more effective as a tool for control of oak competition than dormant-season burns (Brose and Van Lear 1998), and should often be less intense because of more fuel shading, lower litter loads, and higher humidity. In addition, bats in torpor during the growing season may arouse more quickly than in the dormant season given higher ambient temperatures. An interesting feature of growing-season burning relative to smoke exposures will be the effect of the canopy, with smoke expected to disperse less readily through a leafed-out canopy in general and to exit the canopy preferentially through gaps.

Smoke Exposures in Hibernacula

Smoke intrusion into hibernacula is a concern because of the potential for inducing arousal in hibernating bats. Though no Indiana bats were present, one study documented smoke intrusion into hibernacula in Missouri, but no arousal was observed (Caviness 2003). Except at the northernmost part of the distribution of Indiana bats, suitable hibernacula require chimney-effect airflow and large cold-air traps to maintain ideal temperatures, which are below annual mean ambient temperature (Tuttle and Kennedy 2002). Chimney-effect airflow occurs when two cave or mine entrances are at different elevations and outside temperatures fall below the annual mean (which is approximated by the cave walls); air flows out of the upper entrance and in the lower entrance (Tuttle and Taylor 1998). This airflow creates the potential for smoke intrusion into hibernacula

(Carter et al. 2002) perhaps especially during cold fall, winter, and spring nights. Nighttime inversions during this period may be of particular concern and inversion climatologies, where seasonal climate and landscape characteristics are used to determine the potential for smoke accumulation (Ferguson et al. 2003), may be a good place to start for evaluating risk to individual hibernacula.

Fire and Bat Habitat

Fire may have short-term effects on bats through heat and gas exposures, but fire also affects bat habitat. Habitat effects have been assumed to include increased roost availability, facilitation of foraging from reduced clutter, and increased insect prey productivity (USDA FS 2003, USFWS 2007a). Roost availability is dependent on both the quality of individual roosts and the population dynamics of roosts. For Indiana bats, the epitome of a high-quality primary maternity roost appears to be a large dead tree, exposed to solar radiation, with large plates of sloughing bark (Kurta et al. 1993, Foster and Kurta 1999, Carter and Feldhamer 2005, Lacki et al. 2008). Alternate roosts, including live trees and other snags, are also important even though they shelter relatively few bats and seemed to be used mostly during periods of warm ambient temperatures and high precipitation (Humphrey et al. 1977, Gardner et al. 1991, Kurta et al. 1993, Miller et al. 2002). Maternity colonies may occupy one or more primary roosts. Males use smaller trees than females, on average (Kurta 2005).

Published data on summer-roosting behavior of Indiana bats, including nonreproductive males, suggest that bats select roost trees based on size (e.g., diameter) and that stands possessing trees exceeding 40 cm diameter at breast height (d.b.h.) are more likely to provide adequate maternity habitat for this species (Fig. 1). Our literature survey results are based on the roost trees that were available to bats on the landscapes they use. Given the documented preference for larger- than-average roost trees (Kurta 2005), it is likely that even larger roost trees would have been used if they had been available to bats in the published studies. Along these lines, Callahan et al. (1997) recommended promoting the development of forested stands possessing large-diameter, mature trees to provide adequate maternity habitat for the Indiana bat. Further, Carter and Feldhamer (2005) suggested that snag creation within stands of mature timber may be necessary for sustaining maternity habitat of this species in perpetuity. An implication of our results showing the importance of tree size is that, when calculating potential densities of snags and live roosts in forested stands to evaluate quality of maternity habitat for Indiana bats, managers should place the greatest weight on potential roost trees ≥ 40 cm in diameter and ≥ 10 m in height. Further, because Indiana bats prefer roosting sites beneath exfoliating bark to cavities or crevices (Kurta et al. 1993, Carter and Feldhamer 2005, Lacki et al. 2008), the presence of this habitat characteristic on snags should also be used as a criterion for counting a snag as potentially suitable.

