Research Article

Northern Long-Eared Bat Day-Roosting and Prescribed Fire in the Central Appalachians, USA

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ABSTRACT

The northern long-eared bat (*Myotis septentrionalis* Trovessart) is a cavity-roosting species that forages in cluttered upland and riparian forests throughout the oak-dominated Appalachian and Central Hardwoods regions. Common prior to white-nose syndrome, the population of this bat species has declined to functional extirpation in some regions in the Northeast and Mid-Atlantic, including portions of the central Appalachians. Our long-term research in the central Appalachians has shown that maternity colonies of this species form non-random assorting networks in patches of suitable trees that result from long- and short-term forest disturbance processes, and that roost loss can occur with these disturbances. Following two consecutive prescribed burns on the Fernow Experimental Forest in the

RESUMEN

El murciélago orejudo del norte (*Myotis septentrionalis* Trovessart) es una especie que habita en cuevas y se alimenta de insectos que recolecta en el sustrato de áreas altas y riparias en bosques dominados por robles en los Apalaches y en otros bosques deciduos en la región central de Norte América. Comúnmente y antes de ser afectados por el síndrome de la nariz blanca, las poblaciones de este murciélago han declinado hasta su extinción funcional en algunas regiones del Noreste y del Atlántico Medio, incluyendo porciones de los Apalaches centrales. Nuestra investigación a largo plazo en los Apalaches centrales ha mostrado que las colonias maternales forman asociaciones no azarosas en parches de árboles apropiados en el bosque y que resultan de procesos de disturbios a corto y largo plazo, y que la pérdida de lugares para el percheo de los murciélagos puede ocurrir con esos disturbios. Después de dos quemas prescriptas consecutivas en el bosque experimental *Fernow Fire* en los Apalaches centrales en West central Appalachians, West Virginia, USA, in 2007 to 2008, post-fire counts of suitable black locust (*Robinia pseudoacacia* L.; the most selected species for roosting) slightly decreased by 2012. Conversely, post-fire numbers of suitable maple (*Acer* spp. L.), primarily red maple (*Acer rubrum* L.), increased by a factor of three, thereby ameliorating black locust reduction. Maternity colony network metrics such as roost degree (use) and network density for two networks in the burned compartment were similar to the single network observed in unburned forest. However, roost clustering and degree of roost centralization was greater for the networks in the burned forest area. Accordingly, the short-term effects of prescribed fire are slightly or moderately positive in impact to day-roost habitat for the northern long-eared bat in the central Appalachians from a social dynamic perspective. Listing of northern long-eared bats as federally threatened will bring increased scrutiny of immediate fire impacts from direct take as well as indirect impacts from long-term changes to roosting and foraging habitat in stands being returned to historic fire-return conditions. Unfortunately, definitive impacts will remain speculative owing to the species' current rarity and the paucity of forest stand data that considers tree condition or that adequately tracks snags spatially and temporally.

Virginia, EEUU, en 2007 y 2008, el conteo del árboles apropiados de acacia negra (*Robinia pseudoacacia* L.; la especie más elegida para el percheo) mostró un decrecimiento hacia 2012. De manera opuesta, el número de especies post-fuego adecuadas para el percheo (*Acer* spp. L.), fundamentalmente de arce rojo (*Acer rubrum* L.), se incrementó por un factor de tres, y por lo tanto mejoró la reducción causada por la disminución de la acacia. Las asociaciones maternales medidas como el grado de percheo (el uso) y la densidad de dos asociaciones de colonias maternales en el compartimiento quemado fueron similares a una asociación observada en el bosque no quemado. Sin embargo, el agrupamiento en el percheo y su grado de concentración fue mayor para las asociaciones en el área quemada. En concordancia, los efectos a corto plazo de las quemas prescriptas son de pequeño a moderadamente positivos en su impacto sobre el hábitat de percheo diario para el murciélago orejudo en los Apalaches centrales desde la perspectiva de su dinámica social. El listado del murciélago orejudo del norte como amenazado a nivel federal brindará un mayor interés en los efectos inmediatos del fuego tomados de datos directos, como así también de impactos indirectos de cambios a largo plazo en el percheo y el forrajeo en rodales que están retornando a condiciones históricas en su régimen de incendios. Desafortunadamente, los impactos definitivos van a seguir siendo objeto de especulaciones, dada la actual rareza y escasez de los datos de los rodales, que solo consideran las condiciones de los árboles o que relevan adecuadamente espacial y temporalmente a los árboles muertos en pié.

