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ROOSTING ECOLOGY OF BATS IN A DISTURBED LANDSCAPE

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**Dissertation submitted to the
Davis College of Agriculture, Natural Resources and Design
at West Virginia University
in partial fulfillment of the requirements for
the degree of**

**Doctor of Philosophy
In
Forest Resources Science**

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Division of Forestry and Natural Resources

**Morgantown, West Virginia
2010**

**Keywords: Anabat, Fernow Experimental Forest, fission-fusion, *Myotis septentrionalis*,
Myotis sodalis, microsatellite, night-roosting, prescribed fire, roost selection, West Virginia**

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ABSTRACT

Roosting Ecology of Bats in a Disturbed Landscape

Joshua B. Johnson

Increased attention has focused recently on the conservation and management of bats because of their important ecological roles as nocturnal insectivores and as possible bio-indicator species. Worldwide, many bat species have experienced dramatic population declines attributed to numerous anthropogenic environmental changes such as conversion of forests to agricultural or residential uses, and water pollution. In the eastern United States, efforts to promote species recovery largely have focused on protection of hibernacula, which has led to increases in populations of several endangered species. Although protection of hibernacula is undoubtedly important, the full range of habitats used seasonally must be taken into account when considering effective conservation and management strategies. Unfortunately, recovery plans often simply rely on the paradigm of habitat preservation or passive management, rather than proactive attempts at habitat enhancement through modification and management. Indeed, active habitat management may be a more effective means by which to encourage recovery of bat species.

Throughout the Appalachian Mountains and Central Hardwoods forest regions, insufficient retention and/or regeneration of hard-mast producing oaks (*Quercus* spp.) and hickories (*Carya* spp.) in both managed and unmanaged forest stands is a major concern of forest and wildlife managers. Oak regeneration can benefit from a combination of prescribed fire and forest canopy alteration. Following decades of fire suppression in eastern forests, using prescribed fire as a tool to restore or enhance oak-dominated communities is gaining widespread acceptance in the Appalachian Mountains and elsewhere. In addition to fire, overstory thinning by tree removal, girdling, or herbiciding of competitors, can augment oak seedling initiation and survival through reduced competition and increased canopy openness. These methods could increase snag abundance that in turn could benefit snag-dependent wildlife species, including bats. The potential of using prescribed fire to create suitable roost conditions, in either live trees or snags, for bats, largely is an unexplored, but a potentially contributory area of research.

For tree-roosting bats, fire can enhance roosting habitat by creating snags and increasing solar radiation at existing roosts. In 2007 and 2008, I examined roost selection of forest-interior dwelling northern myotis (*Myotis septentrionalis*) maternity colonies in stands treated with prescribed fire (hereafter, fire) and in unburned (hereafter, control) stands on the Fernow Experimental Forest, West Virginia. Using radio telemetry, I tracked 36 female northern myotis to 69 roost trees; 25 in the fire treatment and 44 in the control treatment. Using logistic regression and an information-theoretic model selection approach, I determined that within the fire treatment, northern myotis maternity colonies were more likely to use cavity trees that were smaller in diameter, higher in crown class, and located in stands with lower basal area, gentler slopes, and higher percentage of fire-killed stems than random trees. Moreover, roosts often were surrounded by trees that were in the upper crown classes. In the control treatment, northern myotis were more likely to roost nearer the tops of larger diameter cavity trees in early stages of decay that were surrounded by decaying trees in the upper crown classes than random trees. Roost trees in the fire treatment were associated with larger overall canopy gaps than roost trees within the control treatment. Regardless of treatment, northern myotis maternity colonies roosted

in black locust (*Robinia pseudoacacia*) in greater proportion than its availability. Ambient temperatures recorded at a subset of roost trees in fire and control treatments indicated that daily minimum temperatures were similar, but daily mean and maximum temperatures were higher in the fire treatments, possibly due to larger canopy gaps created by the senescence and decay of the surrounding fire-killed overstory trees. Northern myotis roost-switching frequency, distance between successive roosts, and duration of individual roost tree use were similar between the fire and control treatments, suggesting similar roost tree availability despite a significantly higher proportion of potential roost trees in the fire treatment. Northern myotis readily exploited alterations to forest structure created by the reintroduction of fire, which accelerated snag creation and enlarged existing or created new canopy gaps, but it remains to be determined if these conditions translate into increased recruitment and survivorship.

The influences of reproductive status, weather, and roost tree characteristics on timing of emergence, intra-night activity, and entrance of northern myotis at their diurnal roost trees largely is unknown. I examined nocturnal activity patterns of northern myotis maternity colonies during pregnancy and lactation at diurnal roost trees situated in areas that were and were not subjected to recent prescribed fires at the Fernow Experimental Forest, West Virginia from 2007 to 2009. Data recorded from exit counts and acoustic sampling suggested that northern myotis colony sizes were similar between reproductive periods and roost tree settings. However, intra-night activity patterns differed slightly between reproductive periods and roost trees in burned and non-burned areas. Weather variables poorly explained variation in activity patterns during pregnancy, but precipitation and temperature were negatively associated with activity patterns during lactation.

Throughout the world, maternity groups of bats are known to conform to fission-fusion models; and the movements among roost trees of individual bats belonging to these non-randomly assorting groups form networks of roost trees. That these roost networks may exist as scale-free networks where a central node roost tree is connected more highly to other roost trees suggests a relative importance among roost trees to bat maternity colonies. Also, forest disturbances such as prescribed fire may alter roost networks and characteristics of roost trees and central node roost trees. At the Fernow Experimental Forest in West Virginia, I examined roost networks of northern myotis in forest stands subjected to prescribed fire and those that were not in 2007–2009. I determined that northern myotis did conform to fission-fusion models, forming social groups whose roost areas and roost networks overlapped to some extent. Roost networks largely resembled scale-free network models, 61% of which had single identifiable central node roost trees on which the remainder of the roost trees in the network centered. In control, i.e., unburned, treatments, central node roost trees were in early stages of decay and surrounded by higher basal area than other trees within the networks. In prescribed fire treatments, central node roost trees were smaller in diameter, lower in the forest canopy, and surrounded by lower basal area than other trees in the networks. Compared to central node roost trees in control treatments, those in prescribed fire treatments had higher amounts of bark coverage. My results indicate that northern myotis form social groups that roost in networks of trees that center on a central node roost tree that is selected based on surrounding basal area and decay stage. Forest disturbances such as prescribed fire may result in changes to roost networks through inputs in suitable roost trees by senescence and creation of forest canopy gaps.

Forest disturbances, particularly permanent land use conversions, may fragment, isolate, and concentrate summer populations of philopatric bats, potentially resulting in genetically definable subpopulations. Also, subpopulations may be distinguishable at large spatial scales,

regardless of forest disturbances and other land use conversions. I examined genetic structuring of the forest-interior dwelling northern myotis at multiple spatial scales, from watershed to regional, in West Virginia and New York. I genotyped microsatellites at 18 nuclear loci from 174 individuals. In many cases, loci in subpopulations that I defined *a priori* based on spatial attributes departed from Hardy-Weinberg equilibrium; those loci that were in equilibrium were inconsistent at differentiating subpopulations based on spatial scale. My results indicate that some level of genetic structuring is evident among northern myotis, but this structuring could not be attributed solely to geographic location. It is likely that the ability to migrate relatively long distances, exploit small forest patches, and use networks of swarming sites located throughout the Appalachian Mountain range has allowed northern myotis to maintain high gene flow regardless of forest disturbances resulting in habitat patchiness at local and regional spatial scales.

Understanding the management impact, positive or negative, of prescribed fire on endangered Indiana myotis (*Myotis sodalis*) roosting habitat is of paramount interest to resource managers in the Appalachian Mountains and elsewhere. From 2001 to 2009, we examined roost selection of Indiana myotis in burned and unburned forests in Tucker County, West Virginia. We radio-tracked 16 male and 1 female Indiana myotis to 54 roost trees; 17 in burned stands and 37 in unburned stands. In burned stands, Indiana myotis roosted exclusively in fire-killed maples (*Acer* spp.). In unburned stands, they roosted in live hickories, oaks, and maples. Roost trees in burned stands were surrounded by lower basal area and by trees in advanced stages of decay with larger canopy gaps than at randomly-located potential roost trees in burned stands or actual roost trees located in unburned stands. Compared to randomly-located potential roosts in unburned stands, roost trees in unburned stands were less decayed, had higher percent bark coverage, and were surrounded by lower basal area, also resulting in larger canopy gaps. Roost-switching frequency and distances moved by Indiana myotis among roost trees were similar between burned and unburned stands. Indiana myotis roosted in stands that had initially been burned 1–3 years prior to our observations. Our research indicates that use of fire for forest management purposes, at minimum provoked no response from Indiana myotis in terms of roost tree selection, but rather created additional roost resources, suggesting prescribed fire can be an effective management tool for Indiana myotis.

ACKNOWLEDGMENTS

My research would not have been possible without the collaboration and camaraderie of many individuals and agencies. Firstly, I thank my committee for difficult but fair examinations, and expertise and guidance throughout my pursuit of a doctoral degree. I especially thank Dr. John Edwards for continually supporting me and believing in my abilities. The oft nepenthean Dr. Mark Ford provided much needed raillery and ideas throughout. I thank Dr. Ed Gates for providing me opportunities to advance my career before and after this process. Dr. Todd Petty inspired me in the quantitative side of ecology. I thank Dr. Gerry Hobbs for helping me keep statistics in perspective.

The USDA Forest Service Northern Research Station Joint Venture Agreement 06-JV-11242300-140 provided primary funding for my study from the National Fire Plan to West Virginia University, Division of Forestry and Natural Resources. Funding for prescribed burning was provided by a grant from Florida Power and Light and BHE Environmental to the U.S. Forest Service Northern Research Station through Collection Agreement 06-CO-112331-034. I thank the staff of the USDA Forest Service Monongahela National Forest and the USDA Forest Service Northern Research Station Timber and Watershed Laboratory for conducting the prescribed burns. Field assistance was graciously provided by J. Boyle, K. Boyle, J. DeCarlo, C. McDaniels, T. Smith, A. Stump, and M. Walsh. Jane “Pucker Jean” Rodrigue deserves special recognition for her selfless efforts in the field. I thank Dr. Tom Schuler for allowing me to use the hemispherical camera and familiarizing me with associated software. Freddie Wood provided much needed weather data from the Fernow Experimental Forest. I thank Chris Dobony and fellow graduate student Kathryn Cunningham and her field technicians for collecting wing punches at Fort Drum, New York. I am grateful to Marquette Crockett, Ken Sturm, and their

staff at the Canaan Valley National Wildlife Refuge for field assistance and allowing me to collect samples at the Refuge.

The genetics component of this dissertation would not have been possible without the gracious assistance and expertise provided by Dr. David Ray and his graduate students at West Virginia University, and Dr. Tim King, Mike Eackles, Robin Johnson, Barb Lubinski, Marcus Springmann, and John Switzer at the USGS Leetown Science Center. They presented me with much guidance and support throughout the often frustrating and discouraging process of DNA extraction, amplification, and genotyping. I thank them all for tolerating my ineptitudes in the laboratory setting.

I thank my friends and family from civilization for their constant support and hospitality during this trial.

Lastly, Charles Dickens inadvertently described the process of pursuing a doctoral degree best when he wrote of composing *A Tale of Two Cities* “As the idea became familiar to me, it gradually shaped itself into its present form. Throughout its execution, it has had complete possession of me; I have so far verified what is done and suffered in these pages...”

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Chapter 1

An introduction to and review of bat roosting ecology in disturbed landscapes

Much recent attention has focused on the conservation and management of bats because of their important ecological roles as nocturnal insectivores and as possible bio-indicator species (Fenton 2003, Miller et al. 2003). Worldwide, bats have experienced both real and perceived population declines attributed to numerous anthropogenic environmental changes (e.g., conversion of forests to agricultural or residential uses) and degradation (e.g., water pollution) (Fenton 1997, Pierson 1998, O'Shea et al. 2003). In temperate portions of the eastern United States, three bat species are federally listed as endangered, and several others are species of concern due to population declines (Harvey et al. 1999). Causes for these population declines include human disturbance of hibernacula, environmental pollution, and loss of summer habitat (i.e., forests) (Tuttle 1979, Pierson 1998, Fenton 2003). In the East, efforts to promote species recovery have largely focused on protection of hibernacula, which has led to increases in populations of gray myotis (*Myotis grisescens*), Indiana myotis (*M. sodalis*), and Virginia big-eared bats (*Corynorhinus townsendii virginianus*) (Clawson 2002, Martin et al. 2003, USFWS 2007). Although protection of hibernacula is undoubtedly important, the full range of habitats used by bats during all seasons must be taken into account when considering conservation and management strategies to ensure the perpetuation of a species, at least in the near term. Unfortunately, recovery plans often simply rely on the paradigm of habitat preservation or passive management, rather than proactive attempts at habitat enhancement through modification and management (USFWS 2007). Indeed, active habitat management may be a more effective means by which to encourage recovery of bat species.

In recent decades, numerous studies have investigated bat habitat relations, many of which focused on the effects of forest management practices on roosting and foraging ecology of bats (Miller et al. 2003). Various intensities of forest harvesting methods, from single-tree selection to clearcutting, produce disturbances to forest structure that can affect the roosting and foraging behavior of bats (Owen et al. 2004). Moreover, disturbance intensities vary spatially across the landscape, creating a spatiotemporally heterogeneous mosaic of forest structure or conditions from which bats select roost sites and foraging areas (Andrn 1994, Tang et al. 1997, Turner et al. 2001, Owen et al. 2004, Ford et al. 2005, Perry et al. 2007). Although the majority of bat ecology studies have focused on recent anthropogenic forest disturbances, the nature of these disturbances is not unique to the post-European settlement timeframe (Lorimer 2001). Indeed, natural disturbances such as tree/stand windthrow, or pyrogenic and agricultural activity of Native Americans played large roles in shaping pre-colonial settlement forests (Lorimer 2001, Dyer 2006). Although the significance of the impacts that Native Americans had on pre-colonial forests is debatable (Russell 1983), the consensus is that they had considerable influence on forest structure and succession through clearing for cultivation of crops and setting fires to drive game and clear understories that in effect managed forest conditions to facilitate hunting and to increase soft mast production (Day 1953, Delcourt and Delcourt 1997, Nowacki and Abrams 2008).

In the Central Appalachian Mountains region, major disturbances have occurred since European settlement, including widespread timber harvesting (often exploitative clearcutting), burning, both intentional and uncontrolled wildfires, and other stressors such as Chestnut blight (*Cryphonectria parasitica*) from the late 1800s to the early 1900s. These factors, in concert with Native American impacts during the pre-European settlement period not only perpetuated an oak

(*Quercus* spp.)-dominated forest, but also likely created periodic disturbances to the forest canopy that allowed shade-intermediate and shade-intolerant species to become established in the understory during this gap phase in the forest growth cycle (Yamamoto, 1992; Schuler and Fajvan 1999, Shumway et al. 2001). Fire-suppression efforts, beginning 15–30 years subsequent to the widespread forest harvesting and continuing through the present, resulted in a gradual shift in forest species composition towards more shade-tolerant species, an unprecedented scenario brought on by the lack of disturbance (Schuler and Fajvan 1999, Hutchinson et al. 2008, Nowacki and Abrams 2008).

Undoubtedly, since the early Holocene epoch, bats in North America evolved to adapt to these disturbances that have varied in intensity, frequency, and scale. These adaptations, behavioral and morphological, exist in bat communities today, as species differ in their roosting and foraging behaviors. These differences are both inherited and dictated by morphological characteristics such as echolocation and wing morphology (Aldridge and Rautenbach 1987, Lewis 1995, Ford et al. 2005). Moreover, social interactions in the form of colonial or solitary roosting behaviors and mating systems may be influenced partly by the ephemerality and spatial distribution of habitat (Emlen 1994, Lewis 1995, Burland and Worthington Wilmer 2001, Kerth 2008).

Although the ecological niche occupied by bats in the eastern United States is predominately that of nocturnal insectivores, life histories among species vary in terms of roosting, foraging, and mating behaviors (Barbour and Davis 1969, Harvey et al. 1999). The majority of bat species in the eastern United States roost in trees, either among live canopy foliage or in cavities or under exfoliating bark of live and dead trees. Moreover, bat species partition themselves when foraging among cleared, partially-disturbed, or relatively undisturbed

forested areas according to echolocation and morphological characteristics (Aldridge and Rautenbach 1987, Owen et al. 2004, Ford et al. 2005). Therefore, forest disturbances, either natural or anthropogenic, can alter the availability and distribution of resources with a subsequent reordering of the bat community (Brooks and Ford 2006).

Recent research suggests that in the eastern United States some degree of forest harvesting is tolerated by bats, and may even be favorable for certain species, provided that an adequate number of roost trees is retained (Owen et al. 2004, Ford et al. 2005, Perry and Thill 2007). However, relatively few studies have examined the effects of various forest harvesting regimes on roost selection of bats compared to those investigating foraging habitat selection in partially-harvested or intact forest stands (Sedgeley and O'Donnell 1999, Menzel et al. 2002, Miller et al. 2003, Ford et al. 2005). Limited knowledge of the effects of various forest management practices on availability and selection of roost trees impairs conservation and management decisions regarding bat use.

Throughout the Appalachian Mountains and Central Hardwoods forest regions, insufficient retention and/or regeneration of hard-mast producing oaks and hickories (*Carya* spp.) in managed and unmanaged forest stands are a major concern of forest and wildlife managers. The failure to adequately maintain oak has been attributed in part to fire suppression and uneven-age management practices that favor shade-tolerant tree species such as maples (*Acer* spp.) (Clark 1993, Schuler and Fajvan 1999, Brose et al. 2001, Schuler 2004, Nowacki and Abrams 2008). Oak regeneration can benefit from a combination of prescribed fire and forest canopy alteration. Following decades of fire suppression in eastern forests, using prescribed fire as a tool to restore or enhance oak-dominated communities is gaining widespread acceptance in the Appalachian Mountains and elsewhere. In addition to fire, overstory thinning by tree

removal, girdling, or herbiciding of competitors, can augment oak seedling initiation and survival through reduced competition and increased canopy openness (Miller 1993, Brose et al. 1999, Brose et al. 2001). These methods would increase snag abundance that in turn would favor snag-dependent wildlife species, including bats (Brose et al. 2001, Hallett et al. 2001, Albrecht and McCarthy 2006, Boyles and Aubrey 2006). Prescribed fire is within the accepted management prescriptions for many wildlife species (Kepler et al. 1996, Tucker et al. 2004, Blake 2005, Thatcher et al. 2006); however, the potential of using prescribed fire to create suitable roost conditions, in either live trees or snags, for bats is a largely unexplored topic, but a potentially valuable area of research (Leput 2004, Boyles and Aubrey 2006, Loeb and Waldrop 2008). Based on observational data, both Carter (2006) and Keyser and Ford (2006) hypothesized that periodic fire as a forest disturbance agent may have historically created a shifting mosaic of suitable roosting habitat for the disturbance-dependent Indiana myotis in upland forests of the eastern United States. Indeed, the heterogeneous patches of forest that remain after a fire event are a result of differing fire intensity within a burned area (Turner et al. 1994). Although fire may reduce the longevity or utility of individual roost trees in terms of bat use, it also kills or scars other trees, creating suitable roosting structures in the form of loose bark and cavities (Smith and Sutherland 1999, Russell et al. 2006); fire is a dynamic factor in forest ecosystems (Nowacki and Abrams 2008). Moreover, fire-killed trees leave gaps in the forest canopy, increasing the amount of solar radiation reaching the subcanopy stratum, i.e., lower tree limbs and boles, where bats are roosting (Menzel et al. 2001). Increased solar radiation may be a preferred characteristic of bat roost sites, as warmer temperatures facilitate more rapid development of neonates (Sedgeley 2001, Boyles and Aubrey 2006, Lausen and Barclay 2006). However, loss of foliage from fire-killed trees can reduce the roosting opportunities for foliage-

roosting bats, including the hoary bat (*Lasiurus cinereus*) and eastern red bat (*L. borealis*), but this remains unexamined. Forest management practices attempting to increase the oak component in forest communities may inadvertently be a proactive and effective bat habitat enhancement technique that increases the number of suitable roost trees for cavity- and exfoliating bark-roosting bats (Boyles and Aubrey 2006, Keyser and Ford 2006).

The purpose of my research was to investigate bat roosting ecology in relation to forest management practices, including prescribed fire. Research examining the effects of prescribed fire on various aspects of bat ecology is in its infancy, but has merit in that it will lead to a better understanding of the patterns and processes of bat ecology in the broader context of disturbances and landscape ecology as a whole (Turner et al. 2001, Boyles and Aubrey 2006, Keyser and Ford 2006, Guldin et al. 2007, Loeb and Waldrop 2008).

Objectives

The specific research objectives of my research were to:

- 1) Determine roost selection of female northern myotis in forests subjected to prescribed fire compared to selection in unburned forests.
- 2) Examine night-roosting activity of female northern myotis during the maternity season.
- 3) Determine if northern myotis exhibit non-random, day-roosting association patterns, and examine the characteristics and topology of day roosts from a graph theoretic approach.
- 4) Determine genetic relatedness of northern myotis groups at multiple spatial scales.
- 5) Examine roost selection of Indiana myotis in forests subjected to prescribed and wild fires during summer and autumn.

References

- Albrecht, M. A., and B. C. McCarthy. 2006. Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests. *Forest Ecology and Management* 226:88–103.
- 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.
- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71:355–366.
- Barbour, R. W., and W. H. Davis. 1969. *Bats of America*. University Press of Kentucky, Lexington, Kentucky.
- Blake, J. G. 2005. Effects of prescribed burning on distribution and abundance of birds in a closed-canopy oak-dominated forest, Missouri, USA. *Biological Conservation* 121:519–531.
- 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.
- Brooks, R. T., and W. M. Ford. 2006. Introduction to the special section – bat habitat use in eastern North America temperate forests: site, stand, and landscape effects. *Journal of Wildlife Management* 70:1171–1173.
- Brose, P., T. Schuler, D. VanLear, and J. Berst. 2001. Bringing fire back: the changing fire regimes of the Appalachian mixed-oak forests. *Journal of Forestry* 99:30–35.
- Brose, P. D., D. VanLear, and R. Cooper. 1999. Using shelterwood harvests and prescribed fire to regenerate oak stands on productive upland sites. *Forest Ecology and Management* 113:125–141.

- Burland, T. M., and J. Worthington Wilmer. 2001. Seeing in the dark: molecular approaches to the study of bat populations. *Biological Reviews* 76:389–409.
- Carter, T. C. 2006. Indiana bats in the Midwest: the importance of hydric habitats. *Journal of Wildlife Management* 70:1185–1190.
- Clark, F. B. 1993. An historical perspective of oak regeneration. Pages 3–13 *In* D. Loftis, and C. E. McGee, editors. *Proceedings, Oak regeneration: serious problems, practical recommendations*; 1992 September 8–10; Knoxville, Tennessee. General Technical Report SE-84. USDA Forest Service, Southern Research Station, Asheville, North Carolina.
- Clawson, R. L. 2002. Trends in population size and current status. Pages 2–8 *In* A. Kurta and J. Kennedy, editors. *The Indiana bat: biology and management of an endangered species* Bat Conservation International, Austin, Texas.
- Day, G. M. 1953. The Indiana as an ecological factor in the northeastern forest. *Ecology* 34:329–346.
- Delcourt, H. R., and P. A. Delcourt. 1997. Pre-Columbian Native American use of fire on Southern Appalachian landscapes. *Conservation Biology* 11:1010–1014.
- Dyer, J. M. 2006. Revisiting the deciduous forests of eastern North America. *BioScience* 56:341–352.
- Emlen, S. T. 1994. Benefits, constraints and the evolution of the family. *Trends in Ecology and Evolution* 9:282–285.
- Fenton, M. B. 1997. Science and the conservation of bats. *Journal of Mammalogy* 78:1–14.
- Fenton, M. B. 2003. Science and the conservation of bats: where to next? *Wildlife Society Bulletin* 31:6–15.

- Ford, W. M., M. A. Menzel, J. L. Rodrigue, J. M. Menzel, and J. B. Johnson. 2005. Relating bat species presence to simple habitat measures in a central Appalachian forest. *Biological Conservation* 126:528–539.
- Guldin, J. M., W. H. Emmingham, S. A. Carter, and D. A. Saugey. 2007. Silvicultural practices and management of habitat for bats. Pages 177–205 *In* M. J. Lacki, J. P. Hayes, and A. Kurta, editors. *Bat in forests*. Johns Hopkins University, Baltimore, Maryland.
- Hallett, J. G., T. Lopez, M. A. O’Connell, and M. A. Borysewicz. 2001. Decay dynamics and avian use of artificially created snags. *Northwest Science* 75:378–386.
- Harvey, M. J., J. S. Altenbach and T. L. Best. 1999. *Bats of the United States*. Arkansas Game and Fish Commission and U. S. Fish and Wildlife Service, Little Rock, Arkansas.
- Hutchinson, T. F., R. P. Long, R. D. Ford, and E. K. Sutherland. 2008. Fire history and the establishment of oaks and maples in second-growth forests. *Canadian Journal of Forest Research* 38:1184–1198.
- Kepler, C. B., G. W. Irvine, M. E. Decapita, and J. Weinrich. 1996. The conservation management of Kirtland’s warbler, *Dendroica kirtlandii*. *Bird Conservation International* 6:11–22.
- Kerth, G. 2008. Causes and consequences of sociality in bats. *BioScience* 58:737–746.
- Keyser, P. K., and W. M. Ford. 2006. Influence of fire and mammals in oak forests. Pages 180–190 *In* M. B. Dickenson, editor. *Fire in eastern oak forests: a symposium*. USDA Forest Service, General Technical Report GTR-NRS-1, Northern Research Station. Newtown Square, PA.
- Lausen, C. L., and R. M. R. Barclay. 2006. Benefits of living in a building: big brown bats (*Eptesicus fuscus*) in rocks versus buildings. *Journal of Mammalogy* 87:362–370.

- Leput, D. W. 2004. Eastern red bat (*Lasiurus borealis*) and eastern pipistrelle (*Pipistrellus subflavus*) maternal roost selection: implications for forest management. M.S. Thesis. Clemson University, Clemson, South Carolina.
- Lewis, S. E. 1995. Roost fidelity in bats: a review. *Journal of Mammalogy* 76:481–496.
- 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.
- Lorimer, C. G. 2001. Historical and ecological roles of disturbance in eastern North American forests: 9,000 years of change. *Wildlife Society Bulletin* 29:425–439.
- Martin, K. W., D. M. Leslie, Jr., M. E. Payton, W. L. Puckette, and S. L. Hensley. 2003. Internal cave gating for protection of colonies of the endangered gray bat (*Myotis grisescens*). *Acta Chiropterologica* 5:151–160.
- Menzel, M. A., T. C. Carter, B. R. Chapman, and J. Laerm. 1998. Quantitative comparison of tree roosts used by red bats (*Lasiurus borealis*) and Seminole bats (*L. seminolus*). *Canadian Journal of Zoology* 76:630–634.
- Menzel, M. A., T. C. Carter, W. M. Ford, and B. R. Chapman. 2001. Tree-roost characteristics of subadult and female adult evening bats (*Nycticeius humeralis*) in the upper Coastal Plain of South Carolina. *American Midland Naturalist* 145:112–119.
- Menzel, M. A., S. F. Owen, W. M. Ford, J. W. Edwards, P. B. Wood, B. R. Chapman, and K. V. Miller. 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, D. A., E. B. Arnett, and M. J. Lacki. 2003. Habitat management for forest-roosting bats of North America: a critical review of habitat studies. *Wildlife Society Bulletin* 31:30–44.

- Miller, J. H. 1993. Oak plantation using mechanical, burning, and herbicide treatments. Pages 264–289 *In* D. Loftis, and C. E. McGee, editors. Proceedings, Oak regeneration: serious problems, practical recommendations; 1992 September 8–10; Knoxville, Tennessee. General Technical Report SE-84. USDA Forest Service, Southern Research Station, Asheville, North Carolina.
- Nowacki, G. J., and M. D. Abrams. 2008. The demise of fire and “mesophication” of forests in the eastern United States. *BioScience* 58:123–138.
- O’Shea, T. J., M. A. Bogan, and L. E. Ellison. 2003. Monitoring trends in bat populations of the United States and territories: status of the science and recommendations for the future. *Wildlife Society Bulletin* 31:16–29.
- Owen, S. F., M. A. Menzel, J. W. Edwards, W. M. Ford, J. M. Menzel, B. R. Chapman, P. B. Wood, and K. V. Miller. 2004. Bat activity in harvested and intact forest stands in the Allegheny Mountains. *Northern Journal of Applied Forestry* 21:154–159.
- 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.
- Perry, R. W., R. E. Thill, and D. M. Leslie, Jr. 2007. Selection of roosting habitat by forest bats in a diverse forested landscape. *Forest Ecology and Management* 238:156–166.
- Pierson, E. D. 1998. Tall trees, deep holes, and scarred landscapes; conservation biology of North American bats. Pages 309–325 *In* T. H. Kunz and P. A. Racey, editors. *Bat biology and conservation*. Smithsonian Institution Press, Washington, D.C.
- Russell, E. W. B. 1983. Indian-set fires in the forests of the northeastern United States. *Ecology* 64:78–88.

- Russell, R. E., V. A. Saab, J. G. Dudley, and J. J. Rotella. 2006. Snag longevity in relation to wildfire and postfire salvage logging. *Forest Ecology and Management* 232:179–187.
- Schuler, T. M. 2004. Fifty years of partial harvesting in a mixed mesophytic forest: composition and productivity. *Canadian Journal of Forest Research* 34:985–997.
- Schuler, T. M., and M. A. Fajvan. 1999. Understory tree characteristics and disturbance history of a central Appalachian forest prior to old-growth harvesting. USDA Forest Service, Res. Pap. NE-710, Northeastern Research Station, Radnor, PA.
- Sedgeley, J. A. 2001. Quality of cavity microclimate as a factor influencing selection of maternity roosts by a tree-dwelling bat, *Chalinolobus tuberculatus*, in New Zealand. *Journal of Applied Ecology* 38:425–438.
- 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* 249:437–446.
- Shumway, D. L., M. D. Abrams, and C. M. Ruffner. 2001. A 400-year history of fire and oak recruitment in an old-growth oak forest in western Maryland, U.S.A. *Canadian Journal of Forest Research* 31:1437–1443.
- Smith, K. T., and E. K. Sutherland. 1999. Fire-scar formation and compartmentalization in oak. *Canadian Journal of Forest Research* 29:166–171.
- Tang, S. M., J. F. Franklin, and D. R. Montgomery. 1997. Forest harvest patterns and landscape disturbance processes. *Landscape Ecology* 12:349–363.
- Thatcher, B. S., D. G. Krementz, and M. S. Woodrey. 2006. Henslow's sparrow winter-survival estimates and response to prescribed burning. *Journal of Wildlife Management* 70:198–206.