Boyles and Aubrey (2006) found that reintroduction of prescribed fire into mixed-oak forests after decades of fire suppression resulted in a striking increase in evening bat (*Nycticeius humeralis*) roosting compared with adjacent unburned forest. They attributed the effect on this cavity-roosting bat to the high tree mortality after the first burn, which increased both the exposure of existing snags and the density of snags. MacGregor et al. (1999) found that male Indiana bats did not consistently use prescribed burned units for roosting in greater than expected proportion to their area on the landscape, though it is not clear how fires affected snag availability. Two-age shelterwoods in the same landscape in which snag and live roost retention guidelines were in place showed greater-than-expected roosting by male Indiana bats, lending support for future studies in which Indiana bat responses to shelterwood-burn treatments are analyzed.

Populations of large snags suitable for roosting are the result of a balance between canopy tree mortality rates and how long snags retain their preferred characteristics. In eastern mixed-oak forests, tree mortality rates range from 1-3 percent/year, but much of that mortality is of smaller, suppressed stems (Parker et al. 1985, Wyckoff and Clark 2002). Injury from low-intensity surface fires after long periods of fire suppression in southeastern Ohio appeared to add incrementally to the mortality of large canopy trees that were at risk before burning (Yaussy et al. 2004). Reintroduction of fire to long unburned stands can cause high rates of overstory mortality (Boyles and Aubrey 2006, Anderson and Brown 1983) as can high-intensity fires (Regelbrugge and Smith 1994, Moser et al. 1996). Although bat habitat may be improved over the short term because of these often patchy mortality events, the events tend to occur on sites that support intense fire behavior (e.g., slopes and topographically dry and exposed sites) and a return of high quality roosting habitat to those landscape positions after snags have become unsuitable for roosting would take a very long time. Avoiding high tree mortality adjacent to hibernacula would also be prudent, given ensuing microclimatic changes that may not be favorable to hibernating bats (Carter et al. 2002).

High mortality rates of large, old trees has been recognized where fire has been reintroduced into long-unburned stands of longleaf pine (*Pinus palustris* Mill., ponderosa pine (*Pinus ponderosa*), and larch (*Larix laricina*); extensive duff accumulation results in root consumption and basal heating (e.g., Varner et al. 2005, Kolb et al. 2007). Large, old trees may be inherently more susceptible to dying from a given level of injury because of their physiological characteristics (see Kolb et al. 2007). It is not clear that fire in eastern mixed-oak forests would ever lead to preferential mortality of large trees, as opposed to small trees, if only because of the lack of extensive basal duff accumulation. Efforts to use fuel management (e.g., planned felling or redistribution of tops during shelterwood operations) and ignition strategies to kill individual or small groups of potential roosts would merit attention.

Apart from the creation of snags, the longevity of suitable snags is also an important determinant of snag availability. Studies that follow snags from year to year have found that roosts are used from 2-6 years (Kurta 2005). Of recently dead trees, only a portion will develop patches of exfoliating bark suitable for roosting, though it is not known what fraction that is and what determines the propensity for bark exfoliation. Fires not only create snags by killing trees, some of which may be live roosts, but also fell snags through the structural weakening caused by smoldering combustion (Carter et al. 2002). Experience suggests that snags are drier, and smolder more readily, during late spring burns (Michael Bowden, Ohio Division of Forestry, personal communication). Snag loss may be more of a problem in late summer and fall burns after dry periods when duff is dry and consumes more readily (K. Moore and E.J. Bunzendahl Wayne National Forest (KM), Daniel Boone WF (EJB), personal communication). Bats using maternity roosts in riparian habitat, and the roosts themselves, may be least vulnerable to fire because fire intensities in these landscape positions tend to be low (Carter et al. 2002).

Snag species composition across the range of the Indiana bat suggests that a range of tree species (though not all) form suitable snags and local availability largely determines which tree species bats use (Kurta 2005, USFWS 2007a). Fire-maintained oak-hickory forests would be expected to maintain a species composition suitable for Indiana bats (USFWS 2007a). Tree species that consistently form high quality live roosts include shellbark hickory (*Carya laciniosa*), shagbark hickory (*C. ovata*), and white oak (*Quercus alba*). Oaks, particularly of the white oak group, are favored by low-intensity fire (Abrams 2005) while oak and hickory regeneration has been shown to be favored by repeated fires below open canopies (Iverson et al. 2008). Live roost trees are less ephemeral than snags and provide secondary roosts for maternity colonies and roosts for nonreproductive bats, yet most trees occupied by Indiana bats during the summer are snags (Kurta 2005).