Keywords: central Appalachians, day-roosts, maternity colony, *Myotis septentrionalis,* northern long-eared bat, prescribed fire, roost network

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INTRODUCTION

Over the past decade, efforts to quantify the effects of prescribed fire on many aspects of bat ecology have steadily increased as conservation concern for bats has risen and the use of prescribed fire has become more widespread throughout eastern United States. Post-fire changes in insect prey abundance are variable, with work showing both increases and decreases of species consumed by bats (Swengle 2001, Lacki *et al*. 2009). However, in Eastern landscapes where prescribed burning reduces forest stand density or "clutter," foraging quality as measured by relative abundance of recorded echolocation pulses typically increases for many bat species after fire (Ford *et al*. 2006*a*, Loeb and Waldrop 2008). Presumably, unchanged or even modest decreases in insect abundance are ameliorated by the changes in forest physiognomy that increase bat foraging efficiency (Ford *et al*. 2006*a*). Depending on fire severity, seasonality, and frequency, evidence from the East suggests that fire often can recruit more trees or snags into conditions suitable for day-roosts for bark- and cavity-roosting bat species than are lost (Perry 2012). Indeed, Johnson *et al*. (2010) hypothesized that day-roost use by the federally endangered Indiana bat (*Myotis sodalist* Miller and Allen) at the landscape level in upland habitats may display a shifting disturbance mosaic pattern resulting from fire similar to that observed by Carter (2006), as maintained by flood events in lowland systems throughout the species' distribution. Specifically, periodic landscape-level fires produce requisite site conditions needed by the Indiana bat, such as a pulse recruitment of snags with exfoliating bark, reduced canopy cover, and increased solar radiation on residual boles, as well as factors important over longer periods such as maintenance and regeneration of shagbark hickory (*Carya ovata* [Mill.] K. Koch), an exfoliating bark species highly preferred as roosts (Johnson *et al.* 2010, Perry 2012). The lone example of an Indiana bat maternity colony from the High Allegheny Mountain region of West Virginia, USA, where climate conditions were believed too cool to support a colony (Brack *et al*. 2002), occurred following an intense, stand-changing wildfire in West Virginia (Johnson *et al.* 2010). That being said, evidence of improved habitat conditions for bats from prescribed burning as a forest management or ecosystem restoration tool is largely circumstantial. Although it is reasonable to posit benefits of fire to bats, in the absence of measures of bat recruitment and survival or changes in physiologic condition, most researchers have concluded that their data conclusively reveals only the plasticity of many bat species to readily use burned landscapes as opposed to any conferred ecological advantage (Boyles and Aubrey 2006, Johnson *et al.* 2009, Johnson *et al*. 2010, Karp 2013). Nonetheless, some negative aspects of fire relative to bats in the East have been raised. Though believed to be an uncommon occurrence, smoke entry into caves and mines from dormant-season burning when bats are hibernating has been noted (Carter *et al*. 2002). For non-hibernating migratory species such as the eastern red bat (*Lasiurus borealis* Müller), potential mortality from the inability to rouse from torpor while ground-roosting during dormant-season burning in the upper and mid-South could occur (Perry 2012). Dickinson *et al.* (2010) showed that smoke and heating during early growing season fires in the central Appalachians could exceed acceptable physiological thresholds for the northern long-eared bat. Rodrigue *et al*. (2001) observed that Myotine bats day-roosting in trees are disturbed during burning as flames approach roost sites.

In the central Appalachians, a near century of fire suppression exacerbated by continual diameter-limit harvesting have led to increased mesophication, whereby heavy-seed, shade-intolerant species important to wildlife, such as northern red oak (*Quercus rubra* L.), are being replaced by shade-tolerant tree species such as red maple (*Acer rubrum* L.) that have low value to mast-consuming wildlife (Schuler 2002, Nowacki and Abrams 2008). Additionally, in the Ridge and Valley portion of the region, large areas formerly dominated by montane yellow pine savannas (i.e., pitch pine [*Pinus rigida* Mill.]–bear oak [*Quercus ilicifolia* Wangenh.]) that have unique wildlife and biodiversity values have been type converted by fire suppression or abnormally lengthened fire return intervals. On public lands in the region, such as the Daniel Boone National Forest in Kentucky, the George Washington-Jefferson National Forest in Virginia, and the Monongahela National Forest in West Virginia, prescribed burning programs over the last two decades have increased in frequency and area to reverse these trends.