- Tucker, J. W., Jr., W. D. Robinson, and J. B. Grand. 2004. Influence of fire on Bachman's sparrow, an endemic North American songbird. *Journal of Wildlife Management* 68:1114–1123.
- Turner, M. G., W. W. Hargrove, R. H. Gardner, W. H. Romme. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *Journal of Vegetation Science* 5:731–742.
- Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. *Landscape ecology in theory and practice: pattern and process*. Springer Science + Business Media, New York.
- Tuttle, M. D. 1979. Status, cause of decline, and management of endangered gray bats. *Journal of Wildlife Management* 43:1–17.
- United States Fish and Wildlife Service (USFWS). 2007. Indiana bat (*Myotis sodalis*) draft recovery plan: first revision. USFWS, Region 3, Fort Snelling, Minnesota, USA.
- Yamamoto, S. 1992. The gap theory in forest dynamics. *Botanical Magazine* 105:375–383.

Chapter 2

Roost Tree Selection by Northern Myotis (*Myotis septentrionalis*) Maternity Colonies

Following Prescribed Fire in a Central Appalachian Mountains Hardwood Forest¹

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¹ Forest Ecology and Management 258:233–242

Abstract

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

the fire treatments, possibly due to larger canopy gaps created by the senescence and decay of the surrounding fire-killed overstory trees. Northern myotis roost-switching frequency, distance between successive roosts, and duration of individual roost tree use were similar between the fire and control treatments, suggesting similar roost tree availability despite a significantly higher proportion of potential roost trees in the fire treatment. Northern myotis readily exploited alterations to forest structure created by the reintroduction of fire, which accelerated snag creation and enlarged existing or created new canopy gaps, but it remains to be determined if these conditions translate into increased recruitment and survivorship.

Keywords: bats, northern myotis, *Myotis septentrionalis*, prescribed fire, roost selection, West Virginia

1. Introduction

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

Throughout the Appalachian Mountains and Central Hardwoods forest regions, insufficient retention and/or regeneration of hard-mast producing species such as oaks (*Quercus* spp.) and hickories (*Carya* spp.) in managed and unmanaged forest stands are a major concern of forest and wildlife managers. This failure to adequately maintain oak has been attributed in part to fire suppression and uneven-aged management practices that favor shade-tolerant tree species such as maples (*Acer* spp.) (Clark, 1993; Schuler and Fajvan, 1999; Brose et al., 2001; Schuler, 2004; Nowacki and Abrams, 2008). Oak retention and regeneration can benefit from a combination of prescribed fire and forest canopy thinning by selected removal, girdling, or herbicide of competitors, to augment oak seedling initiation and survival through reduced competition and increased canopy openness (Miller, 1993; Brose et al., 1999; 2001). These methods potentially could result in a net increase in snag abundance that in turn could favor snag-dependent wildlife species, including bats (Brose et al., 2001; Hallett et al., 2001; Albrecht and McCarthy, 2006; Boyles and Aubrey, 2006). Prescribed fire is within the management prescriptions for many wildlife species (Kepler et al., 1996; Brennan et al., 1998; Tucker et al., 2004; Blake, 2005; Thatcher et al., 2006); however, using prescribed fire to create suitable roost conditions, in either live trees or snags, for bats is a largely unexplored, but a potentially valuable area of research (Leput 2004, Boyles and Aubrey 2006, Loeb and Waldrop 2008). Based on observational data, both Carter (2006) and Keyser and Ford (2006) hypothesized that periodic fire as a forest disturbance may have historically created a shifting mosaic of suitable roosting habitat for the disturbance-related endangered Indiana myotis (*Myotis sodalis*) in upland forests of the eastern United States. The heterogeneous patches of forest that remain after a fire event can be attributed to differing fire intensity within a burned area (Turner et al., 1994). Although fire may reduce the longevity or utility of individual roost trees in terms of bat use, it also kills or

scars other trees, creating suitable roosting structures in the form of loose bark and cavities (Smith and Sutherland, 1999; Russell et al., 2006). Moreover, fire-killed trees leave gaps in the forest canopy, increasing the amount of solar radiation reaching the subcanopy, i.e., lower tree limbs and boles, where bats roost (Menzel et al., 2001). Increased solar radiation may be a preferred characteristic of bat roost sites, as warmer temperatures facilitate more rapid development of neonates (Sedgeley, 2001; Boyles and Aubrey, 2006; Lausen and Barclay, 2006). However, loss of foliage from fire-killed trees could reduce the roosting opportunities for foliage-roosting bats, including the hoary bat (*Lasiurus cinereus*) and eastern red bat (*L. borealis*). Forest management practices attempting to increase the oak component in forest communities may inadvertently be a proactive bat habitat enhancement technique that increases the number of suitable roost trees for cavity- and exfoliating bark-roosting bats (Boyles and Aubrey, 2006; Keyser and Ford, 2006).

Northern myotis (northern long-eared bat; *Myotis septentrionalis*) is one of the most common bat species in eastern North America, particularly in the Appalachian Mountains, and is a forest-roosting and foraging obligate species in most areas (Barbour and Davis, 1969; Caceres and Barclay, 2000; Ford et al., 2005; Chapman, 2007). Females form maternity colonies of <100 individuals, roosting in cavities in snags or under exfoliating bark of live or dead trees (Sasse and Pekins, 1996; Foster and Kurta, 1999; Menzel et al., 2002a; Owen et al., 2002). Although many hardwood tree species are used as roost trees, research in the Central Appalachian Mountains has shown that male and female northern myotis selectively roost in black locust (*Robinia pseudoacacia*), a rot-resistant, long-lasting species that remains suitable as a roost for many years, thereby promoting philopatry (Lewis, 1995; Menzel et al., 2002a; Owen et al., 2002; Ford et al., 2006b; Kahler and Anderson, 2006). However, the temporal aspect of forest disturbances,

including fire, and its association with snag dynamics and bat-roost selection remains to be investigated. Although northern myotis maternity roost trees are found in relatively closed-canopy forests, forest manipulation in the form of snag creation, thinning, or patch clearcutting that promotes recruitment of black locust into the subsequent stand, may be tolerated by and augment roosting conditions for northern myotis in the long-term (Sasse and Pekins, 1996; Foster and Kurta, 1999; Cryan et al., 2001; Menzel et al., 2002a; Carter and Feldhamer, 2005; Ford et al., 2006b; Perry and Thill, 2007). The condition, e.g., decay stage, of trees immediately surrounding roost trees, as well as the presence of canopy gaps, also are factors in selection by northern myotis (Cryan et al., 2001; Menzel et al., 2002a; Carter and Feldhamer, 2005; Perry and Thill, 2007; Perry et al., 2007). For northern myotis, the use of prescribed fire to promote oak in forest stands can create snags or modify stand structure, improving existing roost availability or conditions in the near-term, as well as inadvertently promote the establishment of species such as black locust. Whether prescribed fire enhances roost habitat in the longer-term, remains speculative (Leput, 2004; Boyles and Aubrey, 2006). Moreover, it is unclear if northern myotis maternity roost tree availability is a resource that is lacking, and if so can possibly be remedied through proactive forest management strategies, including prescribed fire. Roost tree availability in disturbed and undisturbed forests can be evaluated by examining the roost tree switching behavior of bats (Chaverri et al., 2007).

Whether or not the availability of roost trees, i.e., their frequency of occurrence or distance between trees, has an influence on roost switching behavior such as frequency or distance between roosts has not been well quantified, particularly for bat species of eastern North America (Wilkinson, 1985; Crampton and Barclay, 1998; O'Donnell and Sedgeley, 1999; Kunz and Lumsden, 2003). Extrinsic and intrinsic factors that influence roost switching are

speculative, but undoubtedly include reduced predation risks, parasite loads, distance to foraging areas, or more favorable roost microenvironment (Wilkinson, 1985; Lewis, 1995; O'Donnell and Sedgeley, 1999; Kunz and Lumsden, 2003). Non-random selection of roosts, roost switching frequency and distance traveled between successive roosts are indicators of roost availability (Sedgeley and O'Donnell, 1999; Chaverri et al., 2007). Throughout much of their range, female northern myotis typically switch roost trees every 1–5 days and may travel up to ~2 km between successive roost trees, but roosts are commonly clustered in small (<20 ha) areas (Foster and Kurta, 1999; Menzel et al., 2002a; Carter and Feldhamer, 2005; Broders et al., 2006; Perry and Thill, 2007). How these facets of northern myotis natural history change in forests subjected to prescribed fire is unknown.

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

2. Methods

2.1. Study area

We conducted our research at the Fernow Experimental Forest (FEF) in Tucker County, West Virginia (Fig. 1). The FEF is a 1,900 ha experimental forest managed by the U.S. Forest

Service, Northern Research Station, and is located in the Unglaciaded Allegheny Mountains subsection of the Appalachian Plateau Physiographic Province (Kochenderfer et al., 2007). Elevations range from 530 to 1,100 m. Elklick Run, a 2.4-km fourth-order stream, roughly bisects FEF east to west. Approximately 5.5 km of dendritic intermittent and permanent streams feed into Elklick Run and incise the steep slopes and plateau-like ridgetops, providing all possible slope aspects (Madarish et al., 2002). Mean annual precipitation at FEF is 145.8 cm, ranging from 9.7 cm in October to 14.4 cm in June. Mean annual temperature is 9.2° C, ranging from -18.0° C in January to 20.6° C in July (Kochenderfer, 2006). Vegetation at the FEF is a mosaic of second- and third-growth, mixed-mesophytic and northern hardwood forest that has been managed by even (patch clearcut,)- and uneven (single-tree selection)-aged silviculture since the mid-20th century, or has been left undisturbed following initial harvesting in the Elklick watershed from 1903 to 1911 (Schuler and Fajvan, 1999). Although American chestnut (*Castanea dentata*) and oak species, such as northern red oak (*Q. rubra*), historically dominated the forest overstory, the chestnut blight (*Cryphonectria parasitica*) and subsequent lack of intense disturbance, including fire and clearcutting, since the mid-20th century has allowed forest composition to shift toward shade-tolerant tree species, such as maples and American beech (*Fagus grandifolia*) (Schuler and Fajvan, 1999; Schuler, 2004). Prescribed fire has recently been used to promote oak regeneration in the forest that is currently dominated by sugar maple (*A. saccharum*), red maple (*A. rubrum*), yellow-poplar (*Liriodendron tulipifera*), black cherry (*Prunus serotina*), American beech, sweet birch (*Betula lenta*), and basswood (*Tilia americana*) (Schuler, 2004). In April or May (depending on management compartment) 2007 and 2008, prescribed fire treatments were conducted in management compartments 45 (121ha), 13 (13ha), and 21 (12ha) on FEF (Fig. 1). The three management compartments were burned for 1 day

during each treatment using a strip head fire technique, ignited with hand-held drip torches after fire-blackened perimeters were established. Actual flame heights and combustion varied from dying out to >3.5 m high in some spots, due to variability in leaf litter, slope, and aspect. Additionally, 48, 20-m radius plots were randomly located in each of the three management compartments, and all overstory or midstory trees, other than oak or hickory, were herbicided or girdled (T. Schuler, USDA Forest Service, personal communication).

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

2.2. Radio telemetry

To capture bats, we erected mist nets (Avinet, Inc., Dryden, New York) over stream corridors, small pools, skidder trails, and service roads from May to August 2007 and 2008. Mist netting sites were located within the fire treatment and control treatment. We considered the control treatment to be any area outside the three management compartments where prescribed fires were used. Mist netting was conducted <5 hours following sunset, unless prevented by periods of rain, wind ≥ 20 kph, or temperatures $< 10^{\circ}$ C as these conditions can influence bat activity levels (Erickson and West, 2002). For each captured bat, we determined species, sex, age, weight, forearm length, and reproductive condition (Menzel et al., 2002b). We used Skin Bond[®] (Smith and Nephew, Largo, Florida) surgical cement to affix a 0.35-g radio transmitter (Model LB-2N; Holohil Systems Ltd., Carp, Ontario, Canada) between the scapulae of captured

female northern myotis. Bat capture and handling protocols were approved by the Animal Care and Use Committee of West Virginia University (Protocol No. 08-0504) and followed the guidelines of the American Society of Mammalogists (ACUC, 1998). We used a radio receiver and 3-element Yagi antenna (Wildlife Materials, Inc., Murphysboro, Illinois) to locate roost trees. To record roost tree locations within 10 m of their true geographic location, we used a Garmin GPSmap 60CSx global positioning unit.

2.3. Habitat variables

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

We measured characteristics of each roost tree, the 4 trees (>10 cm dbh) nearest to the roost tree, and the site at which the roost tree was located. For each roost tree, we determined tree species, diameter (cm) at breast height with a diameter (dbh) tape (DBHR), decay class (Cline et al., 1980; i.e., 1 = live, 2 = declining, 3 = recent dead, 4 = loose bark, 5 = no bark, 6 = broken top, 7 = broken bole; DECAYR), crown class (Nyland 1996; i.e., 1 = suppressed, 2 = intermediate, 3 = codominant, 4 = dominant; CROWNR), tree height (m) with a hypsometer (HEIGHT), roost height when known (ROOSTHIGHT), visual estimate of percent bark remaining on the tree (BARK), and roost type (cavity = 1, bark = 0; ROOSTTYPE). For each of 4 trees nearest to the roost tree, we determined tree species, diameter (cm) at breast height (DBHN), distance (m) to the roost tree (DISTN), decay class (DECAYN), and crown class

(CROWN), all of which were averaged for the 4 trees. We photographed the forest canopy at each roost tree with a Nikon Coolpix 8400 camera and FC-E9 fisheye lens (Melville, New York) mounted to a self-leveling mount and tripod (Regent Instruments, Inc., Canada). We used WinScanopy and XLScanopy software (Regent Instruments, Inc., Canada) to analyze each canopy photograph. This software allowed us to analyze the percent canopy gap within the hemispherical photograph of the canopy as a whole (TOTALGAP), as a 45° wedge off the horizon (HORIZGAP), as a 90° wedge centered on the midpoint (OVERHEADGAP), a 90° wedge each centered on the north, east, south, and west aspects (NORTHGAP, EASTGAP, SOUTHGAP, WESTGAP, respectively). We recorded aspect (ASPECT) with a compass, percent slope (SLOPE) with a clinometer at the plot (11.3 m radius centered on the roost tree), and stand basal area with a 20 factor prism (m^2 / ha ; BASAL). At each roost tree in the fire treatment, we also estimated the percent (0, 25, 50, 75, or 100 %) of understory (UNDERSTORY) and midstory (MIDSTORY) trees that were killed by fire. Within fire and control treatments, we located potential roost trees at random coordinates generated with ArcMap. We attempted to sample the same number of random trees as we accumulated roost trees. Potential roost trees were identified as any tree (>10 cm diameter at breast height) that contained either a cavity or exfoliating bark that possibly could be used by a northern myotis maternity colony as described by Owen et al. (2002). We measured the same variables at the potential roost trees as we did at the actual roost trees (Appendix A). Temperature (° C) was measured at a random sample of roost trees located in fire and control treatments with StowAway® Tidbit® (Onset Computer Corp., Pocasset, Massachusetts) data loggers that recorded ambient temperature every minute for 1-week periods from mid-June through mid-July. Data loggers were affixed to the south side of tree boles.

2.4. Statistical analysis

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

and discard actual height of roost trees, which will vary among areas). We used AIC_c for small sample sizes to determine the best approximating candidate model. Candidate models separated by ≤ 2 AIC_c were considered to be competing models. We used Akaike weights, w_{AIC_c} , to indicate the probability that a particular model was the best approximating model in the candidate set. Naglekerke's max-rescaled R^2 was used to evaluate global model fit (Burnham and Anderson, 2002).

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

Lastly, we used a Wilcoxon test to compare the frequency that northern myotis switched roosts, measured as the number of consecutive days spent in a roost tree and total number of roost trees used per bat, between fire and control treatments. We used a Kruskal-Wallis (Proc Npar1way, SAS Institute, Inc., 2004) test to compare distances (m) between consecutive roosts in the fire treatment, in the control treatment, and both directions of between-treatment

movements. We used a sign test (Proc Univariate; SAS Institute, Inc., 2004) to compare minimum, mean, and maximum daily temperatures recorded at roost trees.

3. Results

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

Spearman's rank correlation coefficients exceeded 0.60 for 6 variable pairs within the control treatment contrast, 9 variable pairs within the fire treatment contrast, and 17 variable

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

Within the six belt transects in the fire treatment ($n = 3$) and control treatment ($n = 3$), we tallied 391 trees of 19 species and 369 trees of 23 species, respectively. Northern myotis maternity colonies roosted disproportionately more often in black locust trees and disproportionately less often in oaks and maples than expected in fire and control treatments (Table 4). Availability of roost types (cavity or exfoliating bark) were disproportionately higher

in the fire treatment (Table 5). Available roost trees were smaller in diameter and lower in the canopy, i.e., crown class, but were similar in decay class in the fire treatment than in the control treatment. The majority (68 %) of roost trees in the fire treatment and half of roost trees in the control treatment were either of intermediate or suppressed crown class. The majority of roost trees were of decay class ≥ 4 in the fire treatment (60%) and control treatment (62%). Only 2 and 4 live trees were used in the fire treatment and control treatment, respectively.

At 44 randomly selected roost trees, daily minimum temperatures were similar ($M = -2.0$, $P = 0.618$) between the fire ($n = 15$, mean = 14.26°C , SE = 0.46) and control treatments ($n = 29$, mean = 14.36°C , SE = 0.45). However, daily mean temperatures differed ($M = -11.5$, $P < 0.001$) between fire (mean = 19.58°C , SE = 0.43) and control treatments (mean = 19.03°C , SE = 0.44). Daily maximum temperatures also differed ($M = -7.5$, $P = 0.020$) between fire (mean = 32.16°C , SE = 0.75) and control treatments (mean = 30.83°C , SE = 1.11).

Roost switching frequency by northern myotis was similar ($P = 0.403$) between the fire treatment (mean = 1.43 days, SE = 0.155, switched every 1–6 days) and control treatment (mean = 1.32 days, SE = 0.091, switched every 1–5 days). In the fire treatment, northern myotis used 1–7 (mean = 2.35, SE = 0.402) roost trees for the duration of transmitter retention (mean = 4.36 days, SE = 0.560, range = 2–8). In the control treatment, northern myotis used 1–7 (mean = 3.04, SE = 0.340) roost trees for the duration of transmitter retention (mean = 5.00 days, SE = 0.507, range = 1–9). Distances between consecutive roost trees were similar ($P = 0.115$) among the fire treatment (mean = 152 m, SE = 21.3, $n = 18$, range = 16–314 m), control treatment (mean = 230 m, SE = 24.4, $n = 49$, range = 7–634 m), and between-treatment movements (fire to control treatment: mean = 294 m, SE = 64.1, $n = 8$, range = 136–684 m; control to fire treatment: mean = 249 m, SE = 29.0, $n = 5$, range = 166–341 m).

4. Discussion

Northern myotis responded favorably to prescribed fire by exploiting trees, mostly black locust, that were located in canopy gaps that were created by the senescence and decay of surrounding overstory trees. Northern myotis selection of black locust snags and large-diameter snags of other species as roost trees is typical of findings in the central Appalachian Mountains (Menzel et al., 2002a; Owen et al., 2002). The black locust snags used by northern myotis are a relict of past disturbances on the FEF in the early- to mid-1900s. Ford et al. (2006b) suggested that northern myotis selection of black locust snags as roost trees is a relatively recent phenomenon because historically, black locust was not a prevalent tree species in the Central Appalachian Mountains prior to the widespread harvesting that occurred regionally from the end of the 1800s into the 1920s (Abrams and McCay, 1996; Schuler and Fajvan, 1999). In the pre-settlement forest, northern myotis probably used cavities and exfoliating bark of large-diameter snags, such as American chestnut or sugar maple, located in canopy gaps created by the canopy die off of the roost tree itself or the senescence of surrounding overstory trees killed by natural disturbances such as ice and wind damage. Moreover, frequent fires (<25-year return interval) that were caused by lightning strikes or set by Native Americans not only perpetuated an oak-dominated forest, but also likely created periodic disturbances to the forest canopy that allowed shade-intermediate and intolerant species to become established in the understory during this gap phase in the forest growth cycle (Yamamoto, 1992; Schuler and Fajvan, 1999; Shumway et al., 2001). In the late 1800s and early 1900s, forest disturbances, including exploitative harvesting, frequent and often catastrophic fires, and chestnut blight, created conditions that favored shade-intermediate and intolerant tree species, such as black locust and oaks in the region (Boring et al., 1981; Abrams and McCay, 1996; Schuler and Fajvan, 1999; Shumway et al., 2001; Nowacki

and Abrams, 2008). Fire-suppression efforts 15–30 years subsequent to the widespread harvesting through the present resulted in a gradual shift in forest species composition towards shade-tolerant species (Schuler and Fajvan, 1999; Hutchinson et al., 2008). Black locust trees that established in early 1900s as a result of forest disturbances were eventually overtopped by both shade-tolerant and intolerant species during the building phase of the forest growth cycle and remained in the forest as reliable, long-lasting snags that were used by bats for many consecutive years (Carey, 1983; Yamamoto, 1992; Lewis, 1995). During the mature phase of the forest growth cycle, forest species composition continued to shift toward more shade-tolerant species, such as maples, because of forest fire suppression and uneven-aged forest management practices (Clark, 1993; Brose et al., 2001; Schuler, 2004; Nowacki and Abrams, 2008). Within these mature forests, northern myotis maternity colonies roost in black locust snags and in the cavities or under the exfoliating bark of mature trees, of both shade-tolerant and intolerant species, and typically are associated with canopy gaps (Ford et al., 2002; Owen et al., 2002; this study). Indeed, northern myotis appear to be able to locate roosts in disturbed forests in various phases of the forest growth cycle.

The broader temporal aspect of fire and its association with forest and snag dynamics and bat roost selection has not been considered and remains to be investigated. In our study, the immediate impact of recent prescribed fires included the creation of potential northern myotis roosts by enhancing the exfoliation of bark in live and dead trees (mostly maples and American beech) and possibly made previously unsuitable roost trees suitable by increasing the amount of solar radiation reaching them. Despite the apparent abundance of available roost trees, we observed only one roost tree in the fire treatment that was attributable solely to the recent prescribed fires; a red maple that was fire-killed and had exfoliating bark as a result. All other

roost trees in the fire treatment had cavities that were in existence prior to the fire treatment. Therefore, it is possible that northern myotis philopatry has continued despite prescribed fires, or that they have not had time to respond to the abundance of newly-created roost trees. However, northern myotis on the FEF mostly roosted in cavities, possibly limiting the effectiveness of prescribed fire in creating newly available roosts in the short term, i.e., 1–2 years post-fire. Our fire treatment partially consumed the bases of some roost snags, undoubtedly shortening their useful duration as roosts. The senescence of fire-killed overstory trees allowed increased solar radiation to reach the subcanopy stratum, i.e., lower tree limbs and boles, of a greater number of trees, possibly providing more potential roosts through the improvement of microenvironmental conditions (Menzel et al., 2001; Boyles and Aubrey, 2006; Turbill and Geiser, 2008).

In the control treatment, northern myotis selected roost trees that were surrounded by decaying overstory trees. Clusters of decaying trees may provide alternate roosts and increased solar radiation to reach roost trees (Cryan et al., 2001; Perry and Thill, 2007; Perry et al., 2007). Roost trees located in some areas of the control treatment that had been subjected to light forest thinning is consistent with findings in the Ouachita Mountain region of Arkansas where northern myotis maternity colonies were observed roosting in thinned stands of mixed pine (*Pinus* spp.)-hardwoods (Perry et al., 2007). Prescribed fire may act as a surrogate to mechanical forest thinning or harvesting in that fire-killed mature trees, and consequent crown die off, allow increased solar radiation to reach roost trees. Indeed, the percentage of fire-killed stems surrounding roost trees was positively related to the canopy gap immediately over the roost trees ($\rho = 0.652$, OVERHEADGAP:MIDSTORY; Table 1). Additionally, canopy gaps in the fire treatment were associated with slightly higher maximum daily temperatures at roost trees and undoubtedly inside roost tree cavities. Higher roost temperatures could facilitate more rapid

growth of developing juvenile bats (Sedgeley, 2001; Boyles and Aubrey, 2006; Lausen and Barclay, 2006; Turbill and Geiser, 2008). Roost temperatures can be influenced by the amount of canopy gap as well as by the location of the roost tree with respect to landform (Lacki and Schwierjohann, 2001). Similar to previous studies, northern myotis maternity colonies on the FEF selected roost trees that were located on upper slopes, presumably because of increased intensity and duration of solar radiation (Lacki and Schwierjohann, 2001; Broders and Forbes, 2004). The increased solar radiation in addition to the well-drained upper slopes where black locust is more likely to occur creates an ideal roosting situation for northern myotis (Clarkson, 1958).

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

Despite an apparent abundance of potential roost trees in our fire treatment, northern myotis did not switch roost trees more frequently than found in the control treatment. However, northern myotis in our study did switch roosts more frequently (mean = 1.35 days per roost) than reported previously, both within the Central Appalachian Mountains (Menzel et al., 2002a (mean = 5.3 days per roost); Owen et al., 2002 (mean = 3.0 days per roost)), as well as in other parts of their range (Foster and Kurta, 1999 (mean = 5.6 tracking days and 3.6 roost trees); Cryan et al.,

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

5. Conclusions

The use of prescribed fire as a management tool to restore oak species to forests is amenable to roosting requirements of northern myotis maternity colonies in the Central

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

Acknowledgments

The USDA Forest Service Northern Research Station Joint Venture Agreement 06-JV-11242300-140 provided primary funding for our study from the National Fire Plan to West Virginia University, Division of Forestry and Natural Resources. Funding for prescribed burning was provided by a grant from Florida Power and Light and BHE Environmental to the U.S. Forest Service Northern Research Station through Collection Agreement 06-CO-112331-034. We thank the staff of the USDA Forest Service Monongahela National Forest and the USDA Forest Service Northern Research Station Timber and Watershed Laboratory for conducting the prescribed burns. J. DeCarlo, J. Rodrigue, and T. Smith graciously provided field assistance. We thank 2 anonymous reviewers for helpful comments on this manuscript.

References

- Abrams, M.D., McCay, D.M., 1996. Vegetation-site relationships of witness trees (1780–1856) in the presettlement forests of eastern West Virginia. *Canadian Journal of Forest Research* 26, 217–224.
- Albrecht, M.A., McCarthy, B.C., 2006. Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests. *Forest Ecology and Management* 226, 88–103.
- Animal Care and Use Committee (ACUC). 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79, 1416–1431.
- Barbour, R.W., Davis, W.H., 1969. *Bats of America*. University Press of Kentucky, Lexington, KY, 286 pp.
- Beck, D.E., Hooper, R.M., 1986. Development of a southern Appalachian hardwood stand after clearcutting. *Southern Journal of Applied Forestry* 10, 168–172.
- Blake, J.G., 2005. Effects of prescribed burning on distribution and abundance of birds in a closed-canopy oak-dominated forest, Missouri, USA. *Biological Conservation* 121, 519–531.
- Boring, L.R., Monk, C.D., Swank, W.T., 1981. Early regeneration of a clear-cut southern Appalachian forest. *Ecology* 62, 1244–1253.
- Boyles, J.G., Aubrey, D.P., 2006. Managing forests with prescribed fire: implications for a cavity-dwelling bat species. *Forest Ecology and Management* 222, 108–115.

- Brennan, L.A., Engstrom, R.T., Palmer, W.E., Hurst, G.A., Burger, L.W., Hardy, C.L., 1998. Whither wildlife without fire? Transactions of the 63rd North American Wildlife and Natural Resources Conference. 63, 402-414.
- Broders, H.G., Forbes, G.J., 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., Forbes, G.J., Woodley, S., Thompson, I.D., 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., Schuler, T., VanLear, D., Berst, J., 2001. Bringing fire back: the changing fire regimes of the Appalachian mixed-oak forests. Journal of Forestry 99, 30–35.
- Brose, P.D., VanLear, D., Cooper, R., 1999. Using shelterwood harvests and prescribed fire to regenerate oak stands on productive upland sites. Forest Ecology and Management 113, 125–141.
- Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer, New York, NY, 488 pp.
- Caceres, M.C., Barclay, R.M.R., 2000. *Myotis septentrionalis*. Mammalian Species 634, 1–4.
- Carey, A.B. 1983. Cavities in trees in hardwood forests. In: Davis, J.W., Goodwin, G.A., Ockenfels, R.A. (Eds.), Snag habitat management. USDA Forest Service, General Technical Report RM-99, pp. 167–184.

- Carter, T.C., 2006. Indiana bats in the Midwest: the importance of hydric habitats. *Journal of Wildlife Management* 70, 1185-1190.
- Carter, T.C., Feldhamer, G.A., 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.
- Chapman, B.R., 2007. Northern long-eared myotis. In: Trani-Griep, M., Ford, W.M., Chapman, B.R. (Eds.), *Land managers guide to mammals of the South*. The Nature Conservancy, Durham, NC, pp. 197–204.
- Chaverri, G., Quirós, O.E., Gamba-Rios, M., Kunz, T.H., 2007. Ecological correlates of roost fidelity in the tent-making bat *Artibeus watsoni*. *Ethology* 113, 598–605.
- Clark, F.B., 1993. An historical perspective of oak regeneration. In: Loftis, D., McGee, C. E. (Eds.), *Oak regeneration: serious problems, practical recommendations*; Knoxville, TN. USDA Forest Service, General Technical Report SE-84, Southern Research Station, Asheville, NC, pp. 3–13.
- Clarkson, R.B., 1958. The genus *Robinia* in West Virginia. *Castanea* 23, 56–58.
- Cline, S. P., Berg, A.B., Wight, H.M., 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *Journal of Wildlife Management* 44, 773–786.
- Conover, W.J., 1999. *Practical nonparametric statistics*. 3rd edition. Wiley, New York, NY, 584 pp.
- Crampton, L.H., Barclay, R.M.R., 1998. Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. *Conservation Biology* 12, 1347–1358.
- Cryan, P.M., Bogan, M.A., Yanega, G.M., 2001. Roosting habits of four bat species in the Black Hills of South Dakota. *Acta Chiropterologica* 3, 43–52.