A first step to setting targets for potentially suitable roosting habitat would be to determine adequate roost densities and spatial distribution. Unfortunately, there is a paucity of data available on these topics (Lacki et al. 2008). However, studies of Indiana bat primary and secondary roosting behavior have shown that bats show high fidelity to individual roosts. Even though they switch roosts roughly 2 days, on average, Indiana bats often return to previously used roosts, supporting efforts to protect known roost trees until they become unsuitable. Indiana bats also show fidelity within and among years to roosting areas 1 or more km in extent (Gumbert et al. 2002, Kurta et al. 2002). Because bats in a single maternity colony are dispersed among various roosts at any given time (Kurta 2005) and because of across-year fidelity to roosting areas (also see Humphrey et al. 1977, Kurta and Murray 2002), the supply of primary and secondary roosts must be maintained over areas of tens of square kilometers, an area larger than single burn or harvest units.

Fire and Foraging

Fire may affect foraging habitat in at least two ways: through effects on forest structure and through effects on insect prey productivity and community structure. Foraging habitat, and the effects of fire, may be particularly important for maternity and staging areas, where bats have high demands for insect prey (Carter et al. 2002). Indiana bats are aerial feeders, whose short, broad wings, rounded wingtips, and echolocation characteristics are suitable for foraging in forests (Norberg and Rayner 1987). Indiana bats have been observed to feed primarily around tree crowns, not within them, occasionally descending into the midstory and shrub layers (Humphrey et al. 1977). Lee and McCracken (2004) found that, in sympatry with other *Myotis* bats, Indiana bats foraged higher above ground. For these reason, it has been hypothesized that Indiana bats would prefer foraging in more open stands (e.g., USFWS 2005). Historical forest and uneven-age timber management prescriptions involving low-intensity fire that are being implemented on National Forests in the mixed-oak region would reduce understory and mid-story clutter (Arthur et al. 1998, Elliott et al. 1999, Blake and Schuette 2000, Hutchinson et al. 2005) and, if repeated over the long term, would reduce density of the upper canopy (e.g., Huddle and Pallardy 1996, Peterson and Reich 2001).

Data on Indiana bat foraging casts some doubt on the potential benefits of stand thinning by fire, though Indiana bat foraging in burned forest has not been studied directly. In Appalachian landscapes of West Virginia, Indiana bats were found to use forested riparian habitats most heavily and, where recorded in uplands impacted by a variety of forestry practices, were detected most frequently in areas with the highest canopy cover (e.g., Owen et al. 2004, Ford et al. 2005). Using sonic detectors, Titchenell (2007) found that *Myotis* bats (no identification to species, yet unlikely to have included Indiana bats) showed no difference in foraging behavior between control and shelterwood stands, yet other bat taxa foraged more intensively in shelterwoods. Loeb and Waldrop (2008) found overall preference for thinned pine stands among non-*Myotis* bats, and, again, response varied among species. Complicating matters, interspecific interactions have been shown to affect when and where Indiana bats forage (e.g., Lee and McCracken 2004).

Knowledge of the diet of Indiana bats could help provide a target for monitoring and management. From a limited number of studies, it appears that the diet of Indiana bats foraging primarily in upland forests is dominated by moths (Lepidoptera) and beetles (Coleoptera, see Brack and LaVal 1985, Murray and Kurta 2002). Lepidoptera also dominated diets of bats foraging in riparian habitats (e.g., Belwood 1979, Lee and McCracken 2004), while bats foraging over wetlands in Michigan consumed primarily the adult stages of aquatic insects (Kurta and Whitaker 1998). Diet studies which concurrently sampled both bat diets and nocturnal insect abundances indicated a preference for Lepidoptera by Indiana bats as opposed to a diet determined solely by random encounter rates (e.g., Brack and LaVal 1985, Lee and McCracken 2004).

Unfortunately, there is a paucity of information on insect prey availability for bats in central hardwood forests and its relationship with forest management activities, including fire (Rieske-Kinney 2006). A study of pollinators in oak-dominated stands in the southern Appalachians found that a combination of mechanical shrub control and fire resulted in greater abundances of beetles and butterflies (Lepidoptera) compared with burning or mechanical treatments alone or no treatment, and that these increases were related to increased herbaceous cover where canopy cover was most reduced (Campbell et al. 2007). Whether these increases in abundance would translate into greater (nocturnal) prey availability for bats is not known. Fires in mixed-oak forests have a negative effect on litter-dwelling mites and collembolans and there have been mixed results in using fire to control gypsy moths and acorn-predating weevils (see Rieske-Kinney 2006). Low- to moderate-intensity fire had no effect on palatability of two overstory tree species to gypsy moth larvae (Rieske-Kinney et al. 2002).