Prior to the onset of white-nose syndrome (WNS) in 2006 that has resulted in the loss of >7 million cave-hibernating bats in the East, managers typically only had to address forest management impacts (negative or positive) on the Indiana bat. Examples included tailoring fire prescriptions to avoid take such as conducting growing-season burning when non-volant juvenile bats are not present in day-roosts or limiting dormant-season burning near known hibernacula in the relatively few areas where Indiana bats were known to occur on the landscape. However, with the formerly ubiquitous northern long-eared bat (*Myotis septentrionalis* Trovessart), now listed as federally threatened in deciduous forests in the East, managers on these forests and elsewhere are now tasked with understanding the response of this species to changes in foraging and day-roosting habitat due to burning. In the central Appalachians, northern long-eared bat foraging activity has been reduced by >75 % (Johnson *et al*. 2013), reflective of the overall regional population declines (Frick *et al*. 2015). Similarly, Francl *et al*. (2012) showed a near cessation of juvenile recruitment from surviving northern long-eared bats in the region following the onset of WNS.

Before WNS, northern long-eared bats in the central Appalachians were documented in a wide range of forest conditions—from intensively managed hardwood forests on industrial ownerships to mature or old-growth habitats on public lands (Menzel *et al*. 2002, Owen *et al*. 2002, Ford *et al*. 2006*b*). Foraging occurs largely in moderately to fully stocked upland forests, first-order headwaters, and woodland vernal pools (Owen *et al*. 2003, Owen *et al*. 2004, Ford *et al*. 2005, Brooks and Ford 2006). Although this species day-roosted in numerous tree species in this region, common to all stand conditions was a strong roosting preference for suppressed, small- to medium-sized live black locust (*Robinia pseudoacacia* L.) with cavities, a response seen in other parts of the species' distribution in hardwood-dominated forest types (Silvis *et al*. 2012; B. Hyzy, University of Wisconsin, Stevens Point, Wisconsin, USA, personal communication). A consistent finding was that day-roost availability is not a limiting factor for northern long-eared bats in the central Appalachians. Similarly, Johnson *et al*. (2009) on the Fernow Experimental Forest (FEF) in West Virginia, and Lacki *et al*. (2009) on the Daniel Boone National Forest in Kentucky, concluded that metrics of northern long-eared bat day-roost such as tree size and condition or immediate forest-canopy gap differed somewhat between trees and snags used by bats in burned forests versus those in unburned forests, although species selection was largely unchanged. Moreover, Johnson *et al*. (2011) did not observe any consistent trend relative to the spatial area used for day-roosts by several northern long-eared bat maternity colonies in burned versus unburned stands following two successive prescribed burns in mixed oak and mixed mesophytic stands.

Forest management guidelines provided by the US Fish and Wildlife Service for the listing of the northern long-eared bat under the Endangered Species Act include a 4(d) rule that allows for the continuation of activities in

Eastern forests such as prescribed burning for forest habitat management or ecosystem restoration following the formal and informal consultation process for federal actions or where a federal "nexus" occurs (i.e., management on state lands aided by federal aid or farm bill-related management actions on private land). However, restrictions include limits on burning in June and July in the immediate area around known day-roosts, during the mid- to late-pregnancy period and when juvenile bats are non-volant. Currently, the US Fish and Wildlife Service recognizes that land management practices such as the use of prescribed burning to benefit larger overarching stewardship needs may have conservation benefits to bats. Still, with northern long-eared bat populations projected to continue to decline, an eventual endangered status is likely (Frick *et al*. 2015; T. Carter, Ball State University, Muncie, Indiana, USA, personal communication). And although day-roost and foraging habitat is even less limiting with reduced populations of northern long-eared bats on the landscape, continued provision of high quality summer maternity habitat may be a critical component to reduce any additive mortality and enhance recruitment so that regional populations are as high as possible prior to the hibernating period when WNS is operative. Similarly, identification and modification of any habitat condition or management tool that results in lower fitness are also important. Accordingly, the primary objective of our study was to reexamine northern long-eared bat roost-network metrics from Johnson *et al*. (2011) using two mode network analysis and roost disruption simulation (Silvis *et al*. 2014) as a potential surrogate measure of maternity colony viability, and to evaluate responses to two successive prescribed burns on the FEF. Our secondary objective was to assess long-term change in condition and availability of northern long-eared bat day-roost trees and snags as documented by Johnson *et al*. (2009) and Karp (2013) from these two successive burns. Based on manipulative day-roost elimination studies on northern long-eared bats (Silvis *et al*. 2014, Silvis *et al*. 2015*a*), we hypothesized that northern long-eared bat maternity-roost networks in burned stands on the FEF would be robust against disruption as more potential day-roosts in the years following burning would accrete into the system than would be lost.