- Edwards, J.W., Guynn, D.C., Loeb, S.C., 1993. Seasonal mast availability for wildlife in the Piedmont region of Georgia. USDA Forest Service, Research Paper SE-287, Southern Research Station, Asheville, NC, 20 pp.
- Erickson, J.L., West, S.D., 2002. The influence of regional climate and nightly weather conditions on activity patterns of insectivorous bats. *Acta Chiropterologica* 4, 17–24.
- Ford, W.M., Menzel, J.M., Menzel, M.A., Edwards, J.W., 2002. Summer roost-tree selection by a male Indiana bat on the Fernow Experimental Forest. USDA Forest Service, General Technical Report NE-378, Northeastern Research Station, Newtown Square, PA, 7 pp.
- Ford, W.M., Menzel, J.M., Menzel, M.A., Edwards, J.W., Kilgo, J.C., 2006a. Presence and absence of bats across habitat scales in the upper Coastal Plain of South Carolina. *Journal of Wildlife Management* 70, 1200–1209.
- Ford, W.M., Menzel, M.A., Rodrigue, J.L., Menzel, J.M., Johnson, J.B., 2005. Relating bat species presence to simple habitat measures in a central Appalachian forest. *Biological Conservation* 126, 528–539.
- Ford, W.M., Owen, S.F., Edwards, J.W., Rodrigue, J.L., 2006b. *Robinia pseudoacacia* (black locust) as day-roosts of male *Myotis septentrionalis* (northern bats) on the Fernow Experimental Forest, West Virginia. *Northeastern Naturalist* 13, 15–24.
- Foster, R.W., Kurta, A., 1999. Roosting ecology of the northern bat (*Myotis septentrionalis*) and comparisons with the endangered Indiana bat (*Myotis sodalis*). *Journal of Mammalogy* 80, 659–672.
- Hallett, J.G., Lopez, T., O'Connell, M.A., Borysewicz, M.A., 2001. Decay dynamics and avian use of artificially created snags. *Northwest Science* 75, 378–386.

- Hutchinson, T.F., Long, R.P., Ford, R.D., Sutherland, E.K., 2008. Fire history and the establishment of oaks and maples in second-growth forests. *Canadian Journal of Forest Research* 38, 1184–1198.
- Kahler, H.A., Anderson, J.T., 2006. Tree cavity resources for dependent cavity-using wildlife in West Virginia forests. *Northern Journal of Applied Forestry* 23, 114–121.
- Kepler, C.B., Irvine, G.W., Decapita, M.E., Weinrich, J., 1996. The conservation management of Kirtland's warbler, *Dendroica kirtlandii*. *Bird Conservation International* 6, 11–22.
- Keyser, P.K., Ford, W.M., 2006. Influence of fire and mammals in oak forests. In: Dickenson M.B. (Ed.), *Fire in eastern oak forests: a symposium*. USDA Forest Service, General Technical Report GTR-NRS-1, Northern Research Station. Newtown Square, PA. pp. 180–190.
- Kochenderfer, J.N., 2006. Fernow and the Appalachian hardwood region. In: Adams, M.B., DeWalle, D.R., Horn, J.L. (Eds.), *The Fernow watershed acidification study*. Springer, Dordrecht, Netherlands, pp. 17–39.
- Kochenderfer, J.N., Adams, M.B., Miller, G.W., Helvey, J.D., 2007. Factors affecting large peakflows on Appalachian watersheds: lessons from the Fernow Experimental Forest. USDA Forest Service, Research Paper NRS-3, Northeastern Research Station, Newtown Square, PA, 24 pp.
- Kunz, T.H., Lumsden, L.F., 2003. Ecology of cavity and foliage roosting bats. In: Kunz, T.H., Fenton, M.B. (Eds.), *Bat ecology*. University of Chicago Press, Chicago, IL, pp. 3–89.
- Lacki, M.J., Schweirjohann, J.H., 2001. Day-roost characteristics of northern bats in mixed mesophytic forests. *Journal of Wildlife Management* 65, 482–488.

- Lausen, C.L., Barclay R.M.R., 2006. Benefits of living in a building: big brown bats (*Eptesicus fuscus*) in rocks versus buildings. *Journal of Mammalogy* 87, 362–370.
- Leput, D.W., 2004. Eastern red bat (*Lasiurus borealis*) and eastern pipistrelle (*Pipistrellus subflavus*) maternal roost selection: implications for forest management. M.S. Thesis. Clemson University, Clemson, SC.
- Lewis, S.E., 1995. Roost fidelity in bats: a review. *Journal of Mammalogy* 76, 481–496.
- Loeb, S.C., O’Keefe, J.M., 2006. Habitat use by forest bats in South Carolina in relation to local, stand, and landscape characteristics. *Journal of Wildlife Management* 70, 1210–1218.
- Loeb, S.C., Waldrop, T.A., 2008. Bat activity in relation to fire and fire surrogate treatments in southern pine stands. *Forest Ecology and Management* 255, 3185–3192.
- Madarish, D.M., Rodrigue, J.L., Adams M.B., 2002. Vascular flora and macroscopic fauna on the Fernow Experimental Forest. USDA Forest Service, General Technical Report GTR-NE-291, Northeastern Research Station, Newtown Square, PA, 37 pp.
- Menzel, M.A., Carter, T.C., Ford, W.M., Chapman, B.R., 2001. Tree-roost characteristics of subadult and female adult evening bats (*Nycticeius humeralis*) in the upper Coastal Plain of South Carolina. *American Midland Naturalist* 145, 112–119.
- Menzel, M.A., Owen, S.F., Ford, W.M., Edwards, J.W., Wood, P.B., Chapman, B.R., Miller, K.V., 2002a. 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.
- Menzel, M.A., Menzel, J.M., Castleberry, S.B., Ozier, J., Ford, W.M., Edwards, J.W., 2002b. Illustrated key to skins and skulls of bats in the Southeastern and Mid-Atlantic States.

- USDA Forest Service, Research Note NE-376, Northeastern Research Station, Newtown Square, PA, 18 pp.
- Miller, D.A., Arnett, E.B., Lacki, M.J., 2003. Habitat management for forest-roosting bats of North America: a critical review of habitat studies. *Wildlife Society Bulletin* 31, 30–44.
- Miller, G.W., Schuler, T.M., Smith, H.C., 1995. Method for applying group selection in central Appalachian hardwoods. USDA Forest Service, Research Paper NE-696, Northeastern Research Station, Newtown Square, PA, 11 pp.
- Miller, J.H., 1993. Oak plantation using mechanical, burning, and herbicide treatments. In: Loftis, D., McGee, C.E. (Eds.), *Oak regeneration: serious problems, practical recommendations*. Knoxville, TN, USDA Forest Service, General Technical Report SE-84, Southern Research Station, Asheville, NC, pp 264–289.
- Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and “mesophication” of forests in the eastern United States. *BioScience* 58, 123–138.
- Nyland, R.D., 1996. *Silviculture: concepts and applications*. McGraw-Hill, New York, NY, 633 pp.
- O'Donnell, C.F.J., Sedgeley, J.A., 1999. Use of roosts by the long-tailed bat, *Chalinolobus tuberculatus*, in temperate rainforest in New Zealand. *Journal of Mammalogy* 80, 913–923.
- Owen, S.F., Menzel, M.A., Ford, W.M., Edwards, J.W., Chapman, B.R., Miller, K.V., Wood, P.B., 2002. Roost tree selection by maternal colonies of northern long-eared myotis in an intensively managed forest. USDA Forest Service, General Technical Report NE-292, Northeastern Research Station, Newtown Square, PA, 6 pp.

- Owen, S.F., Menzel, M.A., Edwards, J.W., Ford, W.M., Menzel, J.M., Chapman, B.R., Wood, P.B., Miller, K.V., 2004. Bat activity in harvested and intact forest stands in the Allegheny Mountains. *Northern Journal of Applied Forestry* 21, 154–159.
- Perry, R.W., Thill, R.E., 2007. Roost selection by male and female northern long-eared bats in a pine-dominated landscape. *Forest Ecology and Management* 247, 220–226.
- Perry, R.W., Thill, R.E., Leslie, Jr., D.M., 2007. Selection of roosting habitat by forest bats in a diverse forested landscape. *Forest Ecology and Management* 238, 156–166.
- Russell, R.E., Saab, V.A., Dudley, J.G., Rotella, J.J., 2006. Snag longevity in relation to wildfire and postfire salvage logging. *Forest Ecology and Management* 232, 179–187.
- SAS Institute, Inc. 2004. SAS/STAT 9.1 users guide. Version 9.1. SAS Institute, Inc., Cary, NC, 5,121 pp.
- Sasse, D.B., Pekins, P.J., 1996. Summer roosting ecology of northern long-eared bats (*Myotis septentrionalis*) in the White Mountain National Forest. In: Barclay R.M.R., Brigham, R.M. (Eds.), *Bats and forests symposium*. British Columbia Ministry of Forests Working Paper 23/1996, Victoria, Canada, pp. 91–101.
- Schuler, T.M., 2004. Fifty years of partial harvesting in a mixed mesophytic forest: composition and productivity. *Canadian Journal of Forest Research* 34, 985–997.
- Schuler, T.M., Fajvan, M.A., 1999. Understory tree characteristics and disturbance history of a central Appalachian forest prior to old-growth harvesting. USDA Forest Service, Research Paper NE-710, Northeastern Research Station, Radnor, PA, 12 pp.
- Sedgeley, J.A., 2001. Quality of cavity microclimate as a factor influencing selection of maternity roosts by a tree-dwelling bat, *Chalinolobus tuberculatus*, in New Zealand. *Journal of Applied Ecology* 38, 425–438.

- Sedgeley, J.A., O'Donnell, C.F.J., 1999. Factors influencing roost cavity selection by a temperate rainforest bat (*Chalinolobus tuberculatus*, Vespertilionidae) in New Zealand. *Journal of Zoology* 249, 437–446.
- Shumway, D.L., Abrams, M.D., Ruffner, C.M., 2001. A 400-year history of fire and oak recruitment in an old-growth oak forest in western Maryland, U.S.A. *Canadian Journal of Forest Research* 31, 1437–1443.
- Smith, K.T., Sutherland, E.K., 1999. Fire-scar formation and compartmentalization in oak. *Canadian Journal of Forest Research* 29, 166–171.
- Thatcher, B.S., Krementz, D.G., Woodrey, M.S., 2006. Henslow's sparrow winter-survival estimates and response to prescribed burning. *Journal of Wildlife Management* 70, 198–206.
- Tucker, J.W., Jr., Robinson, W.D., Grand, J.B., 2004. Influence of fire on Bachman's sparrow, an endemic North American songbird. *Journal of Wildlife Management* 68, 1114–1123.
- Turbill, C., Geiser F., 2008. Hibernation by tree-roosting bats. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* 178, 597–605.
- Turner, M.G., Hargrove, W.W., Gardner, R.H., Romme, W.H., 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *Journal of Vegetation Science*, 5, 731–742.
- Wilkinson, G.S., 1985. The social organization of the common vampire bat. *Behavioral Ecology and Sociobiology* 17, 111–121.
- Yamamoto, S., 1992. The gap theory in forest dynamics. *Botanical Magazine* 105, 375–383.

Table 1.

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

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

Table 2.

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

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

Table 3.

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

Parameter	Estimate	SE	Wald χ^2	$P > \text{Wald } \chi^2$	Odds Ratio	95% CL
Fire tree use (vs. fire potential tree use)						
ROOSTTREE+TREECLUSTER+SITE ^{a, b}						
Intercept	12.180	10.249	1.413	0.235		
DBHR	-0.171	0.086	4.020	0.045	0.84	0.71–0.99
DECAYR	0.432	0.390	1.229	0.277	1.54	0.72–3.31
CROWNR	1.454	0.888	2.684	0.101	4.28	0.75–24.37
ROOSTTYPE	3.095	1.899	2.655	0.103	22.09	0.53–913.98
DISTN	-1.772	0.809	4.801	0.028	0.17	0.04–0.83
DECAYN	-0.339	1.093	0.096	0.756	0.71	0.08–6.07
CROWNN	0.775	1.732	0.200	0.655	2.17	0.07–64.72
ASPECT	-0.020	0.013	2.404	0.121	0.98	0.96–1.01
SLOPE ^c	-0.106	0.057	3.525	0.061	0.90	0.81–1.01
BASAL	-0.033	0.016	4.462	0.035	0.97	0.94–0.99
UNDERSTORY ^c	0.025	0.022	1.282	0.258	1.03	0.98–1.07
Control tree use (vs. control potential tree use)						
TREECLUSTER ^d						
Intercept	-6.970	2.806	6.170	0.013		
DBHR	0.019	0.023	0.711	0.399	1.02	0.98–1.07
ROOSTHGHT	0.147	0.088	2.802	0.094	1.16	0.98–1.38

Table 3. Continued.

Parameter	Estimate	SE	Wald χ^2	$P > \text{Wald } \chi^2$	Odds Ratio	95% CL
BARK	-0.016	0.010	2.720	0.099	0.98	0.97–1.00
CROWNR	0.071	0.483	0.022	0.883	1.07	0.42–2.77
ROOSTTYPE	1.755	0.685	6.573	0.010	5.78	1.51–22.12
DISTN	0.178	0.331	0.288	0.591	1.19	0.63–2.28
DBHN	-0.117	0.063	0.711	0.399	0.89	0.79–1.01
DECAYN	1.121	0.419	7.147	0.008	3.07	1.35–6.98
CROWNN	2.201	0.957	5.291	0.021	9.04	1.39–58.95
Fire tree use (vs. control tree use)						
GAP ^c						
Intercept	-9.766	3.121	9.795	0.002		
TOTALGAP ^c	59.497	26.087	5.202	0.023	>999.99	>999.99– >999.99
NORTHGAP ^c	11.995	12.459	0.927	0.336	>999.99	<0.01– >999.99
EASTGAP ^c	28.928	12.141	5.677	0.018	>999.99	169.43– >999.99
OVERHEADGAP ^c	-4.789	6.560	0.533	0.465	0.01	<0.01– >999.99

^a Hosmer-Lemeshow $\chi^2 = 2.397$, $P = 0.935$; Concordance = 92.6%

^b Model-averaged statistics presented.

^c Analyses performed on arcsine-transformed data.

^d Hosmer-Lemeshow $\chi^2 = 13.851$, $P = 0.086$; Concordance = 80.3%

^e Hosmer-Lemeshow $\chi^2 = 10.056$, $P = 0.261$; Concordance = 92.9%

Table 4.

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

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

Table 5.

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

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

^a Includes cavity and exfoliating bark roost trees.

^b Comparison made with Fisher's Exact test.

^c Diameter at breast height.

^d Comparison made with Wilcoxon test.

^e Crown class following Nyland (1996).

^f Decay class following Cline et al. (1980).

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

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

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

Chapter 3

RH: Northern myotis nocturnal activity patterns

Nocturnal roosting activity patterns of northern myotis (*Myotis septentrionalis*) during the maternity season in West Virginia ¹

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ABSTRACT

Nocturnal activity patterns of northern myotis (*Myotis septentrionalis*) at diurnal roost trees remain largely uninvestigated. Moreover, the influences of reproductive status, weather, and roost tree characteristics on timing of emergence, intra-night activity, and entrance at their roost trees is poorly known. We examined nocturnal activity patterns of northern myotis maternity colonies during pregnancy and lactation at diurnal roost trees situated in areas that were and were not subjected to recent prescribed fires at the Fernow Experimental Forest, West Virginia from 2007 to 2009. According to exit counts and acoustic data, northern myotis colony sizes were similar between reproductive periods and roost tree settings. However, intra-night activity patterns differed slightly between reproductive periods and between roost trees in burned and non-burned areas. Weather variables poorly explained variation in activity patterns during

¹ Manuscript formatted for Acta Chiropterologica

pregnancy, but precipitation and temperature were negatively associated with activity patterns during lactation.

Key words: Anabat, bats, *Myotis septentrionalis*, night-roosting, northern myotis, West Virginia

INTRODUCTION

Temperate bat species are nocturnal and exhibit nightly and seasonal activity patterns that vary among species and individuals (Hirshfield et al., 1977; Anthony et al., 1981). During summer nights, bat roost-emergence activity commonly peaks immediately after sunset and can continue for several hours (Kunz, 1973; Barclay, 1982). Typically, a lesser activity peak occurs before sunrise as bats return to their diurnal roosts after foraging (Kunz, 1973). During the night, bats roost at intervals, either at their diurnal roosts or at night roosts nearer their foraging areas (Adam and Hayes, 2000; Johnson et al., 2002; Daniel et al., 2008).

Females of some species form maternity colonies in anthropogenic structures such as buildings and/or trees during summer (Barbour and Davis, 1969; Lewis, 1995). During the maternity season, particularly during the lactation period, females return to their diurnal roosts several times during the night to nurse their young (Henry et al., 2002). Activity at diurnal roosts at night typically is greater during lactation than during pregnancy (Henry et al., 2002).

Very little research has examined bat activity patterns at non-anthropogenic roost sites or activity patterns of northern myotis maternity colonies (Barclay and Cash, 1985; Barclay, 1989; Hickey and Fenton, 1996; Broders et al., 2006). Additionally, how increased solar exposure to roost trees following forest disturbances, including partial-harvesting or prescribed fire, impacts nocturnal bat activity patterns at diurnal roost trees remains uninvestigated (Boyles and Aubrey,

2006; Johnson et al., 2009). Increasing solar exposure may increase roost temperatures, resulting in increased energetic demands on females due to increased growth rates of neonates (Tuttle, 1975; Boyles and Aubrey, 2006; Ruczyński, 2006). Consequently, energetic demands of females would be expected to be greater during lactation, resulting in higher intra-night activity at roosts (Henry et al., 2002). Intra-night activity at maternity colonies may be higher at roost trees experiencing increased solar radiation because females return more frequently to feed their rapidly growing young (Henry et al., 2002).

Our objectives were to determine if nocturnal bat activity at diurnal roost trees of northern myotis differed between pregnancy and lactation reproductive periods; and to examine the influence of weather on activity patterns. Also, we investigated if any differences in bat activity existed between roost trees in areas subjected to prescribed fire compared to those in non-burned areas. We hypothesized: 1) that peak bat activity would occur at dusk and at dawn as bats exited from and returned to their roost trees, 2) that more intra-night activity would be recorded during the lactation period than during the pregnancy period, and 3) that more activity would be recorded at diurnal roost trees located in areas subjected to prescribed fire than those in non-burned areas.

MATERIALS AND METHODS

Study area

We conducted our research at the Fernow Experimental Forest (FEF) in Tucker County, West Virginia. The FEF is a 1,900 ha experimental forest managed by the U.S. Forest Service, Northern Research Station, and is located in the Unglaciated Allegheny Mountains subsection of the Appalachian Plateau Physiographic Province (Kochenderfer et al., 2007). Elevations range from 530 to 1,100 m. Ellick Run, a 2.4-km fourth-order stream, roughly bisects FEF east to

west. Approximately 5.5 km of dendritic intermittent and permanent streams feed into Ellick Run and incise the steep slopes and plateau-like ridgetops (Madarish et al., 2002). Mean annual precipitation at FEF is 145.8 cm, ranging from 9.7 cm in October to 14.4 cm in June. Mean annual temperature is 9.2° C, ranging from –18.0° C in January to 20.6° C in July (Kochenderfer, 2006). Vegetation at the FEF is a mosaic of second- and third-growth, mixed-mesophytic and northern hardwood forest that has been managed by even (patch clearcut)- and uneven (single-tree selection)-aged silviculture since the mid-20th century, or has been left undisturbed following initial harvesting in the Ellick watershed from 1903 to 1911 (Schuler and Fajvan, 1999; Schuler, 2004). In spring 2007 to 2009, prescribed fire treatments were conducted in 3 management compartments totaling ca. 146 ha on FEF. The three management compartments were burned for 1 day during each treatment using a strip head fire technique, ignited with hand-held drip torches. Actual flame heights and combustion varied from dying out to >3.5 m high in some spots, due to variability in leaf litter, slope, and aspect. Additionally, 48, 20-m radius plots were randomly located in each of the three management compartments, and all overstory or midstory trees, other than oak (*Quercus* spp.) or hickory (*Carya* spp.), were herbicided or girdled (T. Schuler, USDA Forest Service, personal communication).

Radio telemetry

To capture bats, we placed mist nets (Avinet, Inc., Dryden, New York) over stream corridors, small pools, skidder trails, and service roads from May to July 2007–2009. For each captured bat, we determined species, sex, age, weight, forearm length, and reproductive condition. We used Skin Bond[®] (Smith and Nephew, Largo, Florida) surgical cement to affix a 0.35-g radio transmitter (Model LB-2N; Holohil Systems Ltd., Carp, Ontario, Canada) between the scapulae of captured female northern myotis. Bat capture and handling protocols were approved by the

Animal Care and Use Committee of West Virginia University (Protocol No. 08-0504) and followed the guidelines of the American Society of Mammalogists (ACUC, 1998). We used a radio receiver and 3-element Yagi antenna (Wildlife Materials, Inc., Murphysboro, Illinois) to locate radio-tagged bats daily.

Acoustic monitoring and exit counts

We used Anabat II (Titely Electronics, Ballina, Australia) broadband, frequency-division, bat detectors to passively monitor for bat echolocation passes, i.e., a series of echolocation pulses, at a random sample of diurnal roost trees (Sasse and Pekins, 1996). We positioned the detector on the ground with the microphone oriented 45–90° angle from horizontal towards the diurnal roost tree. The bat detectors were programmed to monitor from 1 hour prior to sunset to 1 hour after sunrise. We conducted monitoring at diurnal roost trees on the nights we located radio-telemetered bats at those particular trees. Echolocation passes were recorded to an Anabat CompactFlash storage Zero-Crossing Analysis Interface Module (ZCAIM) and downloaded to a computer for analysis using Analook 4.8p software (Corben, 2001). We used qualitative and quantitative echolocation pass identification methods (Fenton and Bell, 1981; O’Farrell et al., 1999; Murray et al., 2001). We identified echolocation passes of some species by comparing our unknowns to a library comprised of echolocation passes collected from hand-released bats marked with chemiluminescent tags collected throughout the southeastern and mid-Atlantic United States. We only attempted identification of echolocation passes containing ≥ 3 pulses. Northern myotis echolocation passes were distinguished from congeners by the characteristic slope ($\Delta \geq 200$ octaves per second) of each pulse. Our identifications were limited to species as no acoustical techniques exist at present to reliably distinguish male/female or adult/juvenile bat echolocation calls. Moreover, number of echolocation passes recorded is an index of activity and

does not necessarily reflect the number of bats being recorded as an individual can be recorded multiple times within a small window of time (Broders, 2003). We conducted exit counts at a random set of roost trees in non-burned and burned areas, and during pregnancy and lactation periods. We commenced exit counts approximately 1 hour before sunset and continued until darkness prevented us from observing emerging bats (Menzel et al., 2002).

Statistical analysis

We used Mann-Whitney tests to compare mean nightly and mean hourly bat passes, defined as the number of echolocation pass sequences recorded, between reproductive periods (pregnancy and lactation) and between roost trees in non-burned and burned areas (Proc Npar1way, SAS Institute, Inc., 2004). We defined pregnancy and lactation periods by examining the reproductive condition of female northern myotis captured during mist-netting efforts that occurred concurrent with acoustic monitoring of roost trees. We noted if roost trees were located in areas that had recently (2007 and thereafter) been burned or were in areas that had not recently been burned (Johnson et al., 2009). Before making comparisons of mean bat passes among hours following sunset within each reproductive period or each roost tree setting (burned or non-burned), we used a time-series analysis to examine hourly means for temporal autocorrelation (RDCT, 2008). Partial autocorrelation coefficients exceeding 5% confidence limits, i.e., partial autocorrelation (PACF) = $|0.59|$, were considered significantly autocorrelated (Montgomery et al., 2008). To determine if hourly mean bat passes within nights differed within reproductive periods and within roost tree settings, we performed a 1-way analysis of variance on ranked data (Proc Rank; Proc GLM, SAS Institute, Inc., 2004). Significant differences among ranked mean bat passes were separated using Duncan's New Multiple Range Test.

We examined possible influence of weather variables on bat activity within the pregnancy and lactation periods using Spearman's correlation coefficients (Proc Corr, SAS Institute, Inc., 2004). Weather variables included hourly precipitation totals (Precip), daily minimum (MinT) and maximum temperatures (MaxT), and mean hourly temperatures (HrT). We obtained precipitation data, and daily minimum and maximum temperatures from a weather station maintained on the FEF (US Forest Service, unpublished data). Mean hourly temperatures were measured at a random sample of roost trees with StowAway[®] Tidbit[®] (Onset Computer Corp., Pocasset, Massachusetts) data loggers that recorded ambient temperature every minute. Lastly, we used Mann-Whitney tests to compare exit counts between roost trees in non-burned and burned areas, and between pregnancy and lactation periods. We used simple regression to evaluate trends in exit counts during summer. Statistical significance for all tests was set at $\alpha = 0.05$.

RESULTS

We radio-tracked 29 female northern myotis (21 pregnant, 8 lactating) to 40 roost trees (28 during the pregnancy period, 13 during the lactation period, 1 roost tree was used during both reproductive periods; and 23 in non-burned areas and 17 in burned areas). We acoustically monitored for 52 sample nights (34 during the pregnancy period and 18 during the lactation period; and 27 in non-burned and 25 in burned areas).

Mean bat passes per hour were similar ($P = 0.916$) between the pregnancy (7.43 ± 2.10 echolocation passes; mean $\pm$ SE), and lactation periods (7.79 ± 2.51). Mean bat passes were similar ($P = 0.226$) at roost trees in non-burned (9.48 ± 2.95) and burned areas (6.00 ± 2.05). Within nights, mean hourly echolocation passes were not serially autocorrelated during the pregnancy ($\text{PACF} \leq |0.293|$) or lactation ($\text{PACF} \leq |0.362|$) periods, or in non-burned ($\text{PACF} \leq$

|0.322| or burned areas ($\text{PACF} \leq |0.349|$). During pregnancy, activity peaked just prior to sunrise (Fig. 1A), with mean bat passes differing between the 10th, and 1st and 7th hours after sunset (Table 1). During lactation, activity peaked during the 3rd hour after sunset (Fig. 1B), which differed from all other hours but the 4th and 10th (Table 1). Among hours between reproductive periods, only the 3rd hour after sunset differed; mean bat passes were higher during lactation (Table 1).

Bat activity was poorly associated with weather variables during pregnancy (Precip: $\rho = -0.013$, MaxT: $\rho = -0.064$, MinT: $\rho = 0.050$, HrT: $\rho = 0.028$) and to some extent during lactation (Precip: $\rho = -0.001$, HrT: $\rho = -0.003$). Maximum daily temperatures ($\rho = -0.347$) and minimum nightly temperatures ($\rho = -0.195$) were negatively associated with bat activity during lactation.

Within non-burned areas, mean hourly bat passes peaked just before sunrise (Fig. 2A). Mean bat passes during the 10th hour after sunset were higher than other hours except for the 3rd, 4th, and 9th hours (Table 2). Within burned areas, mean hourly bat passes peaked in the 3rd and 4th hours following sunset (Fig. 2B). Mean bat passes during the 3rd and 4th hours following sunset were similar to all but the 1st and 11th hours following sunset (Table 2). Among hours between non-burned and burned areas, mean passes differed in the 1st, 10th, and 11th hours; mean bat passes were higher at trees in non-burned areas (Table 2).

Exit counts were similar ($P = 0.461$) between roost trees in non-burned ($n = 6$ samples, range = 2–48 bats, 27.2 ± 9.1 bats) and burned ($n = 11$ samples, range = 1–33 bats, 14.1 ± 2.8 bats) areas. Exit counts also were similar ($P = 0.740$) between pregnancy ($n = 9$ samples, range = 1–48 bats, 21.1 ± 7.2 bats) and lactation ($n = 8$ samples, range = 7–20 bats, 16.0 ± 1.5 bats) periods. Exit counts declined ($\beta = -0.54$) over the summer ($r^2 = 0.13$) (Fig. 3).

DISCUSSION

Nocturnal activity of female northern myotis at diurnal roost trees largely was unaffected by reproductive period or roost tree setting. Exit counts and mean nightly bat passes both indicated that northern myotis colony sizes were similar between reproductive periods and between roost trees in burned and non-burned areas. Colony sizes were slightly less than those recorded previously in West Virginia (Menzel et al., 2002) and Nova Scotia (Garroway and Broders, 2007). Colony size slightly decreased during summer, possibly due to group fission dynamics (Garroway and Broders, 2007). During pregnancy, intra-night activity patterns of northern myotis steadily increased before sunrise, as bats were returning from initial foraging bouts (Henry et al., 2002). A lack of activity peak after sunset during pregnancy may have been due to a gradual emergence of the colonies. Energetic demands during lactation may necessitate prompt foraging after sunset, resulting in more synchronized emergence activity (Anthony and Kunz, 1977; McWilliam, 1989). We did not observe a peak in activity of lactating bats until the 3rd hour following sunset, probably as bats were returning from their first foraging bout to nurse their young (Henry et al., 2002). Thereafter, females may have intermittently emerged and returned from foraging to nurse their young, resulting in similar activity levels throughout the night until a small peak before sunrise as more bats returned for diurnal roosting (Henry et al., 2002). During pregnancy, it is common for female bats to use night-roosts that are not their diurnal roosts (Henry et al., 2002; Murray and Kurta, 2004).

Energetic requirements on female bats during different reproductive periods are well-documented; meeting those demands can be affected by weather conditions and insect availability (Anthony et al., 1981; Barclay, 1982; Hickey and Fenton, 1996). Compared to the lactation period, during pregnancy, weather variables were not strong predictors of bat activity in our study. Absolute energetic demands of bats during pregnancy are less than that during

lactation (Speakman and Thomas, 2003). Therefore, we may expect weather conditions to have less influence on bat activity during the pregnancy period. Similar to our findings, lactating little brown myotis (*Myotis lucifugus*) activity has been shown to be negatively correlated with minimum nightly temperatures (Anthony et al., 1981). During cooler nights, insect activity decreases, causing bats to forage less, and thereby remain in roost trees to conserve energy (Anthony et al., 1981; Hickey and Fenton, 1996). Moreover, cooler nightly temperatures may necessitate females spending more time in their roost trees to maintain internal roost temperatures to foster juvenile growth and survival (Tuttle, 1975). Because bats spent more time in their roosts on cooler nights, we detected fewer echolocation passes on these nights.