Wildlife managers express concern that prescribed fires in the late dormant season and spring reduce bat prey abundances during the critical period when bats

Table 4.—National Forests that consider Indiana bats in their forest plans. Presence of hibernacula in a National Forest, or within its proclamation boundary, and bat summer status were determined from the latest USFS monitoring report, USFS Programmatic Biological Analysis, or USFWS Programmatic Biological Opinion. Number of hibernacula is given in parentheses.

National Forest	State	Forest plan revision	Standards and guidelines	Hibernacula	Bat summer status
Allegheny	Pennsylvania	2007	Part 3	No	Two males captured
Cherokee	Tennessee	2004	Chapter 2	No	Three post-lactating females documented in 2006 (apparently upland roosts)
Daniel Boone	Kentucky	2004	Chapter 2	Yes (>15 w/in Forest)	Seven maternity colonies documented, 90 total records
George Washington and Jefferson	Virginia	2007 (draft)	Chapter 3	Yes (4)	No known maternity colonies, no mistnetting conducted
Hoosier	Indiana	2006	Chapter 3	Yes (1)	Two maternity colonies documented, first in 2004 (apparently upland)
Huron-Manistee	Michigan	2006	Chapter 2	Yes (1)	Two males captured during swarming
Mark Twain	Missouri	2005	Chapter 2	Yes (4)	Two known maternity colonies, male roosts identified
Monongahela	West Virginia	2006	Chapter 2	Yes (15)	One known maternity colony
Nantahala-Pisgah	North Carolina	1994	Amendment 10 (released in 2000)	No	One known maternity colony
Ozark	Arkansas	2005	Part 3	Yes (8)	>1 maternity colony, females foraging in riparian and upland habitat, various male bat captures
Shawnee	Illinois	2006	Appendix H	Yes (2)	Two known maternity colonies in bottomland hardwoods, male roosts in one cave and three mines
Wayne	Ohio	2006	Chapter 2	Yes (2)	Reproductive females captured, maternity colony/colonies assumed present

are coming out of hibernation, are migrating, and females are pregnant. Unanswered questions include the magnitude of reduction in prey abundances, how long those abundances remain depressed, and whether fire ultimately increases foraging success (through both prey availability and improved forest structure for Indiana bat foraging). Another open question is whether increased water yields from fire-maintained watersheds in the central hardwoods would translate into greater insect productivity in riparian areas with benefits to bats foraging on emerging adults (e.g., Beck et al. 2005).

In light of both the potential negative effects of fires on bats over the short term and the potential longer-term benefits, it is useful to consider the size of burn units in relation to the size of bat home ranges. There is a large range in reported mean home ranges, in one review spanning 81 to 668 ha (USDA FS 2007). Indiana bats may travel long distances to foraging areas, so roosting areas may be separated from foraging areas. Burn unit sizes are on par with mean home ranges and, if burning is done near known maternity colonies, it would be prudent to locate burn unit boundaries so that entire home ranges are not burned over in a single year or to conduct the burns in a way that creates a patchwork of burned and unburned areas (e.g., using ridge ignition, which leaves mesic areas unburned).

Fire and Bats on National Forests

We reviewed the current forest plans for the National Forests that lie within the distributional limit of the Indiana bat for information pertaining to standards and guidelines relative to the Indiana bat (Table 4). Forest Plan standards are attainments that must be reached or courses of action that must be followed to mitigate the effects of land management activities while guidelines are expected to be followed in most circumstances. Forest plans are required by the National Forest Management Act and are revised periodically and amended as needed. Individual projects must go through National Environmental Policy Act analysis, including biological assessments for project effects on Indiana bats, where present. Burn plans further specify how burns will be conducted to minimize risk to bats, where applicable.