The effects of prescribed fire around or near diurnal roosts had little effect on the nocturnal activity patterns of northern myotis maternity colonies. At roost trees in both non-burned and burned areas, intra-night activity showed peaks (although not significant in all cases) 3 hours after sunset and again just before sunrise, probably as bats were returning after their first foraging bout and for diurnal roosting, respectively (Henry et al., 2002). Although overall mean bat passes were similar between roost trees within non-burned and burned areas, there were few hourly differences between roost trees in the two treatments during the emergence and entrance periods. Contrary to our predictions, activity during these hours was greater at roost trees in non-burned areas than in burned areas. It is possible that the increased solar exposure at roost trees in burned areas would negatively affect colony size because occupancy by fewer individuals would be necessary to maintain favorable roost temperatures (Johnson et al., 2009). However, according to exit counts and acoustic data, there were no differences in colony size between roost tree settings. Prescribed fire in our study area resulted in canopy gaps over roost trees, resulting in increased temperatures at roost trees during the day (Johnson et al., 2009). Nightly

temperatures did not differ between roost trees in non-burned and burned areas. We would expect the increase in solar exposure to increase energetic demands, similar to that experienced during lactation, which would result in a more concentrated emergence. Canopy gap sizes varied more at roost trees in burned areas than in non-burned areas (Johnson et al., 2009), possibly resulting in less-concentrated emergence events at the former. This phenomenon could be influenced by a combination of factors, including relatively high variation in energetic demand for bats using roost trees in burned areas compared to those in non-burned areas. Or, more simply, variation in perceived twilight times at roost trees in burned areas. Whereas emergence times may be more synchronized in forest stands with intact canopies, or at those with canopy gaps of similar size, they may vary more at trees in burned areas due to variation among canopy gaps. Bat emergence times typically are correlated highly with sunset, but can be shifted earlier during cloudy evenings (McWilliam, 1989). Varying light conditions at roost trees in burned areas may have been significant enough to delay or advance emergence times to different hourly data bins, i.e., 1st or 2nd hour after sunset.

CONCLUSIONS

Our study indicates that northern myotis nocturnal activity patterns are similar to that of other temperate bat species (Henry et al., 2002). Overall nightly activity at diurnal roost trees did not differ between reproductive periods or between roost trees in non-burned and burned areas. Within nights, activity typically peaked 3 hours after sunset as northern myotis presumably returned from their first foraging bout and again prior to sunrise before returning for diurnal roosting. Weather variables were poorly correlated with activity during pregnancy, but negatively correlated with activity during lactation, a particularly energetically-expensive period.

Nocturnal activity patterns were similar overall between roost trees in non-burned and burned areas, but hourly activity was higher at trees in non-burned areas at sunset and before sunrise.

ACKNOWLEDGMENTS

We thank the staff of the USDA Forest Service Monongahela National Forest and the USDA Forest Service Northern Research Station Timber and Watershed Laboratory for conducting the prescribed burns. J. Rodrigue graciously provided field assistance. F. Wood provided much needed weather data from the Fernow Experimental Forest. The USDA Forest Service Northern Research Station Joint Venture Agreement 06-JV-11242300-140 provided primary funding for our study from the National Fire Plan to West Virginia University, Division of Forestry and Natural Resources. Funding for prescribed burning was provided by a grant from Florida Power and Light and BHE Environmental to the U.S. Forest Service Northern Research Station through Collection Agreement 06-CO-112331-034.

LITERATURE CITED

- Adam, M. D., and J. P. Hayes. 2000. Use of bridges as night roosts by bats in the Oregon coast range. *Journal of Mammalogy*, 81:402–407.
- Animal Care and Use Committee (ACUC). 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy*, 79:1416–1431.
- Anthony, E. L. P., and T. H. Kunz. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology*, 58:755–786.
- Anthony, E. L. P., M. H. Stack, and T. H. Kunz. 1981. Night roosting and the nocturnal time budget of the little brown bat, *Myotis lucifugus*: effects of reproductive status, prey density, and environmental conditions. *Oecologia*, 51:151–156.

- Barbour, R. W., and W. H. Davis. 1969. Bats of America. University Press of Kentucky, Lexington, KY. 312 pp.
- Barclay, R. M. R. 1982. Night roosting behavior of the little brown bat, *Myotis lucifugus*. Journal of Mammalogy, 63:464–474.
- 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 K. J. Cash. 1985. A non-commensal maternity roost of the little brown bat (*Myotis lucifugus*). Journal of Mammalogy, 66:782–783.
- 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.
- Broders, H. G. 2003. Another quantitative measure of bat species activity and sampling intensity considerations for the design of ultrasonic monitoring studies. Acta Chiropterologica, 5:235–241.
- 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.
- Corben, C. 2001. Analook. Version 4.8p. Computer software. IBM.
- Daniel, S., C. Korine, and B. Pinshow. 2008. Central-place foraging in nursing, arthropod-gleaning bats. Canadian Journal of Zoology, 86:623–626.
- Fenton, M. B., and G. P. Bell. 1981. Recognition of species of insectivorous bats by their echolocation calls. Journal of Mammalogy, 62:233–243.

- Garroway, C. J., and H. G. Broders. 2007. Nonrandom association patterns at northern long-eared bat maternity roosts. *Canadian Journal of Zoology*, 85:956–964.
- Henry, M., D. W. Thomas, R. Vaudry, and M. Carrier. 2002. Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). *Journal of Mammalogy*, 83:767–774.
- Hickey, M. B. C., and M. B. Fenton. 1996. Behavioural and thermoregulatory responses of female hoary bats, *Lasiurus cinereus* (Chiroptera: Vespertilionidae), to variations in prey availability. *Ecoscience*, 3:414–422.
- Hirshfeld, J. R., Z. C. Nelson, and W. G. Bradley. 1977. Night roosting behavior in four species of desert bats. *Southwestern Naturalist*, 22:427–433.
- Johnson, J. B., J. W. Edwards, W. M. Ford, and J. E. Gates. 2009. Roost tree selection by northern myotis (*Myotis septentrionalis*) maternity colonies following prescribed fire in a Central Appalachian Mountains hardwood forest. *Forest Ecology and Management*, 258:233–242.
- Johnson, J. B., M. A. Menzel, J. W. Edwards, and W. M. Ford. 2002. Gray bat night-roosting under bridges. *Journal of the Tennessee Academy of Science*, 77:91–93.
- Kochenderfer, J. N. 2006. Fernow and the Appalachian hardwood region. Pp. 17–39 in *The Fernow watershed acidification study* (M. B. Adams, D. R. DeWalle, and J. L. Horn, eds.). Springer, Dordrecht, Netherlands. 279 pp.
- Kochenderfer, J. N., M. B. Adams, G. W. Miller, J. D. Helvey. 2007. Factors affecting large peakflows on Appalachian watersheds: lessons from the Fernow Experimental Forest. USDA Forest Service, Research Paper NRS-3, Northeastern Research Station, Newtown Square, PA, 24 pp.

- Kunz, T. H. 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. *Journal of Mammalogy*, 54:14–32.
- Lewis, S. E. 1995. Roost fidelity in bats: a review. *Journal of Mammalogy*, 76:481–496.
- Madarish, D.M., J. L. Rodrigue, and M. B. Adams. 2002. Vascular flora and macroscopic fauna on the Fernow Experimental Forest. USDA Forest Service, General Technical Report GTR-NE-291, Northeastern Research Station, Newtown Square, PA.
- McWilliam, A. N. 1989. Emergence behaviour of the bat *Tadarida (Chaerephon) pumila* (Chiroptera: Molossidae) in Ghana, West Africa. *Journal of Zoology*, 219:698–701.
- Menzel, M. A., S. F. Owen, W. M. Ford, J. W. Edwards, P. B. Wood, B. R. Chapman, and K. V. Miller. 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.
- Montgomery, D. C., C. L. Jennings, and M. Kulachi. 2008. Introduction to time series analysis and forecasting. Wiley, Hoboken, NJ. 445 pp.
- Murray, K. L., E. R. Britzke, and L. W. Robbins. 2001. Variation in search-phase calls of bats. *Journal of Mammalogy*, 82:728–737.
- Murray, S. W., and A. Kurta. 2004. Nocturnal activity of the endangered Indiana bat (*Myotis sodalis*). *Journal of Zoology*, 262:197–206.
- O’Farrell, M. J., B. W. Miller, and W. L. Gannon. 1999. Qualitative identification of free-flying bats using the Anabat detector. *Journal of Mammalogy*, 80:11–23.
- R Development Core Team (RDCT). 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

- 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.
- SAS Institute, Inc. 2004. SAS STAT 9.1 users guide. Version 9.1. SAS Institute, Inc., Cary, NC.
- Sasse, D. B., and P. J. Pekins. 1996. Summer roosting ecology of northern long-eared bats (*Myotis septentrionalis*) in the White Mountain National Forest. Pp. 91–101 in Bats and Forests symposium (R. M. R. Barclay and R. M. Brigham, eds.). British Columbia Ministry of Forests Working Paper 23/1996, Victoria, Canada.
- Schuler, T. M. 2004. Fifty years of partial harvesting in a mixed mesophytic forest: composition and productivity. Canadian Journal of Forest Research, 34:985–997.
- Schuler, T. M., and M. A. Fajvan. 1999. Understory tree characteristics and disturbance history of a central Appalachian forest prior to old-growth harvesting. USDA Forest Service, Res. Pap. NE-710, Northeastern Research Station, Radnor, PA.
- Speakman, J. R., and D. W. Thomas. 2003. Physiological ecology and energetics of bats. Pp. 430–490 in Bat Ecology (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, IL. 779 pp.
- Tuttle, M. D. 1975. Population ecology of the gray bat (*Myotis grisescens*): factors influencing early growth and development. Occasional Papers of the Museum of Natural History. University of Kansas, 36:1–24.

Table 1. Female northern myotis (*Myotis septentrionalis*) night-roosting activity during pregnancy ($n = 34$ samples) and lactation ($n = 18$ samples) reproductive periods at the Fernow Experimental Forest, West Virginia, 2007–2009.

Hour ^a	Pregnant		Lactating		<i>P</i>
	Mean ^b	SE	Mean	SE	
1	3.32 BC	0.91	2.17 BC	0.99	0.119
2	6.82 ABC	1.93	5.44 BC	2.05	0.476
3	7.74 ABC	3.31	19.56 A	7.03	0.041
4	8.24 ABC	4.05	13.28 AB	4.49	0.054
5	7.35 ABC	2.37	8.67 BC	2.84	0.302
6	7.29 ABC	2.51	7.89 BC	3.20	0.186
7	6.06 BC	2.16	6.28 BC	2.71	0.488
8	7.59 ABC	2.52	5.67 BC	2.90	0.228
9	10.85 AB	3.24	7.00 BC	3.27	0.436
10	15.47 A	4.51	9.50 ABC	3.58	0.300
11	0.97 C	0.71	0.22 C	0.22	0.245

^a Hours after sunset.

^b Mean number of echolocation passes per hour detected followed by different capital letters were significantly different according to Duncan's New Multiple Range Test.

Table 2. Female northern myotis (*Myotis septentrionalis*) night-roosting activity at roost trees in non-burned ($n = 27$ samples) and burned ($n = 25$ samples) areas of the Fernow Experimental Forest, West Virginia, 2007–2009.

Hour ^a	Non-burned		Burned		<i>P</i>
	Mean ^b	SE	Mean	SE	
1	4.81 BC	1.14	0.88 B	0.46	0.006
2	9.74 BC	2.42	2.68 AB	1.09	0.086
3	14.70 AB	5.51	8.72 A	3.49	0.829
4	11.59 ABC	5.08	8.24 A	3.32	0.643
5	9.48 BC	2.95	6.00 AB	2.05	0.574
6	9.74 BC	3.05	5.08 AB	2.37	0.147
7	8.41 BC	2.63	3.68 AB	1.97	0.063
8	9.70 BC	3.06	3.92 AB	2.14	0.122
9	13.74 AB	3.90	4.96 AB	2.43	0.125
10	21.52 A	5.56	4.64 AB	1.69	0.030
11	1.37 C	0.89	0.00 B	0.00	0.026

^a Hours after sunset.

^b Mean number of echolocation passes per hour detected followed by different capital letters were significantly different according to Duncan's New Multiple Range Test.

Figure Captions

Fig. 1 Mean (± 1 SE) hourly activity of northern myotis (*Myotis septentrionalis*) during pregnancy (A) and lactation (B) at the Fernow Experimental Forest, West Virginia, 2007–2009.

Fig. 2 Mean (± 1 SE) hourly activity of northern myotis (*Myotis septentrionalis*) at roost trees in non-burned (A) and burned (B) areas of the Fernow Experimental Forest, West Virginia, 2007–2009.

Fig. 3 Exit counts at northern myotis maternity colonies during summer 2008–2009 at the Fernow Experimental Forest, West Virginia.

Fig. 1

Fig. 2

Fig. 3

Chapter 4

Roost networks of non-randomly associating northern myotis (*Myotis septentrionalis*) in a disturbed landscape.

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Abstract

Maternity groups of many bat species are known to conform to fission-fusion models, and the movements among roost trees of individual bats belonging to these groups form networks of roost trees. That these roost networks may exist as scale-free networks, where a central node roost tree is connected more highly to other roost trees, suggests a relative importance among roost trees to bat maternity colonies. Also, forest disturbances such as prescribed fire may alter roost networks and characteristics of roost trees and central node roost trees. At the Fernow Experimental Forest in West Virginia, 2008–2009, we examined roost networks of northern myotis (*Myotis septentrionalis*) in forest stands subjected to prescribed fire and those that were not. We determined that northern myotis conformed to fission-fusion models, forming social groups whose roost areas and roost networks overlapped to some extent. Roost networks largely resembled scale-free network models, 61% of which had a single

identifiable central node roost trees around where the remainder of the roost trees in the network were centered. In control, i.e., unburned, treatments, central node roost trees were in early stages of decay and surrounded by higher basal area than other trees within the networks. In prescribed fire treatments, central node roost trees were smaller in diameter, lower in the forest canopy, and surrounded by lower basal area than other trees in the networks. Compared to central node roost trees in control treatments, those in prescribed fire treatments had higher amounts of bark coverage. Our results indicate that northern myotis form social groups that roost in networks of trees that center on a central node roost tree that is selected based on surrounding basal area and decay stage characteristics. Forest disturbances such as prescribed fire may result in changes to roost networks through inputs of suitable roost trees by senescence and creation of forest canopy gaps.

Key words: bats, fission-fusion, graph theory, *Myotis septentrionalis*, northern myotis, roost selection, West Virginia

Introduction

Nonrandom intraspecific associations among individuals have been documented in a variety of mammals, including bats (Wilkinson 1985, Holekamp et al. 1997, Ottensmeyer and Whitehead 2003, Lehmann and Boesch 2004, Cross et al. 2005). From an evolutionary perspective, the advantages of forming nonrandom associations mostly exceed the disadvantages, and several specific mechanisms underlying the advantages have been posited (Alexander 1974). Groups may form (fusion) as a defensive mechanism, for efficient information transfer, to facilitate food sharing, and cooperative rearing of offspring (Alexander 1974, Wilkinson 1985, Emlen 1994, Kerth 2008). Disadvantages of group formation and causes for group separation (fission) include intra-group competition for resources, increased parasite loads, and disease

transmission (Wilkinson 1985, Krause and Ruxton 2002, Kerth 2008). Therefore, group size may be in constant flux. This fission-fusion dynamic operates to achieve optimal size to maximize individuals' fitness in response to varying intrinsic factors such as reproductive cycle or extrinsic factors such as habitat conditions or weather.

Fission-fusion dynamics have been documented in a number of bat species, yet few studies have investigated causal mechanisms or effects of changing habitat conditions on these dynamics (Wilkinson 1985, O'Donnell and Sedgeley 1999). Indeed, effects of forest structure and degree and type of disturbance on fission-fusion dynamics have been largely ignored, yet the accepted paradigm is that defined social groups of animals should be one of the focal units of conservation (O'Donnell 2000, Willis and Brigham 2004, Rhodes 2007). These bat groups may be regarded as a management unit because females exhibit strong natal philopatry, returning to the same areas, and even specific roost trees, in consecutive years, suggesting selection and possible limitation of roost tree availability or suitable condition (Crampton and Barclay 1998, Sedgeley and O'Donnell 1999, Kurta et al. 2002, Willis and Brigham 2004). Roost switching within a maternity period also is common, and may be dictated in part by availability and ephemerality of roost trees (Lewis 1995, Sedgeley and O'Donnell 1999, Kurta et al. 2002). Northern myotis (*Myotis septentrionalis*) maternity colonies switch roost trees frequently (every 1–5 days), and in the Central Appalachian Mountains, exhibit selection for certain roost tree characteristics, including distinct woody species preferences (Owen et al. 2002, Menzel et al. 2002, Garroway and Broders 2007). Garroways and Broders (2007) confirmed that northern myotis conform to fission-fusion models; however, these observations were not made in the context of forest disturbance and roost availability.

Roost switching patterns can be viewed as networks among trees; a roost topology where roost trees are nodes and daily roost switching movements are edges within a network (Rhodes et al. 2006, Rhodes 2007, Fortuna et al. 2009). Networks can be of many forms, including random and scale-free. In a random network, roost trees are essentially equally connected, with no roost tree being more connected than other roost trees in the network. In a scale-free network, there is an apparent “hub” or central node roost tree within the roost network that is more connected to other roost trees (Rhodes et al. 2006). Roost networks may be specific to social groups of bats and could have implications for roost selection studies and habitat management. Although northern myotis have been shown to select for certain tree characteristics when roosting, the relative importance of trees used by social groups, primarily maternity colonies, has not been examined. Roost selection studies commonly give equal importance to all roost trees, comparing them to potential randomly-located roost trees (Menzel et al. 2002, Miller et al. 2003). Central node roost trees may have specific selected characteristics that may be important in maintaining social organization.

Forest disturbances, including timber harvesting, fires, wind, and other causes, can affect the availability and distribution of roost trees within roost networks (Chaverri et al. 2007, Perry et al. 2007). If roost trees are limited to the extent that extensive intraspecific niche overlap results in negative fitness, survival, or recruitment, then the net effect of forest disturbances to roost tree availability and disruption of roost networks and social organization of bats is an important bat management consideration. Roost niche overlap among bats is more likely to be intraspecific rather than interspecific, particularly among colonial species (Menzel et al. 1998, Carter and Feldhamer 2005, Lacki et al. 2009a, Timpone et al. 2010). During the maternity season, female northern myotis roost colonially in trees or snags with cavities or exfoliating bark

(Arnold 2007, Garroway and Borders 2007). The benefits of roosting together largely counter the potential negative effects of density dependence incurred by limited roost resources (Kerth 2008). Indeed, for some bat species, colonial behavior may be driven more by physiological factors, reproductive status, and genetic relatedness than roost availability (Wilkinson 1985, Sedgeley and O'Donnell 1999, Chaverri et al. 2007). Nevertheless, if forest disturbances result in a short-term net gain in available roosts, roosting networks and social organization of northern myotis may be altered.

Our study objectives were to (1) determine if northern myotis in the central Appalachian Mountains conform to non-random association patterns; (2) determine if northern myotis roost switching patterns resemble random or scale-free networks; and (3) examine the characteristics of roost trees within networks occurring in areas that were and were not disturbed by prescribed fire. We hypothesized that northern myotis would exhibit nonrandom association patterns, as observed by others (Garroway and Broders 2007). Females will roost together non-randomly in definable colonies and form scale-free networks of roost trees with a central node roost tree that is connected to more roost trees through bat movements. Further, we posit that central node roost trees will be physically similar to other roost trees in networks. Lastly, central node roost trees will be physically similar between stands that were and were not subjected to prescribed fire.

Methods

Study area

We conducted our research at the Fernow Experimental Forest (FEF) in Tucker County, West Virginia (Fig. 1). The FEF is a 1,900 ha experimental forest managed by the U.S. Forest Service, Northern Research Station, and is located in the Unglaciaded Allegheny Mountains subsection of the Appalachian Plateau Physiographic Province (Kochenderfer et al. 2007).

Elevations range from 530 to 1,100 m. Ellick Run, a 2.4-km fourth-order stream, roughly bisects FEF east to west. Approximately 5.5 km of dendritic intermittent and permanent streams feed into Ellick Run and incise the steep slopes and plateau-like ridgetops, providing all possible slope aspects (Madarish et al. 2002). Mean annual precipitation at FEF is 145.8 cm, ranging from 9.7 cm in October to 14.4 cm in June. Mean annual temperature is 9.2° C, ranging from –18.0° C in January to 20.6° C in July (Kochenderfer 2006). Vegetation at the FEF is a mosaic of second- and third-growth, mixed-mesophytic and northern hardwood forest that has been managed by even (patch clearcut)- and uneven (single-tree selection variants)-aged silviculture since the mid-20th century, or has been left relatively undisturbed following initial harvesting in the Ellick watershed from 1903 to 1911 (Schuler and Fajvan 1999). Although American chestnut (*Castanea dentata*) and oak species, such as northern red oak (*Q. rubra*), historically dominated the forest overstory, the chestnut blight (*Cryphonectria parasitica*) and subsequent lack of intense disturbance, including fire and clearcutting, since the mid-20th century has allowed forest composition to shift toward shade-tolerant tree species, such as maples and American beech (*Fagus grandifolia*) (Schuler and Fajvan 1999, Schuler 2004). Prescribed fire has recently been used to promote oak regeneration in the forest that is currently dominated by sugar maple (*A. saccharum*), red maple (*A. rubrum*), yellow-poplar (*Liriodendron tulipifera*), black cherry (*Prunus serotina*), American beech, sweet birch (*Betula lenta*), and basswood (*Tilia americana*) (Schuler 2004). In April or May (depending on management compartment) 2007 and 2008, prescribed fire treatments were conducted in management compartments 45 (121 ha), 13 (13 ha), and 21 (12 ha) on FEF. The three management compartments were burned for 1 day during each treatment using a strip head fire technique, ignited with hand-held drip torches after fire-blackened perimeters were established. Due to variability in leaf litter, slope, and aspect,

actual fire conditions throughout varied from failed combustion to flame heights >3.5 m high. Additionally, 48, 20-m radius plots were randomly located in each of the three management compartments, and all overstory or midstory trees, other than oak or hickory, were herbicided or girdled (T. Schuler, USDA Forest Service, personal communication).

Radio telemetry

To capture bats, we erected mist nets (Avinet, Inc., Dryden, New York) over stream corridors, small pools, skidder trails, and service roads from May to August 2007 – 2009. Mist netting sites were located within the fire treatment and control treatment. We considered the control treatment to be any area outside the three management compartments where prescribed fires were used. Mist netting was conducted <5 hours following sunset, unless prevented by periods of rain, wind ≥ 20 kph, or temperatures $< 10^{\circ}$ C as these conditions can influence bat activity levels. We used Skin Bond[®] (Smith and Nephew, Largo, Florida) surgical cement to affix a 0.35-g radio transmitter (Model LB-2N; Holohil Systems Ltd., Carp, Ontario, Canada) between the scapulae of captured female northern myotis. We attempted to locate diurnal roost trees of each transmitted bat on a daily basis until transmitter battery completely discharged or transmitter became detached from the bat. Bat capture and handling protocols were approved by the Animal Care and Use Committee of West Virginia University (Protocol No. 08-0504) and followed the guidelines of the American Society of Mammalogists (ACUC 1998). We used a radio receiver and 3-element Yagi antenna (Wildlife Materials, Inc., Murphysboro, Illinois) to locate roost trees. To record roost tree locations within 10 m of their true geographic location, we used a Garmin GPSmap 60CSx global positioning unit.

Nonrandom association patterns

To determine if northern myotis roosted with nonrandomly with conspecifics, we used daily roosting location data for each transmitted bat. Similar to previous research examining nonrandom association patterns of bats, we calculated a half-weight association index for each pair (dyad) of transmitted bats (Cairns and Schwager 1987, Kerth and König 1999, Garroway and Broders 2007). The half-weight association index (HWI) was calculated as $x/[0.5 \times (n_a + n_b)]$ where x is the number of days that bats a and b were roosting in the same tree on the same day, and n_a and n_b are the number of days the roost trees of bats a and b were located, respectively (Bejder et al. 1998). For each year of data (2008 and 2009), we used SOCPROG 2.4 to compute HWI values for each dyad, resulting in an association matrix (Whitehead 2009). To determine if each dyad was observed roosting together more than expected as determined by a significantly high HWI value, we conducted 20,000 random permutations of each association matrix. We used a cluster analysis with average linkage clustering to assemble individuals into social groups. Only those dyads that exceeded the mean HWI + 1 standard deviation for all dyads within each year were considered to roost together more than expected. We evaluated cophenetic correlation coefficients to determine how well the cluster analyses represented data in the association matrix. The groups assembled with cluster analyses were used in subsequent roost network analyses. We used the 100% minimum convex polygon method to calculate roosting area of each social group for which ≥ 4 roost trees were located. Because transmitter retention time was low (mean ± 1 SE; 5.5 ± 0.3 days), we were unable to perform meaningful analyses on the temporal nature of the fission-fusion dynamics that are known to be exhibited by northern myotis maternity colonies (Garroway and Broders 2007).

Roost network analysis

We used a graph theoretic approach to determine the relative importance of roost trees used by northern myotis social groups. For each social group defined through cluster analysis, we considered bat movements between roost trees on consecutive days to be edges in a roost network. Each roost tree was a node in a roost network linked to other roost trees in the network by edges (Fig. 1). For each roost tree, we determined the number of other roost trees to where it was linked (LINKS). For each social group or roost network with ≥ 3 roost trees, we determined which roost tree had the highest value for LINKS and denoted that tree as a central node. If 2 or more roost trees had identical values, those trees were both considered central nodes. To determine if roost networks followed random or scale-free network patterns, we examined the topology and degree distribution of LINKS in ArcMap (Version 9.2, Environmental Systems Research Institute, Redlands, California).

Roost tree variables

For each roost tree, we determined diameter (cm) at breast height with a diameter tape (DBH), decay class (Cline et al. 1980; i.e., 1 = live, 2 = declining, 3 = recent dead, 4 = loose bark, 5 = no bark, 6 = broken top, 7 = broken bole; DECAY), crown class (Nyland 1996; i.e., 1 = suppressed, 2 = intermediate, 3 = codominant, 4 = dominant; CROWN), tree height (m) with a hypsometer (HEIGHT), visual estimate of percent bark remaining on the tree (BARK), and roost type (cavity = 1, bark = 0; ROOSTTYPE). We determined stand basal area with a 20 factor prism (m^2 / ha ; BASAL). We also noted if each roost tree occurred in areas that had recently been subjected to prescribed fire.

Statistical analysis

We used generalized additive models to determine how or if individual roost tree variables were associated with central node roost trees (Proc Gam; SAS Institute, Inc., 2004).

Before conducting the analyses, we examined all variable pairs for correlation. We removed a member of a variable pair before subsequent analyses if their Spearman's rank (Proc Corr, SAS Institute, Inc., 2004) correlation coefficient was ≥ 0.60 . We removed the variable that either was correlated with several other variables or potentially would be more difficult to replicate or implement when using the model to manage for northern myotis roost trees. For example, we retained crown class, a relative measure, and discarded actual roost tree height which varied among areas. Within each model, we predicted central node versus non-central node trees (binomial link function) using all physical roost tree variables (spline function) except ROOSTTYPE. We performed the analysis 2 times: for roost trees within fire treatments; and for roost trees outside of fire treatments. We used a chi-square test to determine if central and non-central node roost trees were more disproportionately cavity or bark roost trees (ROOSTTYPE) within fire and control treatments (Proc Freq; SAS Institute, Inc., 2004). Lastly, we performed Mann-Whitney U-tests, comparing central node roost tree characteristics in prescribed fire and control treatments (Proc Npar1way; SAS Institute, Inc., 2004). Due to the exploratory nature of our study, we set threshold significance levels for the generalized additive models, chi-square tests, and Mann-Whitney U-tests at $P \leq 0.10$.

Results

In 2008, we radio-tracked 32 female northern myotis to 64 roost trees. Mean HWI (± 1 SD) was 0.024 (0.070), setting a threshold for significant association at 0.094. Cluster analysis placed the 32 bats into 16 social groups ranging in size from 1 to 5 individuals (Table 1, Fig. 2). Cophenetic correlation for the average linkage clustering method was 0.996. Groups roosted in 1 to 11 roost trees; roost areas ranged from 0.39 to 14.77 ha (Table 1, Fig. 3). In 2009, we radio-tracked 38 female northern myotis to 51 roost trees. Mean HWI (± 1 SD) was 0.084 (0.120),

setting a threshold for significant association at 0.204. The 38 bats were clustered into 11 social groups ranging in size from 1 to 12 individuals (Table 1, Fig. 4). Cophenetic correlation for the average linkage clustering method was 0.962. Groups roosted in 1 to 16 roost trees; roost areas ranged from 5.24 to 35.33 ha (Table 1, Fig. 3).

Of the 18 social groups where a roost network was determined, 11 (61%) had a single central node roost tree according to the LINKS metric (Table 2). Central node roost trees were directly linked to 2–6 roost trees in roost networks comprised of 3–16 roost trees (Table 1). The majority of roost trees had 2 links, with fewer being linked to 3 or more roost trees, following the power law $P(k) \approx k^{-1.84}$, ($r^2 = 0.77$) (Fig. 5). The number of bat days (number of bats $\times$ number of days) spent roosting in these trees ranged from 2 to 17. Within control treatments, the following predictor variable pairs were significantly ($\rho > 0.60$) correlated: CROWN, HEIGHT ($\rho = -0.822$); CROWN, DECAY ($\rho = 0.644$); DECAY, BARK ($\rho = -0.702$); DECAY, HEIGHT ($\rho = -0.652$). Within models, we retained CROWN and BARK. Central node roost trees were in early stages of decay and were surrounded by higher basal area than non-central node roost trees (Table 3, Fig 6). Non-central node roost trees were disproportionately cavity trees ($\chi^2 = 3.214$, $P = 0.073$).

Within fire treatments, the following predictor variable pairs were significantly correlated: CROWN, HEIGHT ($\rho = -0.828$); DECAY, BARK ($\rho = -0.670$); DBH, HEIGHT ($\rho = 0.714$). Within models, we retained CROWN, BARK, and DBH. Central node roost trees were small-diameter trees in lower crown classes, in stands of lower basal area (Table 3, Fig. 6). Central node roost trees were not disproportionately cavity trees or those with exfoliating bark ($\chi^2 = 0.972$, $P = 0.324$). Central node roost trees in fire treatments had higher bark coverage than those in control treatments (Table 4).

Discussion

Northern myotis exhibited non-random association patterns, forming social groups nested within networks of roost trees across the landscape. Previous studies have shown that northern myotis roost non-randomly with conspecifics (Garroway and Broders 2007). Our research showed that northern myotis not only form social groups, but that these groups roosted in networks of roost trees that often centered around a central node roost tree. In temperate North America, it is common for female bats of some species to form non-randomly associating colonies during the summer maternity period (Willis and Brigham 2004, Garroway and Broders 2007). Female bats and their female offspring are known to return to the same summer ranges yearly, a phenomenon that may or may not partially drive association patterns (Arnold 2007, Metheny et al. 2008). However, it is clear that some bats are more closely associated with other bats in terms of the characteristics of their spatio-temporal roosting patterns. Average half-weight indices and group sizes of northern myotis in our study were similar to those in Nova Scotia, Canada (0.22; 2.89 bats/group; Garroway and Broders 2007). Several of the social groups in our study were larger than those in the Nova Scotia study, possibly a result of differences in sampling intensity or timing. Reproductive phase has been shown to affect group size and roosting associations (Garroway and Broders 2007), but the relatively short sampling effort, i.e., transmitter retention time, per bat in our study prevented us from determining trends. Regardless, we have shown that some individuals were more likely to roost with certain other individuals; and some individuals did not roost with other bats even though their roosting areas overlapped.

Roosting areas of northern myotis social groups in our study also were similar to those found in Nova Scotia, Canada (0.3 – 31.1 ha; Henderson and Broders 2008). Largely confined to hilltops, the roosting areas of many northern myotis social groups in our study overlapped, with some being entirely enveloped by others. However, the roosting networks of social groups on

separate hilltops never overlapped. Roost trees were sometimes shared among social groups, but not to the extent that individuals from these groups were considered to belong to the same social group. Also, there was some degree of temporal partitioning among social groups using the same roost trees. The temporal difference in roost tree use has implications for the social and behavioral roles that these roost trees fulfill. Sharing roost trees on the same days provides certain benefits to roost mates, including thermal buffering and information exchange about roosting and foraging areas (Wilkinson 1985, Kerth and Reckardt 2003, Kerth 2008). Disadvantages associated with roosting in the same roost trees at the same time include exchange of parasites, disease, and perhaps fungal spores such as those linked with the lethal White Nose Syndrome (*Geomyces destructicans*; Wilkinson 1985, Fortuna et al. 2009). It may be possible that spores, parasite propagules or pupae may persist in roost trees in absence of roosting bats, although this remains to be investigated (Wilkinson 1985). Therefore, bats from different groups may not exchange information at roost trees; however, it is possible that use of the same trees still allows for the exchange of parasites and disease.

Roost tree networks of northern myotis in our study did not fully mimic the perfect scale-free networks observed in *Tadarida australis* in Queensland, Australia (Rhodes et al. 2006). Rather, the roost networks of some northern myotis social groups clearly centered on a central node roost tree; whereas the central node roost trees of other networks were more ambiguous. In a scale-free network, we would expect there to be a single central node roost tree, definable by a large number of links to other roost trees that had fewer links; the degree distribution follows a power curve. In a random network, the degree distribution follows a Poisson distribution (Barbási 2002, Rhodes et al. 2006). The combined northern myotis roost network degree distribution generally fit a power curve, but undoubtedly was confounded by smaller roost

networks consisting of few trees where the limited time period of our observations provided documentation on few links. This was largely due to short transmitter retention time, small group sizes, and resulted in networks consisting of few roost trees. Larger groups and longer transmitter retention times would have allowed us to better identify the full extent of the roost networks, degree distributions, and to specify single central node roost trees.

Across the FEF landscape, central node roost trees differed from other roost trees within networks based on some physical characteristics of the trees themselves and surrounding stands. Within control treatments, central node roost trees were in earlier stages of decay, based on high amounts of bark coverage, and were surrounded by more basal area. Within control treatments at the FEF, northern myotis maternity colonies selected large cavity trees in early stages of decay, compared to randomly-located potential roost trees (Johnson et al. 2009). Within roost networks, non-central node roost trees typically were cavity trees, whereas central node roost trees were more evenly distributed between cavity trees and those with exfoliating bark. That central node roost trees typically were in early stages of decay indicates that northern myotis can locate newly formed snags and establish those trees as hubs within the roost networks. Trees in later stages of decay were connected to fewer trees in the network, possibly because these trees imminently would either decay to the point of unsuitability or collapse, rendering them less reliable nodes within the network. Whereas central node roost trees within control treatments typically had high amounts of bark coverage, those located in fire treatments had even higher amounts of bark coverage by comparison, which is consistent with the trend observed among available and used roost trees across control and fire treatments the FEF (Johnson et al. 2009).

Within stands that were subjected to prescribed fire, central node roost trees were small-diameter trees in lower crown classes, and in areas of lower basal area. This is largely in

agreement with overall roost tree selection within fire treatments at FEF (Johnson et al. 2009). Northern myotis maternity colonies roosted in small-diameter black locust trees (*Robinia pseudoacacia*) that were surrounded by less basal area than randomly-located trees. The persistence of black locust in the forest stand likely promotes the establishment of roost networks that persevere over time (Menzel et al. 2002, Ford et al. 2006, Johnson et al. 2009). Although central node roost trees typically were in lower crown classes, northern myotis at fire treatments at FEF selected trees in higher crown classes compared to those randomly-located trees (Johnson et al. 2009). Prescribed fire created a heterogeneous canopy layer, with gaps allowing solar exposure to reach trees being used as central node roost trees by northern myotis to be positioned in lower crown classes (Turner et al. 1994, Johnson et al. 2009). However, we do not know if roost networks and central node roost trees were similar before and after prescribed fire events.

Potential disruption of roost networks, particularly those resembling scale-free networks, through forest disturbances such as fire can have consequences to bats in terms of roost selection and group fission-fusion dynamics (Boyles and Aubrey 2006, Johnson et al. 2009, Lacki et al. 2009b). Disturbances to roost networks resembling random networks should have minimal effects on social organization because trees with the network are more similar in terms of use and connectivity compared to trees in scale-free networks. Canopy gaps created by the senescence of overstory trees killed by fire are exploited by northern myotis that roost in trees within these gaps (Johnson et al. 2009). Trees that may have been unsuitable as roosts for northern myotis may have been rendered suitable either through the changing of the physical characteristics of the tree itself such as increased exfoliating bark due to senescence or through changes in the stand condition surrounding the tree, e.g., frequent or larger canopy gap creation. These changes in roost tree availability may cause shifts in the roost network and central node roost tree to allow

northern myotis to exploit newly senesced trees in order to maximize use of these trees through time. Consequently, social organization may be reordered to adapt to the new networks depending on the reliability and speed of communication of roost conditions among roost mates and adjacent social groups. As social organization and roost networks change, so may the potential for disease transmission (Fortuna et al. 2009). If roost networks resembling scale-free networks are disrupted by the removal of roost trees either through natural disturbances such as windthrow or anthropogenic disturbances such as timber harvesting, social groups may fission into smaller groups until forests are restored to some semblance of former conditions. Also, if those roost trees that were shared between or among social groups are removed, both communication and disease transmission may be limited among groups. However, the roles that night-roosts play in terms of communication and disease transmission among bats remains unclear (Kunz and Lumsden 2003, Ormsbee et al. 2007). In scale-free networks, central node roost trees may serve as important centers of information and unfortunately, disease and parasite exchange. The removal of these trees from networks may either cause bats to establish their central node roost trees in other trees existing within the network. Also, that central node roost trees often were sites of overlap among social groups suggests that disturbance of these sites potentially could disrupt among-group communication and disease spread; this is an important consequence and potential management implication considering new disease threats such as WNS (Turner et al. 2001, Fortuna et al. 2009).

Acknowledgments

We thank the staff of the USDA Forest Service Monongahela National Forest and the USDA Forest Service Northern Research Station Timber and Watershed Laboratory for conducting the prescribed burns. J. DeCarlo, J. Rodrigue, and T. Smith graciously provided field

assistance. The USDA Forest Service Northern Research Station Joint Venture Agreement 06-JV-11242300-140 provided primary funding for our study from the National Fire Plan to West Virginia University, Division of Forestry and Natural Resources. Funding for prescribed burning was provided by a grant from Florida Power and Light and BHE Environmental to the U.S. Forest Service Northern Research Station through Collection Agreement 06-CO-112331-034.

Literature Cited

- Alexander, R. D. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* 5:325–383.
- Animal Care and Use Committee (ACUC). 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- Arnold, B. D. 2007. Population structure and sex-biased dispersal in the forest dwelling vespertilionid bat, *Myotis septentrionalis*. *American Midland Naturalist* 157:374–384.
- Barbási, A.-L. 2002. Linked. Perseus, Cambridge, Massachusetts.
- Bejder, L., D. Fletcher, and S. Bräger. 1998. A method for testing association patterns of social animals. *Animal Behaviour* 56:719–725.
- 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.
- Cairns, S., and S. Schwager. 1987. A comparison of association indices. *Animal Behaviour* 35:1454–1469.
- 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.

- Chaverri, G., Quirós, O.E., Gamba-Rios, M., Kunz, T.H., 2007. Ecological correlates of roost fidelity in the tent-making bat *Artibeus watsoni*. *Ethology* 113, 598–605.
- Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *Journal of Wildlife Management* 44:773–786.
- Conover, W. J. 1999. Practical nonparametric statistics. 3rd edition. Wiley, New York.
- 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.
- Cross, P. C., J. O Lloyd-Smith, and W. M. Getz. 2005. Disentangling association patterns in fission-fusion societies using African buffalo as an example. *Animal Behaviour* 69:499–506.
- Emlen, S. T. 1994. Benefits, constraints and the evolution of the family. *Trends in Ecology and Evolution* 9:282–285.
- Ford, W. M., S. F. Owen, J. W. Edwards, and J. L. Rodrigue. 2006. *Robinia pseudoacacia* (black locust) as day-roosts of male *Myotis septentrionalis* (northern bats) on the Fernow Experimental Forest, West Virginia. *Northeastern Naturalist* 13:15–24.
- Fortuna, M. A., A. G. Popa-Lisseau, C. Ibáñez, and J. Bascompte. 2009. The roosting spatial network of a bird-predator bat. *Ecology* 90:934–944.
- Garroway, C. J., and H. G. Broders. 2007. Nonrandom association patterns at northern long-eared bat maternity roosts. *Canadian Journal of Zoology* 85:956–964.
- 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.

- Holekamp, K. E., S. M. Cooper, C. I. Katona, N. A. Berry, L. G. Frank, and L. Smale. 1997. Patterns of association among female spotted hyenas (*Crocuta crocuta*). *Journal of Mammalogy* 78:55–64.
- Johnson, J. B., J. W. Edwards, W. M. Ford, and J. E. Gates. 2009. Roost tree selection by northern myotis (*Myotis septentrionalis*) maternity colonies following prescribed fire in a Central Appalachian Mountains hardwood forest. *Forest Ecology and Management* 258:233–242.
- Kerth, G. 2008. Causes and consequences of sociality in bats. *BioScience* 58:737–746.
- Kerth, G., and B. König. 1999. Fission, fusion and nonrandom associations in female Bechstein's bats (*Myotis bechsteinii*). *Behaviour* 136:1187–1202.
- Kerth, G., and K. Reckardt. 2003. Information transfer about roosts in female Bechstein's bats: an experimental field study. *Proceedings of the Royal Society B* 270:511–515.
- Kochenderfer, J. N. 2006. Fernow and the Appalachian hardwood region. Pages 17–39 *In* M. B. Adams, D. R. DeWalle, and J. L. Horn, editors. *The Fernow watershed acidification study*. Springer, Dordrecht, Netherlands. 279 pp.
- Kochenderfer, J. N., M. B. Adams, G. W. Miller, J. D. Helvey. 2007. Factors affecting large peakflows on Appalachian watersheds: lessons from the Fernow Experimental Forest. USDA Forest Service, Research Paper NRS-3, Northeastern Research Station, Newtown Square, PA, 24 pp.
- Krause, J., and G. D. Ruxton. 2002. *Living in groups*. Oxford University Press, Oxford.
- Kummer, H. 1971. *Primate societies: group techniques of ecological adaptation*. Aldine-Atherton, Chicago, Illinois.

- Kunz, T. H. and L. F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. Pages 3–89 *In* T. Kunz and M. Fenton, editors. Bat Ecology. University of Chicago Press, Chicago, Illinois.
- Kurta, T. H., S. W. Murray, and D. H. Miller. 2002. Roost selection and movements across the summer landscape. Pages 118-129 *In* A. Kurta and J. Kennedy, editors. The Indiana bat: biology and management of an endangered species Bat Conservation International, Austin, Texas.
- Lacki, M. J., D. R. Cox, and M. B. Dickinson. 2009. Meta-analysis of summer roosting characteristics of two species of *Myotis* bats. *American Midland Naturalist* 162:318–326.
- Lacki, M. J., D. R. Cox, L. E. Dodd, and M. B. Dickinson. 2009. Response of northern bats (*Myotis septentrionalis*) to prescribed fires in eastern Kentucky forests. *Journal of Mammalogy* 90:1165–1175.
- Lehmann, J., and C. Boesch. 2004. To fission or to fusion: effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organization. *Behavioral Ecology and Sociobiology* 56:207–216.
- Lewis, S. E. 1995. Roost fidelity in bats: a review. *Journal of Mammalogy* 76:481–496.
- Madarish, D.M., J. L. Rodrigue, and M. B. Adams. 2002. Vascular flora and macroscopic fauna on the Fernow Experimental Forest. USDA Forest Service, General Technical Report GTR-NE-291, Northeastern Research Station, Newtown Square, PA.
- Menzel, M. A., T. C. Carter, B. R. Chapman, and J. Laerm. 1998. Quantitative comparison of tree roosts used by red bats (*Lasiurus borealis*) and Seminole bats (*L. seminolus*). *Canadian Journal of Zoology* 76:630–634.

- Menzel, M. A., S. F. Owen, W. M. Ford, J. W. Edwards, P. B. Wood, B. R. Chapman, and K. V. Miller. 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.
- Metheny, J. D., M. C. Kalcounis-Rueppell, C. K. R. Willis, K. A. Kolar, and R. M. Brigham. 2008. Genetic relationships between roost-mates in a fission-fusion society of tree-roosting big brown bats (*Eptesicus fuscus*). *Behavioral Ecology and Sociobiology* 62:1043–1051.
- Miller, D. A., E. B. Arnett, and M. J. Lacki. 2003. Habitat management for forest-roosting bats of North America: a critical review of habitat studies. *Wildlife Society Bulletin* 31:30–44.
- Nyland, R. D. 1996. *Silviculture: concepts and applications*. McGraw-Hill, New York, NY, 633 pp.
- O'Donnell, C. F. J. 2000. Cryptic local populations in a temperate rainforest bat *Chalinolobus tuberculatus* in New Zealand. *Animal Conservation* 3:287–297.
- O'Donnell, C. F. J., and J. A. Sedgely. 1999. Use of roosts by the long-tailed bat, *Chalinolobus tuberculatus*, in temperate rainforest in New Zealand. *Journal of Mammalogy* 80:913–923.
- Ormsbee, P. C., J. D. Kiser, and S. I. Perlmeter. 2007. Importance of night roosts to the ecology of bats. Pages 129–151 *In* M. Lacki, J. Hayes, and A. Kurta, editors. *Bat in Forests*. Johns Hopkins University Press, Baltimore, Maryland.
- Ottensmeyer, C. A., and H. Whitehead. 2003. Behavioural evidence for social units in long-finned pilot whales. *Canadian Journal of Zoology* 81:1327–1338.

- Owen, S. F., M. A. Menzel, W. M. Ford, J. W. Edwards, B. R. Chapman, K. V. Miller, and P. B. Wood. 2002. Roost tree selection by maternal colonies of northern long-eared myotis in an intensively managed forest. General Technical Report NE-292. USDA Forest Service, Northeastern Research Station, Parsons, West Virginia.
- Perry, R. W., R. E. Thill, and D. M. Leslie, Jr. 2007. Selection of roosting habitat by forest bats in a diverse forested landscape. *Forest Ecology and Management* 238:156–166.
- Rhodes, M. 2007. Roost fidelity and fission-fusion dynamics of white-striped free-tailed bats (*Tadarida australis*). *Journal of Mammalogy* 88:1252–1260.
- Rhodes, M., G. W., Wardell-Johnson, M. P. Rhodes, and B. Raymond. 2006. Applying network analysis to the conservation of habitat trees in urban environments: a case study from Brisbane, Australia. *Conservation Biology* 20:861–870.
- SAS Institute, Inc. 2004. SAS/STAT 9.1 users guide. Version 9.1. SAS Institute, Inc., Cary, NC, 5,121 pp.
- Schuler, T. M. 2004. Fifty years of partial harvesting in a mixed mesophytic forest: composition and productivity. *Canadian Journal of Forest Research* 34:985–997.
- Schuler, T. M., and M. A. Fajvan. 1999. Understory tree characteristics and disturbance history of a central Appalachian forest prior to old-growth harvesting. USDA Forest Service, Res. Pap. NE-710, Northeastern Research Station, Radnor, PA.
- 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* 249:437–446.

- Timpone, J. C., J. G. Boyles, K. L. Murray, D. P. Aubrey, and L. W. Robbins. 2010. Overlap in roosting habits of Indiana bats (*Myotis sodalis*) and northern bats (*Myotis septentrionalis*). *American Midland Naturalist* 163:115–123.
- Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. *Landscape ecology in theory and practice: pattern and process*. Springer Science + Business Media, New York.
- Turner, M. G., W. W. Hargrove, R. H. Gardner, W. H. Romme. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *Journal of Vegetation Science* 5:731–742.
- Whitehead, H. 2009. SOCPROG programs: analysing animal social structures. *Behavioural Ecology and Sociobiology* 63:765–778.
- Wilkinson, G. S. 1985. The social organization of the common vampire bat. *Behavioral Ecology and Sociobiology* 17:111–121.
- Willis, C. K. R., and R. M. Brigham. 2004. Roost switching, roost sharing and social cohesion: forest-dwelling big brown bats, *Eptesicus fuscus*, conform to the fission-fusion model. *Animal Behaviour* 68:495–505.

Table 1. Association measures, roost area, and central node roost tree metrics for social groups of northern myotis maternity colonies at the Fernow Experimental Forest, West Virginia, 2008–2009.

Year	Group	Bats	HWI ^a	Roosts	Roost area (ha)	LINKS ^b	CNRT ^c
2008	A	1	–	1	–	–	–
	B	1	–	1	–	–	–
	C	1	–	4	1.70	2	2
	D	1	–	4	0.39	2	2
	E	1	–	3	–	2	1
	F	2	0.28 ± 0.23	4	1.86	2	2
	G	3	0.40 ± 0.17	11	5.65	2	7
	H	1	–	1	–	–	–
	I	1	–	2	–	–	–
	J	4	0.45 ± 0.21	6	1.45	3	1
	K	1	–	5	0.66	2	3
	L	3	0.30 ± 0.02	10	13.42	4	1
	M	1	–	1	–	–	–

	N	1	—	3	—	2	1
	O	5	0.31 ± 0.12	9	10.04	5	1
	P	5	0.35 ± 0.23	7	14.77	5	1
		2.0 ± 1.5		4.5 ± 3.3	5.5 ± 5.7	2.9 ± 1.3	2.0 ± 1.8
2009	Q	9	0.32 ± 0.17	16	23.25	6	1
	R	2	0.66 ± 0.18	5	7.97	2	2
	S	1	—	7	5.24	2	5
	T	4	0.31 ± 0.09	11	35.33	6	1
	U	1	—	1	—	—	—
	V	5	0.40 ± 0.19	8	8.06	5	1
	W	1	—	1	—	—	—
	X	1	—	3	—	2	1
	Y	1	—	1	—	—	—
	Z	1	—	1	—	—	—
	AA	12	0.44 ± 0.23	8	16.78	5	1
		3.5 ± 3.8		5.6 ± 4.9	16.1 ± 11.6	4.0 ± 1.9	1.7 ± 1.5

^a Mean ($\pm$ 1 SD) half weight association index (HWI) of bat dyads within social groups.

^b Number of roost trees that bats moved to or from the central node roost tree.

^c Number of central node roost trees identified within each social group according to the maximum number of LINKS.

Table 2. Number of central node roost trees according to 3 metrics for each social group of northern myotis at the Fernow Experimental Forest, West Virginia, 2008–2009.

Year	Social group	Central node roost tree metrics		
		LINKS ^a	MOVES ^b	DAYS ^c
2008	C	2	2	4
	D	2	2	3
	E	1	1	1
	F	2	2	1
	G	7	1	1
	J	1	1	1
	K	3	2	2
	L	1	1	1
	N	1	1	2
	O	1	2	1
	P	1	1	1
Mean (± 1 SD)		2.00 (1.89)	1.40 (0.52)	1.70 (1.06)
2009	Q	1	1	1
	R	2	1	2
	S	5	5	1
	T	1	1	1
	V	1	1	1
	X	1	1	1

AA	1	1	1
Mean ($\pm$ 1 SD)	1.71 (1.50)	1.57 (1.51)	1.14 (0.38)

^a Number of roost trees that bats moved to or from the central node roost tree.

^b Number of bat movements to or from the central node roost tree.

^c Number of bat days spent roosting in the central node roost tree.

Table 3. Characteristics of central node roost trees of northern myotis maternity colonies in prescribed fire and control treatments at the Fernow Experimental Forest, West Virginia, 2008–2009.

Control treatment				Fire treatment			
Variable	DF	χ^2	<i>P</i>	Variable	DF	χ^2	<i>P</i>
DBH	3.00	0.69	0.875	DBH	3.00	9.72	0.021
CROWN	1.95	0.61	0.729	CROWN	1.98	5.15	0.075
BASAL	3.00	7.28	0.064	BASAL	3.00	10.65	0.014
BARK	3.00	11.15	0.011	BARK	3.00	2.07	0.558

Table 4. Characteristics of central node roost trees used by northern myotis maternity colonies in prescribed fire and control treatments at the Fernow Experimental Forest, West Virginia, 2008–2009.

Variable	Fire treatment		Control treatment		<i>P</i>
	Mean ^a	SE	Mean	SE	
CROWN	3.14	0.18	2.88	0.21	0.423
DECAY	4.21	0.38	4.71	0.36	0.340
DBH (cm)	21.01	1.55	34.85	5.16	0.153
HEIGHT (m)	12.74	1.16	13.22	1.52	0.937
BARK (%)	71.79	7.42	47.65	9.26	0.061
BASAL (m ² /ha)	29.84	2.66	34.02	2.43	0.546

^a Actual values presented. Mann-Whitney tests performed on ranked values.

Fig. 1. Example of roost network of a northern myotis social group at the Fernow Experimental Forest, West Virginia, 2009. Larger dots represent higher number of bat days used.

Fig. 2. Average linkage cluster analysis of non-randomly (half-weight association index >0.09) associating groups of northern myotis at the Fernow Experimental Forest, West Virginia, 2008. Numbers on the y-axis denote individual bats; letters denote social groups.

Fig. 3. Minimum convex polygons (100%) encompassing roost networks of northern myotis social groups at the Fernow Experimental Forest, West Virginia, 2008–2009.

Fig. 4. Average linkage cluster analysis of non-randomly (half-weight association index >0.20) associating groups of northern myotis at the Fernow Experimental Forest, West Virginia, 2009. Numbers on the y-axis denote individual bats; letters denote social groups.

Fig. 5. Degree distribution of roost trees within roost networks of northern myotis social groups at the Fernow Experimental Forest, West Virginia, 2008–2009.

Fig. 6. Relations of roost tree characteristics and central node roost trees of northern myotis maternity colonies in control (A) and prescribed fire (B) treatments at the Fernow Experimental Forest, West Virginia, 2008–2009, as determined by generalized additive models. Spline (variable) values above or below +1 or –1 indicate significant positive or negative associations, respectively.

Chapter 5

Genetic structuring of northern myotis (*Myotis septentrionalis*) in disturbed landscapes and at multiple spatial scales

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Abstract

Forest disturbances, particularly permanent land use conversions, may fragment, isolate, and condense summer populations of philopatric bats, potentially resulting in genetically definable subpopulations. Also, subpopulations may be distinguishable at large spatial scales, regardless of forest disturbances and other land use conversions. We examined genetic structuring of the forest-interior dwelling northern myotis (*Myotis septentrionalis*) at multiple spatial scales, from watershed to regional, in West Virginia and New York. We genotyped

microsatellites at 18 nuclear loci from 174 individuals. In many cases, loci in subpopulations that we defined *a priori* based on spatial attributes often departed from Hardy-Weinberg equilibrium; those loci that were in equilibrium were inconsistent at differentiating subpopulations based on spatial scale. Our results indicate that some level of genetic structuring is evident among northern myotis, but this structuring could not be attributed solely to geographic location. It is likely that the ability to migrate relatively long distances, exploit small forest patches, and use networks of swarming sites located throughout the Appalachian Mountain range has allowed northern myotis to maintain high gene flow regardless of forest disturbances at local and regional spatial scales.

Key words: genetic structuring, microsatellite, *Myotis septentrionalis*, New York, northern myotis, West Virginia

Introduction

The role of genetics in management and conservation of wildlife populations has been a rapidly expanding segment of research that stresses the importance of maintaining genetic diversity among populations – bats are not an exception (Ashley 2003, Racey and Entwistle 2003, Coltman 2008). The degree of genetic relatedness among bat populations typically is higher in sedentary species compared to regional or long-distance migratory species (Burland and Worthington Wilmer 2001, Fleming and Eby 2003). In some species, genetic relatedness among maternity colonies may be driven in large part by natal philopatry exhibited by female bats (Worthington Wilmer et al. 1994, Kerth et al. 2000, Burland and Worthington Wilmer 2001). In this scenario, genetic relatedness is predominantly male-mediated (Burland and Worthington Wilmer 2001, Kerth et al. 2002). However, it is not always possible to genetically differentiate maternity colonies of sedentary species, even by geographic distances that are larger

than known migration distances (Burland et al. 1999, Arnold 2007, Metheny et al. 2008). Moreover, within the context of some fission-fusion dynamics, females within social subgroups may be from different matriline, contributing to genetic diversity across the landscape (Gompper et al. 1997, Burland et al. 1999, Metheny et al. 2008). In most temperate zone cavernicolous bat species, genetic diversity is further augmented because mating occurs at hibernacula where individuals, potentially from different geographic areas, congregate to mate (Kerth et al. 2003, Veith et al. 2004). However, several endangered bat species, such as Bechstein's bats (*Myotis bechsteinii*), do exhibit highly genetically structured (genetically distinct and definable) populations that are spatially separated, even at small spatial scales, and potentially vulnerable to losses of significant genetic information because of relatively small disturbances (Worthington Wilmer et al. 1994, Kerth et al. 2000, Burland and Worthington Wilmer 2001).

The degree of natal philopatry exhibited by female northern myotis (*Myotis septentrionalis*) is unclear, but may be similar to congeners that return to the same areas and roost trees in consecutive years (Barbour and Davis 1969, Lewis 1995, Caceres and Barclay 2000). A higher degree of philopatry, i.e., negligible association among groups across the landscape, over time will be conducive to delineating groups genetically (Kerth et al. 2000, Burland and Worthington Wilmer 2001). Conversely, substantial homogenization of individuals across the landscape will create difficulties in delineating genetically distinguishable groups, notwithstanding spatial scale (Arnold 2007). Similar to other temperate bat species, dispersal in northern myotis may be male-biased, resulting in a higher degree of genetic variation in males than in females within an area (Kerth et al. 2000, Arnold 2007).

At small spatial extents such as the forest stand level, it is unlikely that moderate forest disturbances that retain adequate roost trees, will result in genetically differentiable bat maternity colonies among forest patches (Kerth et al. 2000). However, permanent removal of roost trees could force colonies to relocate to remnant forest patches possibly already occupied by genetically-distinct colonies. Forest management practices create a spatio-temporal mosaic of forest structure and conditions that are continually in flux, undoubtedly forcing colonies to relocate, promoting mixing of maternity colonies. Conversely, relatively permanent forest removal for agricultural purposes or development, may create separations among genetically similar colonies or reinforce separations among colonies that existed prior to forest removal (Kerth et al. 2000). At large spatial extents, separation among colonies due to philopatry either with or without the influence of disturbance potentially creates conditions that are of interest if managing to maintain or enhance genetic diversity essential for the persistence of a species (Awise and Hamrick 1996, Ashley et al. 2003, Racey and Entwistle 2003).

Our objectives were to determine if northern myotis were genetically differentiable at the watershed, intra-county, and interstate spatial scales. Based on their widespread distribution, cosmopolitan forest habitat use, and purported male dispersal, we hypothesized that northern myotis would not exist as genetically definable subpopulations at any spatial scale, regardless of sex.

Methods

Study area

We conducted our research in Tucker County, West Virginia and Jefferson County, New York. Within Tucker County, we sampled four areas, including the Fernow Experimental Forest (FEF), Canaan Valley National Wildlife Refuge (CVNWR), Clover Run, and Olson (Fig. 1).

Tucker County is located in the Unglaciaded Allegheny Mountains subsection of the Appalachian Plateau Physiographic Province (Kochenderfer et al. 2007). Elevations range from 530 to 1,100 m throughout the county. Numerous intermittent and perennial dendritic streams incise the steep slopes and plateau-like ridgetops in the area (Madarish et al. 2002). Vegetation communities in Tucker County are a mosaic of second- and third-growth, mixed-mesophytic, northern hardwood, and subalpine forests. At the FEF, prescribed fire has recently been used to promote oak (*Quercus* spp.) regeneration in the forest that is currently dominated by sugar maple (*A. saccharum*), red maple (*A. rubrum*), yellow-poplar (*Liriodendron tulipifera*), black cherry (*Prunus serotina*), American beech (*Fagus grandifolia*), sweet birch (*Betula lenta*), and basswood (*Tilia americana*) (Schuler 2004). In April or May (depending on management compartment) 2007 and 2008, prescribed fire treatments were conducted in three management compartments, including John B. Hollow, totaling 146 ha. Additionally, 48, 20-m radius plots were randomly located in each of the three management compartments, and all overstory or midstory trees, other than oak or hickory (*Carya* spp.), were herbicided or girdled (T. Schuler, USDA Forest Service, personal communication). Big Springs Cave, a Priority 3 Indiana myotis (*Myotis sodalis*) hibernaculum, is in the southern portion of FEF, and is a known autumn swarming site for northern myotis (J. Johnson, unpublished data). The proximity of sites outside of FEF to swarming sites is unknown. However, Big Springs Cave is within migration distances for northern myotis at sampling sites in Tucker County.

In Jefferson County, New York, we conducted our research at Fort Drum, a U.S. Army installation (about 630 km from the Tucker County sites). Fort Drum lies within the Mohawk subsection of the Appalachian Plateau Physiographic Province and foothills of the Adirondack Mountains. Forest composition is primarily northern hardwood forest dominated by oaks, elms

(*Ulmus* spp.), and black cherry (Dobony and Rainbolt 2008). Sampling occurred in the Cantonment area, which is largely developed for military purposes, but retains considerable acreage of mature forest stands. Elevation at Fort Drum ranges from approximately 130 – 200 m. Two caves, Priority 2 and 4 Indiana myotis hibernacula and known northern myotis hibernacula (and likely swarming sites) are ~15 km from Fort Drum (Fenton 1966).

To capture bats, we erected mist nets (Avinet, Inc., Dryden, New York) over stream corridors, small pools, skidder trails, and service roads from May to August 2008 and 2009. Bat capture and handling protocols were approved by the Animal Care and Use Committee of West Virginia University (Protocol No. 08-0504) and followed the guidelines of the American Society of Mammalogists (ACUC 1998).