Since 1994, nearly all National Forests within the range of the Indiana bat have requested formal consultation with the USFWS relative to their forest plans, resulting in the issuance of non-jeopardy biological opinions and associated incidental take statements (Krusac and Mighton 2002). Formal consultation is a negotiation between the land management agency and the USFWS that is intended to result in a balance between the need to conduct land management activities and the need to minimize, but not eliminate, "take" of Indiana bats (e.g., mortality and disturbance). Thus, forest plan standards and guidelines are not as restrictive as they are when the objective is to eliminate all "take." Many forest plans have been revised recently and often include extensive consideration of Indiana bats (Table 4). Because forest plans are reflective of local conditions and the particular interaction between Forest and USFWS field-office staff, generalization is difficult.

Private and other public landowners can also enter into negotiations with the USFWS to develop Habitat Conservation Plans (HCPs) that would allow incidental take statements to be issued. The state of Indiana's Division of Forestry is currently developing an HCP for Indiana bats and is expected to be the first non-USFS land management entity to receive an incidental take statement.

A sense of bat abundance on Forests can be obtained from monitoring and evaluation reports and biological opinions and assessments (Table 4). Monitoring data are not collected or reported in a standardized fashion across the range and information is often qualitative, so comparisons are difficult. Several Forests have documented only the presence of male bats and others have identified only a few maternity colonies. Maternity colonies occur in both uplands and bottomland/riparian habitat on National Forests. It is apparent from monitoring and evaluation reports that there has been little attempt to follow sampling designs that would allow a Forest to determine whether standards and guidelines were leading to improved Indiana bat performance. Regardless, the relatively few bats documented in many forests would make it difficult to detect effects of habitat modification.

Forest plans in and of themselves do not preclude growing-season burning outside of occupied roosting habitat on most of the National Forests within the range of the Indiana bat. Growing-season burning is well established on the Ozark National Forest in Arkansas. Most Forest Plans prohibit burning in the few known maternity areas (areas that include roosts and associated foraging habitat) during the roosting period. The roosting period, when defined, spans the period from May 1 (earliest date is April 15) to late summer or fall (the earliest end-date is July 31; the latest is Nov. 15). Some Forests require surveys to determine whether bats are present before burning can be done in potential roosting habitat during the roosting period. The most restrictive prescription appears to be that in place for the Shawnee National Forest, where no upland burning is allowed from May 1 to September 1. Even the May 1 restriction allows burning during late spring bud burst. Before 2006, the Monongahela National Forest (West Virginia) was restricted to 120 ha of burning per year (USDA FS 2006), but, as with other Forests in the region, is working to increase their use of fire for oak ecosystem management. Given current restrictions, growing-season burning past the bud-burst stage would appear to be possible on a handful of forests, at least on an experimental basis.

Fire practitioners have expressed concern that date restrictions on live tree and snag removal in recent biological opinions (e.g., Whitebreast Creek and Fort Drum Connector Projects (USFWS 2009b) have been set back to March 31 from mid-April and that burn restrictions may also be tightened to avoid incidental "take" of Indiana bats. Concerns about date restrictions highlight the need for focused research on both the short-term and long-term effects of fires on bats and their habitats so that the negative effects of growing-season burning can be balanced against any positive effects of such burning on habitat.

Forest plans establish standards and guidelines for preventing smoke intrusion into hibernacula. The Wayne National Forest Plan prohibits prescribed burning within a defined hibernacula zone while the George Washington and Jefferson National Forests prohibit burning in a hibernacula zone unless it could be assured that no impact would occur. The Hoosier, Huron-Manistee, and Mark Twain National Forests prohibit burning during swarming and staging periods. The Hoosier, Mark Twain, Ozark-St. Francis, Shawnee, and Wayne National Forests call for best smoke management practices to be used relative to hibernacula. No mention of prescribed burning and hibernacula is made in the Monongahela and Daniel Boone National Forest plans. In these Forests, consideration of smoke management around hibernacula is left to project planning and burn plans. Forests with no known hibernacula (Allegheny, Cherokee, and Nantahala-Pisgah National Forests), of course, make no mention of hibernacula in reference to burning.