DNA extraction and amplification

We used 3 mm diameter biopsy punches to obtain tissue samples from each plagiopatagium of each captured northern myotis. Tissue samples were preserved in a lysis buffer solution (Longmire et al. 1997) or 95% ethanol in the field, and stored at 0° until further processing. All biopsy utensils were sterilized with alcohol and/or flamed between samples to avoid cross-contamination. We extracted genomic DNA from each tissue sample following standard established protocols (Appendix A). We tested 18 microsatellite loci based on markers that were developed for other bat species and from little brown myotis (*Myotis lucifugus*) (Castella and Ruedi 2000, Kerth et al. 2002, Trujillo and Amelon 2009). We used RepeatMasker software to parse the little brown myotis genome for di-, tri-, tetra-, and penta-nucleotide repeats totaling >100 base pairs (Smit et al. 2004). We used Primer3 (<http://frodo.wi.mit.edu/primer3/>) software to develop primer sequences for nine microsatellite loci located in the little brown myotis genome. Primer sequences for one locus (HBD111) were developed from the eastern red

bat (*Lasiurus borealis*) genome (Appendix B; J. Switzer, USGS, unpublished data). Each forward primer was labeled with 6-FAM, VIC, NED, or PET fluorescent dye (Appendix C). Polymerase chain reactions (PCR) were carried out in either 15.0 or 19.5 µl volumes on MJ Research Peltier Thermal Cyclers; and annealing temperatures were either 52° C or 58° C depending on loci (Appendix C). Moreover, PCR master mix reagent concentrations varied depending on loci, which were multiplexed when possible (Appendix C). We used an Applied Biosystems 3130xl Genetic Analyzer to determine allele base pair sizes for each locus among individuals. We used GeneMapper v4.0 to genotype individuals at the 18 nuclear microsatellite loci. We eliminated 3 loci that were either difficult to genotype due to single base pair repeats (HBD111) or failed to reliably amplify (134, from little brown myotis genome, and D09, Trujillo and Amelon 2009).

Statistical analysis

We partitioned our samples into nine hypothetical subpopulations based on geographic distances. Within the FEF, subpopulations were partitioned at the watershed level (John B. Hollow, Wilson Hollow, Watershed 6, Fork Pool, and Camp Hollow; Figure 1), with the assumption that bats captured within watersheds roosted within their respective watersheds, and potentially with family members (Kerth et al. 2000, Johnson et al. 2009). The remaining sites in Tucker County (CVNWR, Clover Run, Olson), were treated as separate subpopulations, as was Fort Drum. Distances between subpopulations within Tucker County ranged from 0.6 to 37.6 km.

We used GenePop (Raymond and Rousset 1995, Rousset 2008) to examine all loci for Hardy-Weinberg equilibrium (HWE) within each subpopulation. Because loci that significantly depart from HWE may be due to null alleles, selection operating at that locus, or that a

population is in genetic flux, we eliminated those loci from further analysis if $P < 0.05$ after sequential Bonferroni adjustment (Rice 1989). We used the remaining loci to determine if our subpopulations that were defined *a priori* were genetically differentiable. We used GenePop to examine fixation indices (F_{ST}) for all pairs of subpopulations. Further, we determined the significance of F_{ST} values by conducting 1,000 permutations of the data (Goudet et al. 1996). Significant F_{ST} values indicate that subpopulations are genetically differentiable using the examined suite of loci.

Because *a priori* partitioning of our sample into subpopulations was based on geographic distances and was potentially arbitrary, we used program Structure to determine if the nine subpopulations we defined could be clustered into groups using genotype data (Pritchard et al. 2000). We programmed Structure to probabilistically assign all individuals into a pre-defined number of clusters after 10,000 permutations of the data. We performed 10 iterations in our analyses of 1 to 9 clusters. For each cluster size, we averaged the estimated log likelihood probability of the data. We plotted the cluster size versus estimated log likelihood probability, and examined the graph for the cluster size with the highest log likelihood probability. We then examined output bar plots associated with the cluster size of highest log likelihood probability for evidence of individuals in our *a priori* groups being assigned into one or more clusters as defined by Structure. Assignment of a large proportion of individuals of an *a priori* subpopulation into the same cluster indicates potential structuring.

We conducted all statistical analyses on 2 datasets; 1 that included all samples, and 1 that included only females. Northern myotis are known to exhibit male-biased dispersal (Arnold 2007). Therefore, females may be more genetically differentiable on a geographic basis than males.

Results

We captured 266 northern myotis (141 males) among all sites. However, for our analyses, we used a 2-off dataset consisting only of individuals for which we were able to genotype ≥ 13 of 15 loci, leaving us with 174 individuals (88 males). When analyzing all individuals, the loci in HWE in all subpopulations were 204, 487, b15, C09, F05, and F19 (Table 1). When analyzing only females, the loci in HWE in all subpopulations were 087, 089, 341, 487, b15, C09, E02, F05, and F19 (Table 2). Subpopulations consisting of a larger number of individuals typically had a larger number of loci that did not conform to HWE. All loci used in our analyses were polymorphic, consisting of ≥ 6 alleles (Appendix B). Within subpopulations and across all individuals, the mean number of alleles per locus ranged from 6.5 at CVNWR to 17.5 at John B. Hollow. Within subpopulations and across females only, the mean number of alleles per locus ranged from 3.8 at Olson to 12.6 at John B. Hollow and Camp Hollow.

Fixation indices indicated that some subpopulations were genetically differentiable from other subpopulations, but this differentiation could not be explained by geographic distance. When considering all individuals, the Camp Hollow subpopulation was different from the most subpopulations (Table 3). The Fort Drum subpopulation was different only from the John B. Hollow subpopulation, but only when considering all individuals regardless of sex (Table 3, 4).

Probabilistic assignment of all individuals resulted in them being grouped into 4 clusters (Figure 2). Although some individuals probabilistically belonged together in the 4 clusters (Figure 3), they were from different *a priori* subpopulations, including those from West Virginia and New York (Figure 4). Probabilistic assignment of only females resulted in them being grouped into 1 cluster (Figure 2).

Discussion

The general lack of genetic relatedness and structure at watershed and regional scales indicates that forest disturbances, including prescribed fire, at the scales we recognized will not disrupt northern myotis from an ecological genetics perspective. We detected no consistent differences between the disturbed John B. Hollow and adjacent watersheds. Genetic variation within subpopulations at the watershed scale was higher than that among subpopulations, similar to that observed in northern myotis in Ohio (Arnold 2007). Moreover, many loci in some subpopulations were not in HWE, possibly indicating that these subpopulations were still in a genetic flux. At the subpopulation level, male northern myotis contributed to overall allelic diversity, adding to the departure from HWE. The Camp Hollow subpopulation, which was the closest subpopulation at FEF to Big Springs Cave, consistently had the most loci that departed from HWE and was genetically differentiable from the most subpopulations. Big Springs Cave is a known autumn swarming site where mating of many bat species, including northern myotis occurs. During summer, male northern myotis are known to roost in proximity to Big Spring Cave in Camp Hollow, year round, possibly influencing our results (Ford et al. 2006). It is unknown if other sites, such as Olson, were as close to swarming sites as Camp Hollow was to Big Springs Cave, as doubtless there are many swarming sites in this karst area that are yet undiscovered or not monitored for northern myotis use. Also, it is unknown if genetic differentiation occurs at such a fine spatial scale that would allow proximity to swarming sites to influence genetic structuring.

Similar to Indiana myotis, female northern myotis probably return to their natal roost areas during the summer maternity period (Kurta and Murray 2002, Kurta et al. 2002). Although this phenomenon may lead to highly genetically structured and discernable familial groups, as observed in Bechstein's bats (Kerth et al. 2000), it may not be applicable to all species.

Individuals within fission-fusion societies of big brown bats showed no matrilineal relationship or relatedness (Metheny et al. 2008). Subpopulations in our study were defined based on where bats were captured that for the most part were the water sources located within the roosting ranges of fission-fusion groups (J. Johnson, unpublished data). Although defining subpopulations based on watersheds may seem capricious, radio-telemetry data on northern myotis maternity colonies in West Virginia indicate that they occupy small roosting ranges that often are isolated in single watersheds (Menzel et al. 2002, Johnson et al. 2009). Although we could reasonably posit that subpopulations may exist at the watershed scale based on philopatry and isolated roosting ranges, relatively low fixation indices among most subpopulations indicate that genetic differentiation at the watershed scale largely is inconsistent.

There are several explanations as to why there is some apparent genetic structuring that exists in our sample, but cannot be wholly attributed to our definition of subpopulations based on watershed delineations and spatial proximity. The foundation of population genetics analysis based on microsatellites is the occurrence of shared alleles among individuals and that the loci at which these alleles occur are selectively neutral (Lowe et al. 2004). Therefore, some individuals in our sample that were members of different *a priori* subpopulations shared alleles to the extent of being considered related and in discernable subpopulations. However, individuals belonging to the same modeled subpopulations often were from West Virginia and New York, indicating that genetic relatedness was not associated with the spatial scales that we sampled. We analyzed some loci that were developed from the little brown myotis genome that may or may not be under selection; alleles at those loci may not be distributed among individuals wholly based on non-assortative mating. However, we observed no trends in allelic diversity at those loci among *a priori* subpopulations.

The mating system of northern myotis certainly influences gene flow among subpopulations and our results indicate that sexes differed in degree of genetic structuring, i.e., differentiation among subpopulations. Sex-biased dispersal has been observed in northern myotis, with males exhibiting less genetic structure geographically than females (Arnold 2007). It has also been suggested that gene flow may be mediated in part by females, as observed in big brown bats (*Eptesicus fuscus*; Vonhof et al. 2008). It is likely that the mating system of northern myotis is similar to that of the little brown myotis in that non-assortative mating occurs at cave and mine swarming sites mostly during autumn, and to a lesser extent in spring (Myers 1964, Thomas et al. 1979). Bats may visit many swarming sites and mate with several bats during a single mating season, increasing gene flow potential (Fenton 1969, Kerth et al. 2003). Consequently, the network of swarming sites that exists in the Appalachian Mountains probably facilitates gene flow throughout this region, reducing our ability to attribute minor genetic differences to spatial proximity of hypothetical subpopulations (Griffin 1945). The ability to migrate long distances (~100 km) and exploit relatively isolated and small forest fragments within migrating distances mitigates the effects the forest disturbance from fragmentation, and consequent potential for genetic isolation (Caceres and Barclay 2000, Henderson et al. 2008, Johnson et al. 2008). Disturbance of a forest stand may cause philopatric bats to roost in adjacent forest stands, possibly adding allelic diversity to subpopulations that already existed in those stands. However, northern myotis in John B. Hollow, an area recently disturbed by two successive spring prescribed fire treatments and herbicide treatments since 2007, had the highest allelic diversity among *a priori* subpopulations (Johnson et al. 2009). Disturbance of forest stands should not disrupt mate selection or swarming site selection as gene flow will continue uninterrupted, unless some disturbance event occur at the swarming location. It is unclear if

forest disturbances at swarming sites affect selection or use by mating bats. Therefore, contrary to the conclusions of Arnold (2007), forest disturbances at the stand level should have little, if any, role in the genetic structuring of northern myotis.

Acknowledgments

I thank C. Dobony and fellow graduate student K. Cunningham and her field technicians for collecting wing punches at Fort Drum, New York. J. Rodrigue graciously provided field assistance. M. Crockett, K. Sturm, and their staff at the Canaan Valley National Wildlife Refuge provided field assistance collecting samples and access to the Refuge. I thank Dr. D. Ray and his graduate students at West Virginia University, and Dr. T. King, M. Eackles, R. Johnson, B. Lubinski, M. Springmann, and Dr. J. Switzer at the USGS Leetown Science Center for assistance with lab procedures and data analysis. The USDA Forest Service Northern Research Station Joint Venture Agreement 06-JV-11242300-140 provided primary funding for our study from the National Fire Plan to West Virginia University, Division of Forestry and Natural Resources. Funding for prescribed burning was provided by a grant from Florida Power and Light and BHE Environmental to the U.S. Forest Service Northern Research Station through Collection Agreement 06-CO-112331-034.

Literature Cited

- Animal Care and Use Committee (ACUC). 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- Arnold, B. D. 2007. Population structure and sex-biased dispersal in the forest dwelling vespertilionid bat, *Myotis septentrionalis*. *American Midland Naturalist* 157:374–384.

- Ashley, M. V., M. F. Willson, O. R. W. Pergams, D. J. O'Dowd, S. M. Gende, and J. S. Brown. 2003. Evolutionarily enlightened management. *Biological Conservation* 111:115–123.
- Awise, J. C., and J. L. Hamrick. 1996. *Conservation genetics: case histories from nature*. Chapman and Hall, New York.
- Barbour, R. W., and W. H. Davis. 1969. *Bats of America*. University Press of Kentucky, Lexington, Kentucky.
- Burland, T. M., and J. Worthington Wilmer. 2001. Seeing in the dark: molecular approaches to the study of bat populations. *Biological Reviews* 76:389–409.
- Burland, T. M., E. M. Barratt, M. A. Beaumont, and P. A. Racey. 1999. Population genetic structure and gene flow in a gleaner bat, *Plecotus auritus*. *Proceedings of the Royal Society of London, Series B-Biological Sciences* 266:975–980.
- Caceres, M. C., and R. M. R. Barclay. 2000. *Myotis septentrionalis*. *Mammalian Species* 634:1–4.
- Castella, B., and M. Ruedi. 2000. Characterization of highly variable microsatellite loci in the bat *Myotis myotis* (Chiroptera: Vespertilionidae). *Molecular Ecology* 9:1000–1002.
- Coltman, D. W. 2008. Molecular ecological approaches to studying the evolutionary impact of selective harvesting in wildlife. *Molecular Ecology* 17:221–235.
- Dobony, C. A., and R. E. Rainbolt. 2008. American woodcock on Fort Drum Military Installation, New York. *Northeastern Naturalist* 15:241–248.
- Fenton, M. B. 1966. *Myotis sodalis* in caves near Watertown, New York. *Journal of Mammalogy* 47:526.
- Fenton, M. B. 1969. Summer activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec. *Canadian Journal of Zoology* 47:597–602.

- Fleming, T. H., and P. Eby. 2003. Ecology of bat migration. Pages 156–208 *In* T. H. Kunz and M. B. Fenton, editors. Bat ecology. University of Chicago Press, Chicago, Illinois.
- Ford, W. M., S. F. Owen, J. W. Edwards, and J. L. Rodrigue. 2006. *Robinia pseudoacacia* (black locust) as day-roosts of male *Myotis septentrionalis* (northern bats) on the Fernow Experimental Forest, West Virginia. *Northeastern Naturalist* 13:15–24.
- Gompper, M. E., J. L. Gittleman, and R. K. Wayne. 1997. Genetic relatedness, coalitions and social behaviour of white-nosed coatis, *Nasua narica*. *Animal Behaviour* 53:781–797.
- Goudet, J., M. Raymond, T. DeMeeüs, and F. Rousset. 1996. Testing differentiation in diploid populations. *Genetics* 144:1933–1940.
- Griffin, D. R. 1945. Travels of banded cave bats. *Journal of Mammalogy* 26:15–23.
- Henry, M., D. W. Thomas, R. Vaudry, and M. Carrier. 2002. Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). *Journal of Mammalogy* 83:767–774.
- Hickey, M. B. C., and M. B. Fenton. 1996. Behavioural and thermoregulatory responses of female hoary bats, *Lasiurus cinereus* (Chiroptera: Vespertilionidae), to variations in prey availability. *Ecoscience* 3:414–422.
- Hirshfeld, J. R., Z. C. Nelson, and W. G. Bradley. 1977. Night roosting behavior in four species of desert bats. *Southwestern Naturalist* 22:427–433.
- Holekamp, K. E., S. M. Cooper, C. I. Katona, N. A. Berry, L. G. Frank, and L. Smale. 1997. Patterns of association among female spotted hyenas (*Crocuta crocuta*). *Journal of Mammalogy* 78:55–64.
- Johnson, J. B., J. W. Edwards, W. M. Ford, and J. E. Gates. 2009. Roost tree selection by northern myotis (*Myotis septentrionalis*) maternity colonies following prescribed fire in a

- Central Appalachian Mountains hardwood forest. *Forest Ecology and Management* 258:233–242.
- Johnson, J. B., J. E. Gates, and W. M. Ford. 2008. Distribution and activity of bats at local and landscape scales within a rural-urban gradient. *Urban Ecosystems* 11:227–242.
- Kerth, G., A. Kiefer, C. Trappmann, and M. Weishaar. 2003. High gene diversity at swarming sites suggest hot spots for gene flow in the endangered Bechstein's bat. *Conservation Genetics* 4:491–499.
- Kerth, G., F. Mayer, and B. König. 2000. Mitochondrial DNA (mtDNA) reveals that female Bechstein's bats live in closed societies. *Molecular Ecology* 9:793–800.
- Kerth, G., F. Mayer, and E. Petit. 2002. Extreme sex-biased dispersal in the communally breeding nonmigratory Bechstein's bat (*Myotis bechsteinii*). *Molecular Ecology* 11:1491–1498.
- Kochenderfer, J. N., M. B. Adams, G. W. Miller, J. D. Helvey. 2007. Factors affecting large peakflows on Appalachian watersheds: lessons from the Fernow Experimental Forest. USDA Forest Service, Research Paper NRS-3, Northeastern Research Station, Newtown Square, PA.
- Kurta, A., and S. W. Murray. 2002. Philopatry and migration of banded Indiana bats (*Myotis sodalis*) and effects of radio transmitters. *Journal of Mammalogy* 83:585–589.
- Kurta, T. H., S. W. Murray, and D. H. Miller. 2002. Roost selection and movements across the summer landscape. Pages 118-129 *In* A. Kurta and J. Kennedy, editors. *The Indiana bat: biology and management of an endangered species* Bat Conservation International, Austin, Texas.
- Lewis, S. E. 1995. Roost fidelity in bats: a review. *Journal of Mammalogy* 76:481–496.

- Longmire, J. L., M. Maltbie, and R. J. Baker. 1997. Use of “lysis buffer” in DNA isolation and its implication for museum collections. *Occasional Papers of the Museum of Texas Tech University* 163:1–3.
- Lowe, A., S. Harris, and P. Ashton. 2004. *Ecological genetics: design, analysis, and application*. Blackwell: Malden, Massachusetts.
- Madarish, D. M., J. L. Rodrigue, and M. B. Adams. 2002. Vascular flora and macroscopic fauna on the Fernow Experimental Forest. USDA Forest Service, General Technical Report GTR-NE-291, Northeastern Research Station, Newtown Square, PA.
- Menzel, M. A., S. F. Owen, W. M. Ford, J. W. Edwards, P. B. Wood, B. R. Chapman, and K. V. Miller. 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.
- Metheny, J. D., M. C. Kalcounis-Rueppell, C. K. R. Willis, K. A. Kolar, and R. M. Brigham. 2008. Genetic relationships between roost-mates in a fission-fusion society of tree-roosting big brown bats (*Eptesicus fuscus*). *Behavioral Ecology and Sociobiology* 62:1043–1051.
- Myers, R. F. 1964. Ecology of three species of Myotine bats in the Ozark Plateau. Ph.D. Dissertation, University of Missouri, Columbia, Missouri. 209 pp.
- Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155:945–959.
- Racey, P. A., and A. C. Entwistle. 2003. Conservation ecology of bats. Pages 680–743 *In* T. H. Kunz and M. B. Fenton, editors. *Bat ecology*. University of Chicago Press, Chicago, Illinois.

- Raymond, M., and F. Rousset. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity* 86:248-249.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- Rousset, F. 2008. Genepop'007: a complete reimplementation of the Genepop software for Windows and Linux. *Molecular Ecology Resources* 8: 103-106.
- Schuler, T. M. 2004. Fifty years of partial harvesting in a mixed mesophytic forest: composition and productivity. *Canadian Journal of Forest Research* 34:985–997.
- Schuler, T. M., and M. A. Fajvan. 1999. Understory tree characteristics and disturbance history of a central Appalachian forest prior to old-growth harvesting. USDA Forest Service, Res. Pap. NE-710, Northeastern Research Station, Radnor, PA.
- 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* 249:437–446.
- Sherman, P. W., and M. C. Runge. 2002. Demography of a population collapse: the northern Idaho ground squirrel (*Spermophilus brunneus brunneus*). *Ecology* 83:2816–2831.
- Shumway, D. L., M. D. Abrams, C. M. Ruffner. 2001. A 400-year history of fire and oak recruitment in an old-growth oak forest in western Maryland, U.S.A. *Canadian Journal of Forest Research* 31:1437–1443.
- Smit, A. F. A., R. Hubley, and P. Green. 2004. RepeatMasker Open 3.0.
<http://www.repeatmasker.org>
- Thomas, D. W., M. B. Fenton, and R. M. R. Barclay. 1979. Social behavior of the little brown bat, *Myotis lucifugus*. I. Mating behaviour. *Behavioural Ecology and Sociobiology* 6:129–136.

- Trujillo, R. G., and S. K. Amelon. 2009. Development of microsatellite markers in *Myotis sodalis* and cross-species amplification in *M. grisescens*, *M. leibii*, *M. lucifugus*, and *M. septentrionalis*. *Conservation Genetics* 10:1965–1968.
- Veith, M., N. Beer, A. Kiefer, J. Johannesen, and A. Seitz. 2004. The role of swarming sites for maintaining gene flow in the brown long-eared bat (*Plecotus auritus*). *Heredity* 93:342–349.
- Vonhof, M. J., C. Strobeck, and M. B. Fenton. 2008. Genetic variation and population structure in big brown bats (*Eptesicus fuscus*): is female dispersal important? *Journal of Mammalogy* 89:1411–1420.
- Worthington Wilmer, J., C. Moritz, L. Hall, and J. Toop. 1994. Extreme population structuring in the threatened ghost bat, *Macroderma gigas*: evidence from mitochondrial DNA. *Proceedings of the Royal Society of London, Series B-Biological Series* 257:193–198.

Table 1. Observed and expected (H_O/H_E) heterozygosity, and test for departure from Hardy-Weinberg equilibrium of 15 nuclear microsatellite loci for 9 *a priori* subpopulations of northern myotis (*Myotis septentrionalis*) in Tucker County, West Virginia and Fort Drum, New York, 2008–2009.

Locus	Subpopulation								
	Camp Hollow ($N = 41$)	Clover Run ($N = 16$)	Canaan Valley NWR ($N = 5$)	Fort Drum ($N = 22$)	Wilson Hollow ($N = 24$)	Fork Pool ($N = 6$)	John B. Hollow ($N = 36$)	Olson ($N = 8$)	Watershed 6 ($N = 16$)
087	0.325/0.489*	0.500/0.627	0.600/0.733	0.429/0.587	0.375/0.504	0.000/0.303	0.500/0.656*	0.375/0.342	0.625/0.683
089	0.763/0.972	0.875/0.978	1.000/0.964	0.773/0.973	0.826/0.968	0.500/0.955	0.727/0.955*	0.750/0.942	0.750/0.968
204	0.700/0.942	0.875/0.933	0.600/0.911	0.790/0.916	0.792/0.934	0.667/0.909	0.861/0.948	0.875/0.925	0.750/0.942
233	0.171/0.229*	0.125/0.123	0.000/0.000	0.286/0.308*	0.261/0.415*	0.000/0.303	0.206/0.242	0.125/0.342	0.250/0.431
341	0.512/0.462	0.688/0.466	0.500/0.571	0.455/0.554*	0.167/0.479*	0.500/0.409	0.306/0.469	0.667/0.485	0.400/0.480
439	0.343/0.856*	0.400/0.807	0.800/0.711	0.167/0.862*	0.150/0.850*	0.167/0.803	0.333/0.827*	0.125/0.825	0.357/0.878*
487	0.732/0.845	0.875/0.837	0.800/0.844	0.682/0.877	0.652/0.856	0.667/0.788	0.750/0.824	0.625/0.825	0.875/0.895
910	0.667/0.946*	0.400/0.908*	1.000/0.956	0.765/0.954	0.429/0.938*	0.667/0.924	0.406/0.952*	0.167/0.924	0.733/0.945
b15	0.805/0.946	0.938/0.964	1.000/0.978	0.909/0.978	0.783/0.947	1.000/0.939	0.917/0.944	0.750/0.958	0.688/0.950
C01	0.366/0.775*	0.375/0.740*	0.200/0.822	0.273/0.720*	0.458/0.738	0.333/0.652	0.333/0.640*	0.250/0.742	0.313/0.762*
C09	0.868/0.882	0.875/0.823	1.000/0.822	0.810/0.899	0.917/0.834	0.833/0.909	0.829/0.837	0.875/0.750	0.750/0.929
D02	0.539/0.920*	0.571/0.905	0.500/0.893	0.650/0.935	0.375/0.927*	0.167/0.864	0.781/0.946*	0.500/0.933	0.600/0.899
E02	0.707/0.891	0.800/0.920*	1.000/0.889	0.909/0.889	0.667/0.901	0.833/0.909	0.722/0.889*	0.500/0.883	0.938/0.897
F05	0.775/0.867	0.938/0.873	1.000/0.889	0.909/0.854	0.750/0.855	0.833/0.955	0.829/0.830	1.000/0.800	0.813/0.808
F19	0.875/0.930	0.813/0.933	1.000/0.889	0.909/0.923	0.870/0.927	1.000/0.955	0.833/0.938	0.875/0.933	0.938/0.960

* $P < 0.05$ after sequential Bonferroni correction

Table 2. Observed and expected (H_O/H_E) heterozygosity, and test for departure from Hardy-Weinberg equilibrium of 15 nuclear microsatellite loci for 9 *a priori* subpopulations of female northern myotis (*Myotis septentrionalis*) in Tucker County, West Virginia and Fort Drum, New York, 2008–2009.

Locus	Subpopulation								
	Camp Hollow (<i>N</i> = 24)	Clover Run (<i>N</i> = 6)	Canaan Valley NWR (<i>N</i> = 3)	Fort Drum (<i>N</i> = 5)	Wilson Hollow (<i>N</i> = 9)	Fork Pool (<i>N</i> = 6)	John B. Hollow (<i>N</i> = 21)	Olson (<i>N</i> = 3)	Watershed 6 (<i>N</i> = 9)
087	0.375/0.558	0.500/0.667	0.667/0.800	0.400/0.644	0.400/0.513	0.000/0.303	0.524/0.571	0.667/0.600	0.667/0.667
089	0.773/0.974	1.000/0.970	1.000/1.000	0.600/0.956	0.800/0.975	0.500/0.955	0.850/0.955	0.667/0.933	0.778/0.967
204	0.609/0.923*	1.000/0.909	0.333/0.733	0.750/0.857	0.800/0.954	0.667/0.909	0.905/0.949	1.000/0.933	0.889/0.935
233	0.208/0.305*	0.167/0.167	0.000/0.000	0.000/0.000	0.286/0.434	0.000/0.303	0.238/0.220	0.333/0.733	0.333/0.614
341	0.583/0.479	0.833/0.530	0.500/0.500	0.600/0.556	0.200/0.517	0.500/0.409	0.333/0.452	1.000/0.667	0.375/0.492
439	0.450/0.883*	0.500/0.833	0.667/0.800	0.250/0.893	0.250/0.801*	0.167/0.803	0.353/0.736*	0.000/0.800	0.375/0.908
487	0.750/0.832	0.833/0.833	1.000/0.933	0.600/0.733	0.800/0.901	0.667/0.788	0.857/0.871	0.667/0.800	0.889/0.941
910	0.708/0.952*	0.400/0.867	1.000/1.000	0.800/0.933	0.308/0.911*	0.667/0.924	0.316/0.940*	0.500/0.833	0.667/0.935
b15	0.708/0.930	0.833/0.939	1.000/0.933	1.000/1.000	0.800/0.931	1.000/0.939	0.905/0.962	1.000/1.000	0.778/0.954
C01	0.458/0.758*	0.500/0.818	0.333/0.867	0.200/0.689	0.467/0.802	0.333/0.652	0.333/0.630*	0.000/0.800	0.222/0.817*
C09	0.826/0.865	0.833/0.848	1.000/0.867	1.000/0.889	0.933/0.818	0.833/0.909	0.850/0.824	1.000/0.867	0.667/0.928
D02	0.478/0.897*	0.200/0.689	0.500/0.833	0.400/0.889	0.400/0.897*	0.167/0.864	0.684/0.937*	0.000/0.800	0.667/0.850
E02	0.708/0.885	0.833/0.924	1.000/0.933	0.800/0.844	0.600/0.880	0.833/0.909	0.762/0.883	0.000/0.533	1.000/0.882
F05	0.833/0.885	1.000/0.939	1.000/0.933	1.000/0.933	0.867/0.851	0.833/0.955	0.850/0.814	1.000/0.800	0.778/0.810
F19	0.917/0.931	0.500/0.879	1.000/0.867	1.000/0.933	0.857/0.892	1.000/0.955	0.810/0.930	0.667/0.933	1.000/0.948

* $P < 0.05$ after sequential Bonferroni correction

Table 3. Fixation indices between *a priori* subpopulations of northern myotis (*Myotis septentrionalis*) in Tucker County, West Virginia and Fort Drum, New York, 2008–2009.

Subpopulation	Subpopulation								
	Camp Hollow	Clover Run	Canaan Valley NWR	Fort Drum	Wilson Hollow	Fork Pool	John B. Hollow	Olson	Watershed 6
Camp Hollow	0.000								
Clover Run	0.001	0.000							
Canaan Valley NWR	0.004	0.007	0.000						
Fort Drum	-0.001	0.001	0.011	0.000					
Wilson Hollow	0.006*	0.004	0.021*	0.002	0.000				
Fork Pool	-0.003	-0.010	-0.011	0.001	0.004	0.000			
John B. Hollow	0.004*	0.003	0.014	0.005*	-0.001	0.004	0.000		
Olson	0.013*	0.001	0.014*	0.014	0.003	0.004	0.009	0.000	
Watershed 6	0.001*	0.004	0.012	-0.007	0.002	-0.005	0.003*	0.010	0.000

* indicates significance at $P < 0.05$

Table 4. Fixation indices between *a priori* subpopulations of female northern myotis (*Myotis septentrionalis*) in Tucker County, West Virginia and Fort Drum, New York, 2008–2009.

	Subpopulation								
	Camp Hollow	Clover Run	Canaan Valley NWR	Fort Drum	Wilson Hollow	Fork Pool	John B. Hollow	Olson	Watershed 6
Camp Hollow	0.000								
Clover Run	-0.007	0.000							
Canaan Valley NWR	-0.028	-0.014	0.000						
Fort Drum	0.001	-0.007	-0.039	0.000					
Wilson Hollow	0.015*	-0.001	-0.002	-0.002	0.000				
Fork Pool	0.005*	-0.008	-0.014	0.004	0.008	0.000			
John B. Hollow	0.006*	0.003	-0.026	-0.002	0.008*	-0.002	0.000		
Olson	0.016	0.008	-0.014	-0.001	-0.003	0.005	-0.006	0.000	
Watershed 6	-0.004	-0.004	-0.022	-0.013	0.002	-0.001	-0.007	0.006	0.000

* indicates significance at $P < 0.05$

Figure captions

Figure 1. *A priori* subpopulations of northern myotis in Tucker County, West Virginia and Fort Drum, New York, 2008–2009. FEF = Fernow Experimental Forest.

Figure 2. Mean (± 1 SD) estimated log likelihood probability of all individual northern myotis (A) and only females (B) belonging to K clusters, based on genotype data collected from northern myotis in Tucker County, West Virginia and Fort Drum, New York, 2008–2009.

Figure 3. Probabilistic assignment of all individual northern myotis into 4 clusters based on genotype data collected from northern myotis in Tucker County, West Virginia and Fort Drum, New York, 2008–2009.

Figure 4. Probabilistic assignment of all individual northern myotis from 9 *a priori* subpopulations into 4 clusters based on genotype data collected from northern myotis in Tucker County, West Virginia and Fort Drum, New York, 2008–2009. CVNWR = Canaan Valley National Wildlife Refuge.

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Appendix A. Procedure for extracting genomic DNA from bat wing punches.

Cell Lysis

1. Add 600 μ l PureGene Cell Lysis Solution to each 1.5 ml tube
2. Remove wing punch from vial and dry on Kimwipe before adding to Cell Lysis Solution (sterilize forceps between samples).
3. Heat samples in oven for 30 minutes at 65°C.
4. Homogenize with microfuge tube pestle (sterilize pestle between samples).
5. Add 10 μ l Proteinase K Solution (20 mg/ml) to the lysate and mix by inverting 25 times; incubate at 55°C overnight (water bath). Invert tube periodically during incubation.

RNASE Treatment

1. Add 3 μ l RNaseIT to the cell lysate.
2. Mix by inverting tube 25 times and incubate at 37°C for 30 minutes in oven.

Protein Precipitation

1. Cool sample to room temperature.
2. Add 200 μ l Protein Precipitation Solution to the RNase-treated cell lysate.
3. Vortex for 20 seconds. Place in ice bath for 30 minutes.
4. Centrifuge 13,000 for 10 minutes. The precipitated proteins will form a tight pellet. If the protein pellet is not visible or tight, repeat Step 3 followed by incubation on ice for 5 minutes, then repeat Step 4.

DNA Precipitation

1. Pour supernatant containing the DNA (leaving behind the precipitated protein pellet) into a 1.5 ml microfuge tube containing 600 μ l 100% Isopropanol (2-propanol).
2. Mix sample by inverting gently 50 times. Place in freezer for 30 minutes.
3. Centrifuge at 13,000 for 10 minutes; depending on yield, the DNA may or may not be visible as a small white pellet.
4. Pour off supernatant and drain tube on Kimwipe. Add 600 μ l 70% Ethanol and invert the tube several times to wash the DNA pellet.
5. Centrifuge at 13,000 for 10 minutes. Carefully pour off the ethanol. Pellet may be loose so pour slowly and watch pellet.
6. Invert and drain the tube on Kimwipe. Place in Speed-Vac on medium heat for 15-20 minutes.

DNA Hydration

1. Add 25 μ l DNA Hydration Solution.
2. Rehydrate DNA by incubating sample 1 hour at 65°C and overnight at room temperature.
If possible, tap tube periodically to aid in dispersing DNA.
3. Store DNA at 4°C. For long-term storage, store at -20°C or -80°C.

Appendix B. Primer sequences, repeat motifs, number of alleles (A), observed base pair lengths for 15 nuclear microsatellite loci used for population genetics analysis of northern myotis (*Myotis septentrionalis*) in Tucker County, West Virginia and Fort Drum, New York, 2008–2009. (F: = forward primer; R: = reverse primer).

Locus	Primer sequences	Repeat motif	A	Size range	Source
087	F: GTGGGTTTGATCCCTGATTG R: CACACCACCAGGCTGTCTAA	(TTCTC) _Y ...(CT) _Z	16	130–182	This study
089	F: GTGGGTTTGATCCCTGATTG R: CACACCACCAGGCTGTCTAA	(ATCT) _X ...(TATC) _Y ...(ATCT) _Z	64	216–436	This study
204	F: GTGGGTTTGATCCCTGATTG R: CACACCACCAGGCTGTCTAA	(TAGA) _X ...(GATA) _Y ...(GATA) _Z	34	153–285	This study
233	F: GTGGGTTTGATCCCTGATTG R: CACACCACCAGGCTGTCTAA	(TTTAT) _V (TTATT) _W (TATTT) _X (ATTTT) _Y ...(ATTTT) _Z	11	150–195	This study
341	F: GTGGGTTTGATCCCTGATTG R: CACACCACCAGGCTGTCTAA	(GATA) _X ...(TAGA) _Y T(GATA) _Z	6	121–165	This study
439	F: GTGGGTTTGATCCCTGATTG R: CACACCACCAGGCTGTCTAA	(GATA) _Y ...(GATA) _Z	14	177–225	This study
487	F: GTGGGTTTGATCCCTGATTG R: CACACCACCAGGCTGTCTAA	(GATA) _Z	24	156–236	This study

910	F: GTGGGTTTGATCCCTGATTG R: CACACCACCAGGCTGTCTAA	(GATA) _W ...(GATA) _X ...(GATA) _Y (ATAG) _Z	31	206–344	This study
b15	F: GTGGGTTTGATCCCTGATTG R: CACACCACCAGGCTGTCTAA	(CT) _Y (CA) _Z	43	106–178	Kerth et al. (2002)
C01	F: GTGGGTTTGATCCCTGATTG R: CACACCACCAGGCTGTCTAA	(TG) _Z	14	330–366	Trujillo and Amelon (2009)
C09	F: GTGGGTTTGATCCCTGATTG R: CACACCACCAGGCTGTCTAA	(ATAG) _V ...(GATA) _W (GAT) _X (GATA) _Y ...(GATA) _Z	20	154–230	Trujillo and Amelon (2009)
D02	F: GTGGGTTTGATCCCTGATTG R: CACACCACCAGGCTGTCTAA	(AC) _X	23	187–232	Trujillo and Amelon (2009)
E02	F: GTGGGTTTGATCCCTGATTG R: CACACCACCAGGCTGTCTAA	(AC) _Z	23	368–432	Trujillo and Amelon (2009)
F05	F: GTGGGTTTGATCCCTGATTG R: CACACCACCAGGCTGTCTAA	(AC) _Z	19	294–332	Trujillo and Amelon (2009)
F19	F: GTGGGTTTGATCCCTGATTG R: CACACCACCAGGCTGTCTAA	(CA) _Z	22	192–238	Castella and Ruedi (2000)

Appendix C. Polymerase chain reaction reagent concentrations and volumes, and annealing temperatures for 8 master mixes comprised of 18 nuclear microsatellite loci used to determine genetic differentiation of northern myotis (*Myotis septentrionalis*) in Tucker County, West Virginia and Fort Drum, New York, 2008–2009.

PCR master mix (annealing temperature)	Reagents	Stock concentration	Final concentration	Rxn Volume
A (52° C)	dH ₂ O	–	–	0.55
	5X buffer	5X	1.60 X	4.80
	MgCl ₂	25mM	3.75 mM	2.75
	dNTP	10mM	0.32 mM	2.25
	BSA	5 units/ul	0.33 units/ul	0.40
	487 F (6-FAM) R ^a	5uM	0.23 uM	0.10
	910 F (VIC) R ^a	5uM	0.23 uM	0.26
	b15 F (NED) R ^a	5uM	0.20 uM	0.45
	204 F (PET) R ^a	5uM	0.20 uM	0.45
	<i>Taq</i> polymerase	5 units/ul	0.08 units/ul	0.24
	Template	~20 ng/ul	~20.00 ng/ul	1.50
B (58° C)	dH ₂ O	–	–	2.68
	5X buffer	5X	1.60 X	4.90
	MgCl ₂	25mM	3.75 mM	5.00
	dNTP	10mM	0.32 mM	2.50

	BSA	5 units/ul	0.33 units/ul	0.40
	HBD111 F (6-FAM) R ^a	5uM	0.23 uM	0.45
	439 F (VIC) R ^a	5uM	0.23 uM	0.15
	087 F (NED) R ^a	5uM	0.20 uM	0.30
	F19 F (PET) R ^a	5uM	0.20 uM	0.20
	<i>Taq</i> polymerase	5 units/ul	0.08 units/ul	0.32
	Template	~20 ng/ul	~20.00 ng/ul	1.50
C (58° C)	dH ₂ O	—	—	1.81
	5X buffer	5X	1.60 X	5.00
	MgCl ₂	25mM	3.75 mM	2.50
	dNTP	10mM	0.32 mM	2.25
	BSA	5 units/ul	0.33 units/ul	0.40
	134 F (VIC) R ^a	5uM	0.20 uM	0.15
	D09 F (NED) R ^a	5uM	0.45 uM	0.30
	<i>Taq</i> polymerase	5 units/ul	0.08 units/ul	0.24
	Template	~20 ng/ul	~20.00 ng/ul	1.50
D (58° C)	dH ₂ O	—	—	
	5X buffer	5X	1.60 X	5.00
	MgCl ₂	25mM	3.75 mM	2.50
	dNTP	10mM	0.32 mM	2.25
	BSA	5 units/ul	0.33 units/ul	0.40

E (58° C)	C09 F (VIC) R ^a	5uM	0.23 uM	0.30
	F05 F (NED) R ^a	5uM	0.20 uM	0.60
	<i>Taq</i> polymerase	5 units/ul	0.08 units/ul	0.32
	Template	~20 ng/ul	~20.00 ng/ul	1.50
	dH ₂ O	—	—	2.26
	5X buffer	5X	1.60 X	4.80
	MgCl ₂	25mM	3.75 mM	2.75
	dNTP	10mM	0.32 mM	2.25
	BSA	5 units/ul	0.33 units/ul	0.40
	233 F (6-FAM) R ^a	5uM	0.20 uM	0.20
F (58° C)	C01 (VIC) R ^a	5uM	0.45 uM	0.20
	<i>Taq</i> polymerase	5 units/ul	0.08 units/ul	0.24
	Template	~20 ng/ul	~20.00 ng/ul	1.50
	dH ₂ O	—	—	5.83
	5X buffer	5X	1.60 X	5.00
	MgCl ₂	25mM	3.75 mM	2.50
	dNTP	10mM	0.32 mM	2.25
	BSA	5 units/ul	0.33 units/ul	0.40
	341 F (6-FAM) R ^a	5uM	0.20 uM	0.60
	E02 (6-FAM) R ^a	5uM	0.45 uM	0.20
	089 (6-FAM) R ^a	5uM	0.45 uM	0.34

G (58° C)	<i>Taq</i> polymerase	5 units/ul	0.08 units/ul	0.24
	Template	~20 ng/ul	~20.00 ng/ul	1.50
	dH ₂ O	—	—	6.91
	5X buffer	5X	1.60 X	5.00
	MgCl ₂	25mM	3.75 mM	2.50
	dNTP	10mM	0.32 mM	2.25
	BSA	5 units/ul	0.33 units/ul	0.40
	D02 F (6-FAM) R ^a	5uM	0.20 uM	0.60
	<i>Taq</i> polymerase	5 units/ul	0.08 units/ul	0.24
	Template	~20 ng/ul	~20.00 ng/ul	1.50

^a Locus name, (fluorescent dye), and Forward or Reverse primer

Chapter 6

Roost Selection by Indiana Myotis Following Forest Fires in Central Appalachian Hardwoods Forests

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¹ Manuscript formatted for submission as a USDA Forest Service Research Paper

ABSTRACT

Despite the potential for prescribed fire and natural wildfire to increase snag abundance in hardwood forests, few studies have investigated fire effects on bat roosting habitat, particularly the endangered Indiana myotis (*Myotis sodalis*). From 2004 to 2009, we examined roost selection of Indiana myotis in burned and unburned forests in Tucker County, West Virginia. We radio-tracked 16 male and 1 female Indiana myotis to 54 roost trees; 17 in burned stands and 37 in unburned stands. In burned stands, Indiana myotis roosted exclusively in fire-killed maples (*Acer* spp.). In unburned stands, they roosted in live hickories (*Carya* spp.), oaks (*Quercus* spp.), and maples. Roost trees in burned stands were surrounded by less basal area and by trees in advanced stages of decay with larger canopy gaps than at randomly-located potential roost trees in burned stands or actual roost trees located in unburned stands. Compared to randomly-located potential roosts in unburned stands, roost trees in unburned stands were less decayed, had higher percent bark coverage, and were surrounded by less basal area, also resulting in larger canopy gaps. Roost-switching frequency and distances moved by Indiana myotis among roost trees were similar between burned and unburned stands. Indiana myotis roosted in stands that had initially been burned 1–3 years prior to our observations. Our research indicates that use of fire for forest management purposes, at minimum provoked no response from Indiana myotis in terms of roost tree selection, but rather created additional roost resources, suggesting prescribed fire can be an effective management tool for Indiana myotis.

Johnson, J.B.; Ford, W.M.; Rodrigue, J.L.; Edwards, J.W.; Johnson, C.M. 2010. Roost selection by Indiana myotis following forest fires in Central Appalachian Hardwoods forests. Res. Pap. NRS-XXX. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. XX p.

KEY WORDS: Fernow Experimental Forest, forest fire, Indiana myotis, *Myotis sodalis*, prescribed fire, roost selection, West Virginia

INTRODUCTION

Formerly discouraged as a forest management practice in many hardwood forest types, use of prescribed fire has gained increasing acceptance among managers as a tool to help regenerate and retain hard-mast producing species such as oaks (*Quercus* spp.) and hickories (*Carya* spp.) in the Appalachian Mountains and Central Hardwoods forest regions, respectively (Brose et al. 1999, 2006). Competitors of hard-mast producing tree species, such as maples (*Acer* spp.) and yellow-poplar (*Liriodendron tulipifera*) are fire-sensitive. Often, these species are injured or killed during forest fires, creating better under- and mid-story conditions, i.e., increased solar radiation, for extant and future oak regeneration to succeed in the next stand following regeneration or be in a position to capture current canopy gaps (Brose et al. 2001, Nowacki and Abrams 2008). Although the effects of fire have been examined mostly from a forest management perspective regionally, its role is often overlooked relative to life histories and developing management strategies for wildlife species (Brennan et al. 1998), especially in the Appalachian Mountains (Keyser and Ford 2006).

Depending upon season, severity and micro-site conditions, fire can result in an increased abundance of senescent trees, which typically has positive implications for tree-dwelling wildlife species with an affinity for snags (Tucker et al. 2004, Blake 2005, Boyles and Aubrey 2006, Hayes and Loeb 2007). Bats in temperate forests are no exception, as recent research indicates that prescribed fires alter forest structure in a way that is favorable to bats that roost in tree cavities or under exfoliating bark (Boyles and Aubrey 2006, Johnson et al. 2009, Lacki et al. 2009). Fire can create additional snags in a forest stand, as well as favorable micro-site conditions through the enlargement of canopy gaps (Johnson et al. 2009). Canopy gaps created or enlarged by the senescence of fire-killed overstory trees allow more solar radiation to reach roost trees. Whereas empirical data exist indicating that fire positively affects roosting habitat of common species such as evening bats (*Nycticeius humeralis*) and northern myotis (*Myotis septentrionalis*), no work has specifically examined this condition relative to roost selection and habitat of the federally-endangered Indiana myotis (*M. sodalis*) (MacGregor et al. 1999, Gumbert 2001, Dickinson et al. 2009).

The geographic range of the Indiana myotis largely overlaps the oak-dominated forest communities in the Midwest, mid-Atlantic, and northeastern United States (Braun 1950, Thomson 1982). Past Indiana myotis population declines have been attributed to human disturbance of hibernacula during winter, environmental pollution and loss of summer habitat (i.e., forests) (Menzel et al. 2001, USFWS 2007). Recent population stabilization and in some cases modest population increases are being reversed at present by the rapidly spreading enzootic white-nose syndrome (WNS). This pathogen has reduced Indiana bats and other *Myotis* species by >75% where outbreaks have occurred (USFWS 2009, E. Britzke, US Army Corps of Engineers, pers. comm.). Heretofore, successful efforts to promote species recovery have

focused largely on protection of hibernacula (Clawson 2002, USFWS 2007, 2009). Although protection of hibernacula is undoubtedly important, the full range of habitats used by bats during all seasons must be taken into account when considering conservation and management strategies to ensure the perpetuation of the species (Menzel et al. 2001). Indeed, following population declines due to WNS, protection of critical summer maternity habitat will be imperative for species recovery. Many studies have focused on characteristics of Indiana myotis summer roosting habitat, and fewer have examined spring and autumn roosting habitat (Menzel et al. 2001, Brack 2006, Britzke et al. 2006, Carter 2006). Regardless of season, Indiana myotis generally select large-diameter trees, roosting under exfoliating bark of either snags or live trees, particularly shagbark hickory (*C. ovata*) (Callahan et al. 1997, MacGregor et al. 1999, Gumbert 2001, Menzel et al. 2001, Ford et al. 2002). Although roost trees have been documented in areas subjected to prescribed fire by previous researchers, it is unclear if the Indiana myotis actually roosted in fire-killed trees (MacGregor et al. 1999). Indiana myotis are known to return to the same areas (and sometimes roost trees) in successive summers (Gumbert et al. 2002, Kurta and Murray 2002, Kurta et al. 2002, Johnson and Gates 2010). Forest alterations and consequent changes in summer roosting habitat due to fire therefore can have lasting impacts on local bat populations. For example, fire may negatively impact Indiana myotis roosting habitat through a reduction in roost resources or by creating unsuitable conditions at existing roost trees. Alternatively, fire may disturb a forest stand in a way similar to that in flooded forests, where snag abundance increases several-fold over preexisting conditions, thereby providing additional roosting resources for Indiana myotis (Kurta et al. 1996, Carter 2006).

Current recovery efforts and planning documents do not address the use of prescribed fire to beneficially alter Indiana myotis roosting habitat (USFWS 2007). Potentially, prescribed fire

may create favorable roosting conditions for Indiana myotis, similar to that observed with more common species (Carter and Feldhamer 2005). Indeed, fire might be an effective tool to foster recovery of this species, as Indiana myotis may benefit from additional snags and canopy disturbances provided by active management (Carter 2006, Keyser and Ford 2006). However, it is unclear what the minimum threshold roost tree density is for Indiana myotis occupancy, although recommendations of up to 64 potential roosts per ha have been proposed (Gardner et al. 1991, Menzel et al. 2001). Also, an increase in the availability of roost trees may not necessarily result in increased use (Menzel et al. 2001). Non-random selection of roosts, roost switching frequency, and distance traveled between successive roosts are indicators of roost availability, but have not been well researched in the eastern United States (Wilkinson 1985, Crampton and Barclay 1998, Sedgeley and O'Donnell 1999, Kunz and Lumsden 2003, Chaverri et al. 2007).

Our objectives were to: (1) compare roost tree selection of Indiana myotis in forest stands subjected to fire (wildfire and prescribed burning) and in unburned stands in the central Appalachian Mountains based on the physical characteristics of roost trees and potential roost trees, and (2) examine roost tree abundance and availability by comparing roost-switching frequency and distances traveled between successive roosts located in burned and unburned forest stands. Consistent with other bat species in the region and existing ecological observations of the Indiana myotis, we predicted that Indiana myotis would select roost trees within forest gaps created by fire, and that roost-switching frequency would be higher and distances travelled shorter in forest stands subjected to fire (Boyles and Aubrey 2006, Johnson et al. 2009).

MATERIALS AND METHODS

Study Area

We conducted our research at the Fernow Experimental Forest (FEF) and the Petit Farm in Tucker County, West Virginia (Fig. 1). The FEF is a 1,900 ha experimental forest managed by the U.S. Forest Service, Northern Research Station. The Petit Farm is located on private land, approximately 8 km southeast of FEF. Both areas are located in the Unglaciaded Allegheny Mountains subsection of the Appalachian Plateau Physiographic Province (Kochenderfer et al. 2007). Elevations range from 530 to 1,100 m at FEF and 750 to 1,000 m at the Petit Farm and to nearly 1,300 m on portions of the surrounding national forest. On the FEF, Elklick Run, a 2.4-km fourth-order stream, roughly bisects the area east to west. Approximately 5.5 km of dendritic intermittent and permanent streams feed into Elklick Run and incise the steep slopes and plateau-like ridgetops, providing all possible slope aspects (Madarish et al. 2002). The Petit Farm contains several first- and second-order streams that drain into Glady Fork. Slopes are less steep at Petit Farm than at FEF. Overall mean annual precipitation in the area is 145.8 cm, ranging from 9.7 cm in October to 14.4 cm in June. Mean annual temperature is 9.2° C, ranging from -18.0° C in January to 20.6° C in July (Kochenderfer 2006). Vegetation at FEF and Petit Farm largely is a mosaic of second- and third-growth, mixed-mesophytic and northern hardwood forest. Forests on the FEF, largely resembling those in the surrounding region, have been managed by even (patch clearcut)- and uneven (single-tree selection)-aged silviculture since the mid-20th century, or has been left undisturbed following initial harvesting in the Elklick watershed from 1903 to 1911 (Schuler and Fajvan 1999). On the Petit Farm, small portions of the forests at lower-elevations were cleared for pastoral grazing and hay production, but recent diameter-limit harvesting has occurred on much of the ca. 400-ha area within the past decade.

Northern red oak (*Q. rubra*), black cherry (*Prunus serotina*), and sugar maple (*A. saccharum*) equal of greater than 46 cm minimum diameter were harvested, whereas red maple (*A. rubrum*) of all sizes were not. In March 2003, an escaped campfire burned through a portion of the forest stand that had been diameter-limit harvested in 2001 at the Petit Farm, and onto the adjacent Monongahela National Forest. Fire intensity was variable as well, but flame heights and residual overstory mortality was greater than that observed at FEF, in large part due to abundant downed tops and slash from the recent logging. American chestnut (*Castanea dentata*) and oak species, such as northern red oak, historically were significant components the forest overstory at both areas. The chestnut blight (*Cryphonectria parasitica*) and subsequent fire suppression, white-tailed deer (*Odocoileus virginianus*) herbivory, and use of uneven-aged harvesting systems with no regard for regeneration has allowed forest composition to shift toward shade-tolerant tree species, such as maples and American beech (*Fagus grandifolia*) (Schuler and Fajvan 1999, Schuler 2004). At the FEF, prescribed fire recently has been used to promote oak regeneration in stands currently dominated by sugar maple, red maple, yellow-poplar (*Liriodendron tulipifera*), black cherry, American beech, sweet birch (*Betula lenta*), and basswood (*Tilia americana*) (Schuler 2004). In spring 2007–2009, prescribed fire treatments were conducted in management compartments 45 (121 ha), 13 (13 ha), and 21 (12 ha) on FEF (Fig. 1). The compartments were burned using strip head-fires, ignited with hand-held drip torches. Actual flame heights and combustion varied from immediately dying out to >3.5 m high in some spots, due to great variability in leaf litter, slope, and aspect. Additionally, 48, 20-m radius plots were randomly located in each of the three management compartments, and all overstory or midstory trees, other than oak or hickory species, were treated with herbicides or girdled (T. Schuler, USDA Forest Service, personal communication).

From spring through autumn, the extant bat community consists of northern myotis, little brown myotis (*M. lucifugus*), big brown bats (*Eptesicus fuscus*), tri-colored bats (*Perimyotis subflavus*), eastern red bats (*Lasiurus borealis*), silver-haired bats (*Lasionycteris noctivagans*), and hoary bats (*Lasiurus cinereus*) (Owen et al. 2004, Ford et al. 2005). A small number of Indiana myotis and endangered Virginia big-eared bats (*Corynorhinus townsendii virginianus*) that hibernate in cave systems on or near both FEF and the Petit Farm remain in the area during summer (Owen et al. 2001, Ford et al. 2002).

Radio telemetry

We captured bats in mist nets (Avinet, Inc., Dryden, New York) erected over stream corridors, small pools and ponds, skidder trails, and service roads during summer 2004–2006 at the Petit Farm and 2008–2009 at FEF. During autumn 2007–2008 at FEF, we used a harp trap to capture bats during the autumn swarm at Big Springs Cave, an Indiana myotis hibernaculum. For each captured bat, we determined species, sex, age, weight, forearm length, and reproductive condition (Menzel et al. 2002). We used Skin Bond[®] (Smith and Nephew, Largo, Florida) surgical cement to affix a 0.35-g radio transmitter (Model LB-2N; Holohil Systems Ltd., Carp, Ontario, Canada) between the scapulae of captured Indiana myotis. Bat capture and handling protocols were approved by the Animal Care and Use Committee of West Virginia University (Protocol No. 08-0504) and followed the guidelines of the American Society of Mammalogists (ACUC 1998). We used a radio receiver and 3-element Yagi antenna (Wildlife Materials, Inc., Murphysboro, Illinois) to locate roost trees. To record the geographic locations of roost trees, we used global positioning units (various models).

Habitat variables

We measured the physical characteristics of each roost tree and, using a point-quarter sampling method, the 4 trees (>10 cm dbh) nearest to the roost tree, as well as the site at which the roost tree was located. Measurements were taken within a few weeks of the bat roosting in a tree. For each roost tree, we determined tree species, diameter (cm) at breast height with a diameter (dbh) tape (DBHR), decay class (Cline et al. 1980; i.e., 1 = live, 2 = declining, 3 = recent dead, 4 = loose bark, 5 = no bark, 6 = broken top, 7 = broken bole; DECAYR), crown class (Nyland 1996; i.e., 1 = suppressed, 2 = intermediate, 3 = codominant, 4 = dominant; CROWNR), tree height (m) with a hypsometer (HEIGHT), roost height when known (ROOSTHGT), and visually estimated percent bark remaining on the tree (BARK). For each of 4 trees nearest to the roost tree, we determined tree species, diameter (cm) at breast height (DBHN), distance (m) to the roost tree (DISTN), decay class (DECAYN), and crown class (CROWNN), all of which were averaged for the 4 trees irrespective of species. We measured percent canopy gap either with a densiometer or through photographic methods (Johnson et al. 2009; GAP). We recorded aspect (ASPECT) with a compass, percent slope (SLOPE) with a clinometer at the plot (11.3 m radius centered on the roost tree), and stand basal area with a 20 factor prism (m^2 / ha ; BASAL).

Within burned and unburned areas, we located potential roost trees at random coordinates generated with ArcMap (Version 9.2, Environmental Systems Research Institute, Redlands, California). We considered unburned areas to be any area outside the three management compartments on FEF where prescribed fires were used or the forest stand on the Petit Farm where the wildfire occurred. Potential roost trees were identified as any tree (>10 cm diameter at breast height) that had exfoliating bark that possibly could be used by an Indiana myotis as

described by Menzel et al. (2001). We measured the same variables at the potential roost trees as we did at the actual roost trees.

In ArcMap, we determined the elevation (ELEV) for each roost tree and each roost tree's distance from the closest permanent water source (WATER). We also used ArcMap to determine distances that bats moved among successive roost trees.

Statistical analysis

We used the Mann-Whitney test (Proc Npar1way, SAS Institute, Inc. 2004) to make the following comparisons of tree and site characteristics: (1) roost trees located within burned areas to those in unburned areas; (2) roost trees in burned areas to potential roost trees in burned areas; (3) roost trees in unburned areas to potential roost trees in unburned areas; and (4) roost trees used in autumn to those used in summer. We used a Fisher's Exact Test (Proc Freq, SAS Institute, Inc. 2004) to determine if roost trees were more frequently located on any slope aspects. We also used a Mann-Whitney test to compare the frequency that Indiana myotis switched roosts (as measured as the number of consecutive days spent in a roost tree, between burned and unburned areas) and to compare distances (m) travelled between consecutive roost trees in the burned and unburned areas.

RESULTS

From 2004 to 2009, we captured and radio-tracked 16 Indiana myotis (1 female, 15 males), and located 51 roost trees (24 at FEF and 27 at the Petit Farm); 17 in burned areas and 37 in unburned areas. Eleven of the bats were captured and tracked to roosts during summer (May–August). All roost trees used by bats captured at FEF during the autumn swarm were located on or near FEF except 1 roost located on the Petit Farm, approximately 9 km from Big Springs Cave (Figure 1). In burned areas, Indiana myotis roosted exclusively in fire-killed sugar maple and red

maple snags. In unburned areas, Indiana myotis roosted in a variety of live tree species, predominately hickories, oaks, and maples (Table 1). The single female Indiana myotis that we tracked roosted in a large-diameter (31.0 cm) , fire-killed red maple with about 45 other bats, presumably also Indiana myotis (A. Stump, USDA Forest Service, pers. comm.). At FEF and the Petit Farm, some Indiana myotis roosted in fire-killed trees in stands that had initially been burned 1–3 years prior to our observation (Table 1).

Roost trees in burned stands were surrounded by less basal area and by trees in more advanced stages of decay, resulting in larger canopy gaps than at randomly-located potential roost trees in burned stands and at roost trees located in unburned stands (Table 2). Compared to randomly-located potential roost trees in unburned stands, roost trees in unburned stands were less decayed, had higher percent bark coverage, and were surrounded by lower basal area, resulting in larger canopy gaps (Table 2). In burned areas, roost trees were more frequently located on south-facing slopes ($P = 0.043$). In unburned areas, roost trees were more frequently located on west- and south-facing slopes ($P = 0.014$). Compared to summer roost trees, roost trees used in autumn had a higher percentage of bark coverage, were surrounded by greater basal area and by trees that were larger in diameter and less decayed, resulting in smaller canopy gaps surrounding these trees (Table 2). Roost trees used in summer were closer to water and on gentler slopes than roost trees used in autumn (Table 2).

Roost-switching frequency was similar ($P = 0.945$) between burned (mean = 1.25 days, SE = 0.25, switched every 1–4 days) and unburned areas (mean = 1.08 days, SE = 0.06, switched every 1–2 days). Distances that Indiana myotis moved among roost trees was similar ($P = 1.000$) between burned (mean = 219.62 m, SE = 49.65, range = 21–435 m) and unburned (mean = 476.95 m, SE = 177.23, range 1–2,420 m) areas.

DISCUSSION

Our observations indicate that Indiana myotis will respond favorably to structural changes in forests caused by fire. The characteristics of roost trees and surrounding trees in burned areas were important in roost selection. Typically, Indiana myotis roost under the exfoliating bark of live trees such as shagbark hickory or senescent trees that are taller and larger in diameter than surrounding trees (Menzel et al. 2001). Burning created additional roost trees as the bark of live trees tends to peel away from the sapwood from heated sap in the phloem/cambium layer. We observed Indiana myotis roosting in spaces under exfoliating bark of fire-killed trees, primarily sugar and red maples, species particularly susceptible to fire-induced damage or mortality (Brose et al. 1999). Within burned areas, Indiana myotis selected trees that were taller and larger in diameter, similar to that reported by others (Menzel et al. 2001). Roost trees were surrounded by trees that were in more advanced stages of decay, possibly providing additional roosting structure. Also, the senescence of roost trees and surrounding trees resulted in an enlarged canopy gap, allowing more solar radiation to reach the roost tree (Johnson et al. 2009). Roost trees in summer and autumn occurred mostly on southern or southwestern slopes, augmenting solar exposure.