Standards and guidelines governing snags and potential live roosts differ among Forests and among silvicultural treatments within Forests. Live roost retention (e.g., shagbark and shellbark hickory and other trees with suitable bark characteristics) varies from retention of all shagbark and shellbark hickories (e.g., Allegheny and George Washington and Jefferson National Forests) to their retention in the context of the availability of other live roosts and the silvicultural system being employed. The regeneration system of most interest relative to burning in mixed-oak forests is some form of shelterwood (e.g., Brose et al. 1998, 1999), though there is some potential for using fire in clearcuts to benefit oaks (Michael Bowden, personal communication). Shelterwood standards and guidelines, where provided, include provisions for future snags and provide targets for snag densities by size class. Often the lower size limit on snags is between 10 and 25 cm d.b.h., a size that is considerably smaller than the median Indiana bat roost (Fig. 1).

Apart from forest plans, forestwide (programmatic) biological assessments (e.g., USDA FS 2005) and their associated biological opinions (e.g., USFWS 2005) are available for Forests and are good places for state and private land managers to find information on the Indiana bat and land management as they develop their own programs. The Indiana Bat Recovery Plan (USFWS 2007a) has rangewide scope and is also a good source of information. The USFWS website dedicated to the Indiana bat contains a variety of documents and other useful information (USFWS 2009a).

CONCLUSIONS AND RECOMMENDATIONS

Prescribed fires cause roost-switching behavior in tree-roosting bats that would reduce their exposure to smoke. Extensive use of torpor by roosting males and nonreproductive females would increase their risk of smoke exposure, though use of torpor and arousal times under typical burning conditions are unknown. Reproductive females are generally expected to maintain high body temperatures and, thus, be able to respond quickly to fires. However, use of torpor by pregnant female bats during spring storms has been demonstrated. Forest managers can reduce risk to tree-roosting bats by reducing fuel consumption, which determines the quantity of smoke produced, and fireline intensity, which drives smoke transport. Burning under relatively high ambient temperatures, for example, from late April through May, after bats have dispersed to their summer habitat, may also reduce risk, though data on the use of torpor are needed. Given demonstrated roost switching behavior, the critical risk period for bats may not be when maternity colonies are formed, but later, when flightless young are present. Further research may show that early growing-season burning, as opposed to burning during the vegetative dormant season, may be done at lower intensities during warmer weather and may result in more desirable fire effects on vegetation with manageable risks for bats.

Smoke exposures in hibernacula would be expected to pose problems if they cause extra arousals, though arousal thresholds for hibernating bats are unknown. Given treatment of hibernacula as smoke-sensitive targets, and the smoke management efforts that this designation entails, it is unlikely that toxicity from high gas concentrations themselves will be problematic, only arousal from exposures to relatively low smoke concentrations. Smoke intrusion into hibernacula of species other than Indiana bats has been documented. For Indiana bat hibernacula, smoke intrusion is most likely when hibernacula are exchanging air under conditions when nighttime temperatures drop below the annual mean. A better understanding of risk requires increased knowledge of arousal response to smoke by hibernating Indiana bats and information on air flow in individual hibernacula.

Fires in upland mixed-oak forests are expected to improve roosting and foraging habitat for Indiana bats by increasing the availability of suitable snags, reducing canopy clutter, and increasing long-term insect prey availability. Unfortunately, the data basis for these expectations is poor to mixed. For instance, the long-term tradeoff between snag creation and snag loss in mixed-oak forests under burning regimes is unknown. Data on foraging activity show Indiana bat preference for relatively closed-canopy stands, casting doubt on the benefits to foraging that would arise from the stand thinning caused by forest burning. Explicit studies on the benefits of forest burning on Indiana bat foraging habitat are needed.

Fire has been recommended on National Forests in two relatively incompatible contexts: as a tool for well regulated oak silviculture and as an imperative for oak ecosystem restoration and maintenance. Given Indiana bat fidelity to roosting and foraging areas, upland maternity areas might serve, on an experimental basis at first, as focal areas for oak ecosystem restoration and maintenance where burning is used to try to increase local roosting populations and their reproductive success. A regional approach to oak ecosystem conservation and monitoring on National Forests has been proposed (Yaussy et al. 2008) and, if designed properly, has the potential to add to our understanding of Indiana bat response to forest thinning and burning. Currently, adaptive management relative to Indiana bats is not possible because monitoring programs are poorly funded and not designed to assess the effects of land management activities on bat populations. Furthermore, few research projects have addressed the central questions about fire and Indiana bat habitat. The current state of knowledge is a poor foundation on which to base upland management activities and to determine whether existing, or any further, date restrictions on burning on National Forests are counterproductive for Indiana bat conservation.

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