Roost trees in unburned areas occurred in naturally-existing canopy gaps. However, roost trees were less decayed than random trees in unburned areas, and were comprised of a larger number of species than in burned areas. Although we did not investigate tree species selection, the diversity of tree species used in unburned areas was more typical of previous observations of Indiana myotis roosts (Menzel et al. 2001). In unburned areas, Indiana myotis selected trees surrounded by less basal area than randomly-located trees, and occurred in large canopy gaps. In burned areas, canopy gaps were larger than those in unburned areas. From our observations,

mean canopy gap size over roost trees in burned areas and those used during summer were >30%, but it remains unclear if enlarged canopy gaps such as those in burned areas provide actual fitness benefits for Indiana myotis beyond roost use in unburned areas. Also, because our study included data from only 1 female Indiana myotis, we were unable to make any substantive male-female roost selection comparisons. Nonetheless, the characteristics of roost trees used by males in our study are very similar to those reported for Indiana myotis maternity colonies elsewhere within the species' distribution (Menzel et al. 2001, Britzke et al. 2003, Carter 2006, Watrous et al. 2006).

During autumn, male Indiana myotis selected roost trees that were less decayed, and in smaller canopy gaps than roost trees used during summer. In the mountains of western Virginia to the east of our study area, almost half of the roost trees used during autumn were shagbark hickory (Brack 2006). Although we documented no bats roosting in burned areas during autumn, Indiana myotis have been reported roosting in burned areas in Kentucky, although it is unclear if those bats roosted in fire-killed trees (Gumbert 2001). In that study, summer and autumn roost areas also were similar in terms of canopy gap, aspect, slope, and distance to water. We found that most differences in site characteristics, including slope and distance to water likely were attributable to differences between the Petit Farm and FEF rather than selection *per se*, as the majority of autumn roost trees were located in or near the FEF and the majority of summer roost trees were located at the Petit Farm. Also, fire intensity and forest harvesting (basal area removal) at the Petit Farm were greater than at FEF. Compared to autumn roost trees, the larger canopy gaps at summer roost trees were due to more summer roosts being located in burned areas. The seasonal differences in the canopy gap sizes and consequent increased amounts of solar radiation reaching roost trees may have some physiological significance. During autumn

when insect availability may be unstable, male Indiana myotis may select relatively shaded, cooler roosts that allow them to conserve energy by lowering their body temperature near ambient air temperatures to a state of torpor (Henshaw and Folk 1966). Conversely, during summer, insect availability may be more consistent, allowing male Indiana myotis to maintain a higher body temperature during the day by selecting warm trees in canopy gaps on favorable aspects. Female Indiana myotis maternity colonies typically select roost trees with high solar exposure, presumably to facilitate juvenile growth rates (Callahan et al. 1997). Consequently, burning may have a more beneficial impact on summer roosting conditions for both sexes.

We believe that our observations suggest that efforts to manage forests with prescribed fire to enhance oak regeneration appear to be compatible with Indiana myotis habitat management. The immediate effects of forest fires are minimal in terms of disturbance to bats roosting in trees within a burned stand, but may affect species, e.g., eastern red bats, that roost in forest leaf litter (Rodrigue et al. 2001, Dickinson et al. 2009). The short-term (<10 years) effects of forest fires include the increase in roost tree abundance resulting in more trees with exfoliating bark and favorable conditions such as enlarged canopy gaps at trees that may have been previously unsuitable for Indiana myotis. Relative to bat-roosting habitat, the effects of fire on upland hardwood forest stands perhaps are functionally similar to the disturbance impacts following flood damage and mortality in bottomland and riparian forests, as many trees are killed and become suitable snags for roosts, with surrounding senescent trees and canopy gaps (Kurta et al. 1996, Carter 2006). In the Midwest, for example, Indiana myotis maternity colonies often use snags within floodplains or in ponds created by beavers (*Castor canadensis*). Forest fires in upland stands mimic floods in systems dominated by hydric disturbance and their effects on forest stands in terms of snag, i.e., roost tree, creation and forest structure change (Carter 2006).

However, floods may be more spatially extensive, providing a more abundant source of snag resources than forest fires, which may be more rarefied over the montane landscape where our study occurred. Although it is unknown if there is a minimum density of roost trees required for Indiana myotis occupancy of an area, our roost-switching data and that of others indicate that there usually are a sufficient number of roost trees in burned and unburned stands (Menzel et al. 2001, Gumbert et al. 2002, Kurta et al. 2002, Britzke et al. 2006). Fire-killed trees may be suitable Indiana myotis roosts for few to many years. Nonetheless, the ephemerality of these roost trees remains to be quantified, depending on species and site conditions, i.e., susceptibility to windthrow. Our results indicate that Indiana myotis do respond to the effects of fire on forest stands, roosting in fire-killed trees 1–3 years post-fire, thus maximizing the utility of the newly-created roost trees while they are suitable. Certainly, the exfoliating bark will gradually or quickly slough from the trees depending on species (Hallett et al. 2001), eventually rendering the tree unsuitable for Indiana myotis. Therefore, the intermediate- to longer-term benefits of fire are uncertain for Indiana myotis. A short-term increase in roost tree density was created by fire, but stand conditions may return to pre-fire densities in absence of additional disturbance as roost trees lose their bark and therefore much of their Indiana myotis roost-specific suitability. However, adjacent or nearby forest stands can be subjected to burning, or herbicide or girdling treatments to create additional roost trees in the short term. Systematic rotation of fire treatments among adjacent forest stands would maintain or even increase the density of roost trees for Indiana myotis populations at stand to landscape scales. By temporally staggering prescribed fire treatments among adjacent forest stands, potential roost trees could be maintained in an area for the foreseeable future (Rudolph and Conner 1996). In the long-term, canopy gap creation and reduction or elimination of fire-sensitive tree species due to fires will favor an oak-dominated

forest that is beneficial to many other wildlife species (McShea and Healy 2002). However, it is important to note that this will also aid in the regeneration and retention of hickories, a preferred roost tree genera of Indiana myotis (Brose et al. 1999, Nowacki and Abrams 2008). Because it will take several decades for shagbark hickories to reach roost tree size, burning adjacent stands on systematic rotation will create and retain snags and other large trees with exfoliating bark in the interim. Certainly, additional research is needed to fully assess the spatial and temporal dynamics of snags and burning in relation to Indiana myotis roosting habitat requirements relative to foreseeable management regimes in the central Appalachians and elsewhere.

Although we observed no annual reuse of roost trees, Indiana myotis have been documented returning to roost trees within specific roost areas for several consecutive years (Gumbert et al. 2002, Kurta et al. 2002). The mechanisms behind the initial use of a roost tree remain unclear (Wilkinson 1992, Ruczyński et al. 2009), but our observations indicate that Indiana myotis likely were using trees in or near the areas impacted by fires prior to the disturbances, then roosting in fire-killed trees >1 year following forest fires. Indeed, Indiana myotis were roosting in trees at FEF in 2001, before prescribed fires occurred (Ford et al. 2002). Although we did not observe the same individuals for multiple years, the fact that Indiana myotis roosted in fire-killed trees in burned areas suggests that they selected these new roost trees over those used in previous years, i.e., roost selection took precedence over roost fidelity. Apparently, Indiana myotis maternity colonies rarely or infrequently occur in the local area despite continued extensive mist netting efforts and the presence of hibernacula in the area (Ford et al. 2005, Johnson et al. 2009). Therefore, although selection may take precedence over fidelity at a local scale, it may not translate to regional scales. This would require a substantial shift in the summer ranges and migration behavior of bats (Fleming and Eby 2003). Habitat changes due to fire may

benefit local Indiana myotis populations that already occur in an area. If these changes do benefit Indiana myotis in terms of greater fitness, significant increases in the Indiana myotis population as a whole would occur only if prescribed fire treatments were expanded to include more of their geographic range, particularly the core population in the Midwest (Carter 2006).

ACKNOWLEDGMENTS

The USDA Forest Service Northern Research Station Joint Venture Agreement 06-JV-11242300-140 provided primary funding for our study from the National Fire Plan to West Virginia University, Division of Forestry and Natural Resources. Funding for prescribed burning was provided by a grant from Florida Power and Light and BHE Environmental to the U.S. Forest Service Northern Research Station through Collection Agreement 06-CO-112331-034. We thank the staff of the USDA Forest Service Monongahela National Forest and the USDA Forest Service Northern Research Station Timber and Watershed Laboratory for conducting the prescribed burns. Field assistance was graciously provided by J. Boyle, K. Boyle, C. McDaniels, A. Stump, and M. Walsh.

REFERENCES

- Animal Care and Use Committee (ACUC). 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy*. 79: 1416–1431.
- Blake, J.G. 2005. Effects of prescribed burning on distribution and abundance of birds in a closed-canopy oak-dominated forest, Missouri, USA. *Biological Conservation*. 121: 519–531.
- Boyles, J.G.; Aubrey, D.P. 2006. Managing forests with prescribed fire: implications for a cavity-dwelling bat species. *Forest Ecology and Management*. 222: 108–115.

- Brack, V., Jr. 2006. Autumn activity of *Myotis sodalis* (Indiana bat) in Bland County, Virginia. *Northeastern Naturalist*. 13: 421–434.
- Braun, E.L. 1950. Deciduous forests of eastern North America. New York, NY, McGraw-Hill, 596 p.
- Brennan, L.A.; Engstrom, R.T.; Palmer, W.E.; Hurst, G.A.; Burger, L.W.; Hardy, C.L. 1998. Whither wildlife without fire? Transactions of the 63rd North American Wildlife and Natural Resources Conference. 63: 402-414.
- Britzke, E.R.; Harvey, M.J.; Loeb, S.C. 2003. Indiana bat, *Myotis sodalis*, maternity roosts in the southern United States. *Southeastern Naturalist*. 2: 235–242.
- Britzke, E.R.; Hicks, A.C.; Von Oettingen, S.; Darling, S.R. 2006. Description of spring roost trees used by female Indiana bats (*Myotis sodalis*) in the Lake Champlain Valley of Vermont and New York. *American Midland Naturalist*. 155: 181–187.
- Brose, P.H.; Schuler, T.M.; Van Lear, D.H.; Berst, J. 2001. Bringing back fire: the changing fire regimes of the Appalachian mixed-oak forests. *Journal of Forestry*. 99: 30–35.
- Brose, P.H.; Schuler, T.M.; Ward, J. S. 2006. Responses of oak and other hardwood regeneration to prescribed fire: what we know as of 2005. In: Dickinson, M.B. ed., *Fire in Eastern Oak Forests: Delivering Science to Land Managers*. General Technical Report GTR-NRS-P-1, Newtown Square, PA, U.S. Department of Agriculture, Forest Service, Northern Research Station: 123–135.
- Brose, P.H.; Van Lear, D.H.; Keyser P.D. 1999. A shelterwood-burn technique for regenerating productive upland oak sites in the Piedmont region. *Southern Journal of Applied Forestry*. 23: 158–163.

- Callahan, E.V.; Drobney R.D.; Clawson, R.L. 1997. Selection of summer roosting sites by Indiana bats (*Myotis sodalis*) in Missouri. *Journal of Mammalogy*. 78: 818–825.
- Carter, T.C. 2006. Indiana bats in the Midwest: the importance of hydric habitats. *Journal of Wildlife Management*. 70: 1185-1190.
- Carter, T.C.; Feldhamer G.A. 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.
- Chaverri, G.; Quirós, O.E.; Gamba-Rios, M.; Kunz, T.H. 2007. Ecological correlates of roost fidelity in the tent-making bat *Artibeus watsoni*. *Ethology*. 113: 598–605.
- Clawson, R.L. 2002. Trends in population size and current status. In: Kurta, A.; Kennedy, J., eds., *The Indiana bat: biology and management of an endangered species*. Austin, TX, Bat Conservation International: 2–8.
- Cline, S.P.; Berg, A.B.; Wight, H.M. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *Journal of Wildlife Management*. 44: 773–786.
- Crampton, L.H.; Barclay, R.M.R. 1998. Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. *Conservation Biology*. 12: 1347–1358.
- Dickinson, M.B.; Lacki, M.J.; Cox, D.R. 2009. Fire and the endangered Indiana bat. In: Hutchinson, T.F., ed., *Proceedings of the 3rd fire in eastern oak forests conference*. General Technical Report GTR-NRS-P-46, Newtown Square, PA, U.S. Department of Agriculture, Forest Service, Northern Research Station: 51–75.
- Fleming, T.H.; Eby P. 2003. Ecology of bat migration. In Kunz, T.H.; Fenton, M.B., eds., *Bat ecology*. Chicago, IL, University of Chicago Press: 156–208.

- Ford, W.M.; Menzel, J.M.; Menzel, M.A.; Edwards, J.W. 2002. Summer roost-tree selection by a male Indiana bat on the Fernow Experimental Forest. General Technical Report NE-378, Newtown Square, PA, U.S. Department of Agriculture, Forest Service, Northeastern Research Station, 7 p.
- Ford, W.M.; Menzel, M.A.; Rodrigue, J.L.; Menzel, J.M.; Johnson, J.B. 2005. Relating bat species presence to simple habitat measures in a central Appalachian forest. *Biological Conservation*. 126: 528–539.
- Gardner, J.E.; Garner, J.D.; Hofmann, J.E. 1991. Summer roost selection and roosting behavior of *Myotis sodalis* (Indiana bat) in Illinois. Champaign, IL, Illinois Natural History Survey and Illinois Department of Conservation: 56 p.
- Gumbert, M.W. 2001. Seasonal roost tree use by Indiana bats in the Somerset Ranger District of the Daniel Boone National Forest, Kentucky. Richmond, KY: Eastern Kentucky University, 136 p. M.S. Thesis.
- Gumbert, M.W.; O'Keefe, J.M.; MacGregor, J.R. 2002. Roost fidelity in Kentucky. In Kurta, A.; Kennedy, J., eds., *The Indiana bat: biology and management of an endangered species*. Austin, TX, Bat Conservation International: 143–152.
- Hallett, J.G.; Lopez, T.; O'Connell, M.A.; Borysewicz, M.A. 2001. Decay dynamics and avian use of artificially created snags. *Northwest Science*. 75: 378–386.
- Hayes, J.P.; Loeb, S.C. 2007. The influences of forest management on bats in North America. In Lacki, M.J.; Hayes, J.P.; Kurta, A. eds., *Bats in forests: conservation and management*, Baltimore, MD, Johns Hopkins University Press: 207–234.

- Henshaw, R.E.; Folk, G.E., Jr. 1966. Relation of thermoregulation to seasonally changing microclimate in two species of bats (*Myotis lucifugus* and *M. sodalis*). *Physiological Zoology*. 39: 223–236.
- Johnson, J.B.; Edwards, J.W.; Ford, W.M.; Gates, J.E. 2009. Roost tree selection by northern myotis (*Myotis septentrionalis*) maternity colonies following prescribed fire in a Central Appalachian Mountains hardwood forest. *Forest Ecology and Management*. 258: 233–242.
- Johnson, J.B.; Gates, J.E. 2010. Observations of Indiana myotis roosting and foraging behavior in Carroll County, Maryland. *The Maryland Naturalist*. In press.
- Keyser, P.K.; Ford, W.M. 2006. Influence of fire and mammals in oak forests. In: Dickenson, M.B., ed., *Fire in eastern oak forests: delivering science to land managers*. General Technical Report GTR-NRS-1, Newtown Square, PA. U.S. Department Agriculture, Forest Service, Northern Research Station: 180–190.
- Kochenderfer, J.N. 2006. Fernow and the Appalachian hardwood region. In: Adams, M.B.; DeWalle, D.R.; Horn, J.L., eds., *The Fernow watershed acidification study*. Dordrecht, Netherlands, Springer: 17–39.
- Kochenderfer, J.N.; Adams, M.B.; Miller, G.W.; Helvey, J.D. 2007. Factors affecting large peakflows on Appalachian watersheds: lessons from the Fernow Experimental Forest. Research Paper NRS-3, Newtown Square, PA, U.S. Department Agriculture, Forest Service, Northeastern Research Station, 24 p.
- Kunz, T. H.; Lumsden, L.F. 2003. Ecology of cavity and foliage roosting bats. In Kunz, T.H.; Fenton, M.B., eds., *Bat ecology*. Chicago, IL, University of Chicago Press: 3–89.

- Kurta, A.; Murray, S.W. 2002. Philopatry and migration of banded Indiana bats (*Myotis sodalis*) and effects of radio transmitters. *Journal of Mammalogy*. 83: 585–589.
- Kurta, A.; Murray, S.W.; Miller, D.H. 2002. Roost selection and movements across the summer landscape. In Kurta, A.; Kennedy, J., eds., *The Indiana bat: biology and management of an endangered species*. Austin, TX, Bat Conservation International: 118–129.
- Kurta, A.; Williams, K.J.; Mies, R. 1996. Ecological, behavioural, and thermal observations of a peripheral population of Indiana bats (*Myotis sodalis*). In: Barclay, R.M.R.; Brigham, R.M., eds., *Bats and forests symposium, Working Paper 23/1996*, Victoria, Canada, British Columbia Ministry of Forests: 91–101.
- Lacki, M.J.; Cox, D.R.; Dodd, L.E.; Dickinson, M.B. 2009. Response of northern bats (*Myotis septentrionalis*) to prescribed fires in eastern Kentucky forests. *Journal of Mammalogy*. 90: 1165–1175.
- MacGregor, J.; Kiser, J.D.; Gumbert, M.W.; Reed, T.O. 1999. Autumn roosting habitat of male Indiana bats (*Myotis sodalis*) in a managed forest setting in Kentucky. In: Stringer, J.W.; Loftis, D.L., eds., *General Technical Report SRS-24*, Asheville, NC, U.S. Department of Agriculture, Forest Service, Southern Research Station: 169–170.
- Madarish, D.M.; Rodrigue, J.L.; Adams, M.B. 2002. Vascular flora and macroscopic fauna on the Fernow Experimental Forest. *General Technical Report GTR-NE-291*, Newtown Square, PA, U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 37 p.
- McShea, W.J.; Healy, W.M. 2002. *Oak forest ecosystems: ecology and management for wildlife*. Baltimore, MD, Johns Hopkins: 432 p.

- Menzel, M.A.; Menzel, J.M.; Carter, T.C.; Ford, W.M.; Edwards, J.W. 2001. Review of the forest habitat relationships of the Indiana bat (*Myotis sodalis*). General Technical Report NE-284, Newtown Square, PA, U. S. Department of Agriculture, Northeastern Research Station: 21 p.
- Menzel, M.A.; Menzel, J.M.; Castleberry, S.B.; Ozier, J.; Ford, W.M.; Edwards, J.W. 2002. Illustrated key to skins and skulls of bats in the Southeastern and Mid-Atlantic States. Research Note NE-376, Newtown Square, PA, U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 18 p.
- Nowacki, G.J.; Abrams, M.D. 2008. The demise of fire and “mesophication” of forests in the eastern United States. *Bioscience*. 58: 123–138.
- Nyland, R.D. 1996. *Silviculture: concepts and applications*. New York, NY, McGraw-Hill: 633 p.
- Owen, S.F.; Menzel, M.A.; Ford, W.M.; Chapman, B.R.; Miller, K.V.; Edwards, J.W.; Wood, P. B. 2001. First summer record of a female Indiana bat, *Myotis sodalis*, in West Virginia. *Journal of the Elisha Mitchell Scientific Society*. 117: 132–134.
- Owen, S.F.; Menzel, M.A.; Edwards, J.W.; Ford, W.M.; Menzel, J.M.; Chapman, B.R.; Wood, P.B.; Miller, K.V. 2004. Bat activity in harvested and intact forest stands in the Allegheny Mountains. *Northern Journal of Applied Forestry*. 21: 154–159.
- Rodrigue, J.L.; Shuler, T.M.; Menzel, M.A. 2001. Observations of bat activity during prescribed burning in West Virginia. *Bat Research News* 42: 48–49.
- Ruczyński, I.; Kalko, E.K.V.; Siemers, B.M. 2009. Calls in the forest: a comparative approach to how bats find tree cavities. *Ethology*. 115: 167–177.

- Rudolph, D.C.; Conner, R.N. 1996. Red-cockaded woodpeckers and silvicultural practice: is uneven-aged silviculture preferable to even-aged? *Wildlife Society Bulletin* 24:330–333.
- SAS Institute, Inc. 2004. SAS/STAT 9.1 users guide. Version 9.1. Cary, NC, SAS Institute, Inc.: 5,121 p.
- Schuler, T.M. 2004. Fifty years of partial harvesting in a mixed mesophytic forest: composition and productivity. *Canadian Journal of Forest Research*. 34: 985–997.
- Schuler, T.M.; Fajvan, M.A.. 1999. Understory tree characteristics and disturbance history of a central Appalachian forest prior to old-growth harvesting. Research Paper NE-710, Radnor, PA, U. S. Department of Agriculture, Forest Service, Northeastern Research Station: 12 p.
- Sedgeley, J.A.; O'Donnell, C.F.J. 1999. Factors influencing roost cavity selection by a temperate rainforest bat (*Chalinolobus tuberculatus*, Vespertilionidae) in New Zealand. *Journal of Zoology*. 249: 437–446.
- Thomson, C.E. 1982. *Myotis sodalis*. *Mammalian species*. 163: 1–5.
- Tucker, J.W., Jr.; Robinson, W.D.; Grand, J.B. 2004. Influence of fire on Bachman's sparrow, an endemic North American songbird. *Journal of Wildlife Management*. 68: 1114–1123.
- United States Fish and Wildlife Service (USFWS). 2007. Indiana bat (*Myotis sodalis*) draft recovery plan: first revision. Fort Snelling, MN, Region 3, USFWS: 258 p.
- United States Fish and Wildlife Service (USFWS). 2009. Indiana bat (*Myotis sodalis*), 5-year review: summary and evaluation. Bloomington, IN, Region 3, USFWS, 13 p.

- Watrous, K.S.; Donovan, T.M.; Mickey, R.M.; Darling, S.R.; Hicks, A.C.; Von Oettingen, S.L.
2006. Predicting minimum habitat characteristics for the Indiana bat in the Champlain
Valley. *Journal of Wildlife Management*. 70: 1228–1237.
- Wilkinson, G.S. 1985. The social organization of the common vampire bat. *Behavioral Ecology
and Sociobiology*. 17: 111–121.
- Wilkinson, G.S. 1992. Information transfer at evening bat colonies. *Animal Behaviour*. 44: 501–
518.

Table 1. Indiana myotis roost tree use in forest stands that were and were not subjected to fire at the Fernow Experimental Forest (FEF) and Petit Farm in Tucker County, West Virginia, 2004–2009.

Year	Radio-tracked bats	Tree species used		Habitat alterations	Comments
		In burned area	In unburned area		
2003	–	–	–	Petit Farm: escaped campfire burns through forest stand subjected to diameter-limit harvest	–
2004	Petit Farm: 1 female in summer	<i>A. rubrum</i> (n = 1)	–	–	At least 45 individuals using roost tree
2005	Petit Farm: 4 males in summer	<i>A. rubrum</i> (n = 8) <i>A. saccharum</i> (n = 2)	<i>A. rubrum</i> (n = 2) <i>C. cordiformis</i> (n = 1) <i>Sassafras albidum</i> (n = 1) <i>Quercus rubra</i> (n = 1) <i>Q. prinus</i> (n = 1) <i>Betula lenta</i> (n = 1)	–	
2006	Petit Farm: 3 males in summer	<i>A. rubrum</i> (n = 1) Undetermined (n = 1)	<i>A. saccharum</i> (n = 2) <i>A. rubrum</i> (n = 1) <i>Betula lenta</i> (n = 1) <i>Q. rubra</i> (n = 1) <i>Robinia pseudoacacia</i> (n = 1) Undetermined (n = 1) <i>C. ovata</i> (n = 4) <i>Fagus grandifolia</i> (n = 2)	–	–
2007	FEF: 2 males in autumn	–	<i>Q. rubra</i> (n = 2) <i>Prunus serotina</i> (n = 1) <i>Liriodendron tulipifera</i> (n = 1)	FEF: all 3 compartments received prescribed fire treatment	–

Table 1. Continued.

Year	Radio-tracked bats	Tree species used		Habitat alterations	Comments
		In burned area	In unburned area		
2008	FEF: 1 male in summer, 3 males in autumn	–	Summer roosts: <i>C. glabra</i> (<i>n</i> = 1) <i>F. grandifolia</i> (<i>n</i> = 1) <i>A. rubrum</i> (<i>n</i> = 1) Autumn roosts: <i>C. ovata</i> (<i>n</i> = 4) <i>L. tulipifera</i> (<i>n</i> = 1) <i>A. saccharum</i> (<i>n</i> = 1) <i>Ulmus rubra</i> (<i>n</i> = 1)	FEF: compartment 45 received prescribed fire treatment	1 male in autumn roosted in <i>A. saccharum</i> in unburned area of Petit Farm
2009	FEF: 2 males in summer	<i>A. rubrum</i> (<i>n</i> = 4)	–	FEF: compartments 13 and 21 received prescribed fire treatment	1 roost tree in compartment 13 3 roost trees in compartment 45

Table 2. Characteristics of roost trees used by Indiana myotis and randomly located trees subjected and not subjected to fire in Tucker County, West Virginia, 2004–2009. Mann-Whitney and Fisher’s Exact tests were used to determine significance (*P*-value) differences between means.

Comparison and variables	Mean	SE	Mean	SE	<i>P</i> -value
Fire roost vs. fire random					
Fire roost (<i>n</i> = 17)			Fire random (<i>n</i> = 6)		
DBHR (cm)	40.72	2.47	26.63	4.85	0.020
HEIGHT (m)	20.51	1.54	12.92	2.17	0.011
DECAYN	3.60	0.29	2.21	0.42	0.032
GAP (%)	32.77	5.43	11.43	0.71	0.008
BASAL (m ² /ha)	11.32	2.68	26.86	3.63	0.012
SLOPE (%)	29.53	2.77	43.50	5.12	0.021
ELEV (m)	837.82	11.06	680.17	26.26	<0.001
Fire roost vs. non-fire roost					
Fire roost (<i>n</i> = 17)			Non-fire roost (<i>n</i> = 34)		
BARK (%)	64.25	6.73	76.79	5.31	0.029
DBHN (cm)	25.21	1.48	30.79	1.54	0.019
DECAYN	3.60	0.29	1.54	0.14	<0.001
GAP (%)	32.77	5.43	14.63	3.10	0.002
BASAL (m ² /ha)	11.32	2.68	23.55	2.08	0.001
WATER (m)	89.12	22.69	272.97	47.70	0.023
Non-fire roost vs. non-fire random					
Non-fire roost (<i>n</i> = 34)			Non-fire random (<i>n</i> = 15)		
DECAYR	2.95	0.29	4.27	0.36	0.010
BARK (%)	76.79	5.31	46.67	8.20	0.006
GAP (%)	14.63	3.10	8.49	0.45	<0.001
BASAL (m ² /ha)	23.55	2.08	32.52	3.29	0.041

Comparison and variables	Mean	SE	Mean	SE	<i>P</i> -value
ELEV (m)	812.59	16.66	721.27	20.58	0.002
Summer roosts vs. autumn roosts					
Summer roost (<i>n</i> = 34)	Autumn roost (<i>n</i> = 17)				
BARK (%)	68.59	4.80	80.41	8.11	0.014
DBHN (cm)	26.72	1.28	33.20	2.18	0.026
DECAYN	2.68	0.26	1.32	0.11	0.001
GAP (%)	30.33	7.27	11.66	0.62	0.008
BASAL (m ² /ha)	15.68	2.58	24.34	2.15	0.021
SLOPE (%)	26.59	2.15	42.00	4.88	0.006
WATER (m)	127.08	37.70	380.88	52.56	<0.001

Figure 1. Indiana myotis roost tree locations within burned and unburned areas on the Fernow Experimental Forest (FEF) and Petit Farm, Tucker County, West Virginia, 2004–2009.

CHAPTER 7

Conclusion

The role of forest disturbances in the context of landscape ecology and implications for forest dwelling bats is of significant importance and should be considered when developing land management strategies and conceptual frameworks for species conservation. My research provides insight into the roosting ecology of northern myotis and Indiana myotis following prescribed fire, a forest disturbance that potentially affects roost tree availability and distributions at local spatial and immediate temporal scales. My findings indicate that northern myotis, a forest-interior dwelling species presumed most sensitive of extant bat species in West Virginia to disturbance, at worst was neutral in its response to prescribed fire, but probably benefits from a temporary increase in snag availability and canopy gaps over roost trees. Indeed, prescribed fire caused overstory tree mortality, resulting in large canopy gaps that allowed increased solar exposure to reach roost trees and likely provided thermal benefits to northern myotis maternity colonies. Similar to northern myotis, Indiana myotis may have benefitted from both forest fires and prescribed fires, which created similar forest conditions from a physical structure and site perspective. Indiana myotis roosted in red and sugar maples that were fire-killed, indicating that these bats recognized the increase in snag availability on the landscape and exploited those conditions in the near term. Forest fires likely create similar forest conditions to those in flooded riparian areas, where Indiana myotis roost in snags created through flooding.

My research utilizing a graph theoretic approach to examining roost switching behavior indicates that social groups of northern myotis have established networks of roost trees, with few central node roost trees within those networks being more connected than others. Northern myotis form social groups that roost in networks of trees that center on a central node roost tree

that is selected based on surrounding basal area and decay stage. Forest disturbances such as prescribed fire may result in changes to roost networks through inputs in suitable roost trees by senescence and creation of forest canopy gaps. The role of forest disturbance in the social organization and roost networks of bat remains a compelling area of research going forward.

Although northern myotis in my study formed social groups that restricted their roost areas to small watersheds, and these social groups were presumed family members based on the philopatric tendencies of this species, I found no consistent indication that bats among watersheds were genetically differentiable subpopulations. Moreover, using genotype data to model and sort individuals from presumed subpopulations into clusters indicated that these individuals were structured, but not based on spatial attributes. Lastly, due to the mating system of northern myotis where networks of mating sites are maintained and isolated forest patches can be exploited during summer, I find no evidence that indicated that forest disturbances such as prescribed fire disrupt gene flow among individuals.

Prescribed fire apparently has no negative effect on the roosting ecology of cavity-roosting bats, but it remains to be investigated how this type of forest disturbance affects foliage-roosting bat species such as eastern red bats. In the broader context of forest habitat – wildlife relationships, prescribed fires will promote hard mast producing tree species, including oaks and hickories, thus benefitting a wide range of wildlife species.