METHODS

We examined data for northern long-eared bat day-roosts that were originally collected by Johnson *et al*. (2008, 2011) and Karp (2013) from the FEF in Tucker County, West Virginia, USA. The FEF is a 1900 ha experimental forest managed by the US Forest Service, Northern Research Station, and is located in the unglaciated Allegheny Plateau. Topography is characterized by steep slopes and plateau-like ridgetops. Elevations range from 530 m to 1100 m (Ford *et al*. 2005). Approximately 8 km of dendritic intermittent and permanent streams are present on the FEF. Mean annual precipitation at FEF is 145.8 cm and mean annual temperature is 9.2 °C, ranging from a mean of –18.0 °C in January to 20.6 °C in July (Madarish *et al*. 2002). Vegetation at FEF is a mosaic of second- and third-growth, mixed mesophytic and Northern hardwood forest stands that have been managed by various even- and uneven-aged harvesting practices or has been left undisturbed following initial harvesting in the early twentieth century (Schuler 2004, Ford *et al*. 2005). Although American chestnut (*Castanea dentata* [Marshall] Borkh.) and oak species such as northern red oak historically dominated the forest overstory, chestnut blight, caused by *Cryphonectria parasitica* (Murr.) Barr, and subsequent lack of intense disturbance (including fire and harvesting) since the mid-twentieth century has allowed forest composition in unmanaged stands to shift toward shade-tolerant tree species, such as maples (*Acer* spp.) and American beech (*Fagus grandifolia* Ehrh.)

(Schuler 2004). Prescribed fire recently has been used to promote oak regeneration in FEF forests that are currently dominated by sugar maple (*Acer saccharum* Marshall), red maple , yellow poplar (*Liriodendron tulipifera* L.), black cherry (*Prunus serotina* Ehrh.), American beech, sweet birch (*Betula lenta* L.), and basswood (*Tilia americana* L.) (Ford *et al*. 2006*b*, Johnson *et al*. 2009). In April to May 2007 and 2008, consecutive prescribed fires were conducted in a 121 ha compartment on the FEF that had been relatively free of management for the past two decades except for a small strip-clearcut (≤5 ha) and scattered light timber stand improvement entries (T. Schuler, US Forest Service, Northern Research Station, Parsons, West Virginia, USA, personal communication). Treatment stands were burned 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, fire intensity as assessed by *post hoc* flame height measurement ranged from a few centimeters to >3.5 m (Johnson *et al.* 2009).

To capture bats, we erected mist nets (Avinet, Inc., Dryden, New York, USA[1]) over stream corridors, small pools, skidder trails, and service roads from May to August 2008 and 2009. We located mist netting sites within both the fire compartment and adjacent unburned stands on the FEF. Mist netting was conducted opportunistically for 3 hr to 5 hr following sunset, unless prevented by periods of rain, wind >20 km hr^{-1}, or temperatures <10 °C as these conditions can influence bat activity levels. We used Skin Bond® (Smith and Nephew, Largo, Florida, USA) 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 long-eared bats. Bat capture and handling protocols were approved by the Animal Care and Use Committee of West Virginia University (Protocol Number 08-0504). We used a radio receiver and 3-element Yagi antenna (Wildlife Materials Inc., Murphysboro, Illinois, USA) to locate roost trees. If individual females were successfully tracked to their diurnal roost tree, we then erected triple-high mist nets around the day-roost to catch as many of the females in the maternity colony as possible for subsequent radio tagging and characterization of maternity colony networks (Johnson *et al*. 2012*a*, Silvis *et al*. 2014). Additional bats were then tracked daily to the same or subsequent new day-roosts. We recorded the location of all day-roosts within 10 m of their true geographic location, using a Garmin GPSmap 60CSx global positioning unit (Garmin, Olathe, Kansas, USA). Although numerous metrics were recorded to describe day-roost characteristics between the burned compartment and adjacent unburned stands such as diameter at breast height, crown class, condition class, bark retention, cavity presence, roost type (cavity or bark), and tree height of day-roost as well as surrounding basal area, these data are presented elsewhere by Johnson *et al*. (2009, 2011). The findings of Johnson *et al*. (2009) showed that black locust, maple (primarily red maple), and oak (primarily northern red oak and black oak [*Quercus velutina* Lam.]) in condition classes 2 to 6 (Cline *et al*. 1980, as modified by Johnson *et al.* [2009]: 1 = live, 2 = declining, 3 = recent dead, 4 = loose bark, 5 = no bark, 6 = broken top, 7 = broken bole) composed 48.8 %, 14.0 % and 13.1 % of day-roosts used on the FEF by northern long-eared bats, respectively, and were the only species selected more than availability would suggest. Accordingly, we tallied pre- and post-fire counts every other year from 2006 to 2012 of potential day-roosts (≥10 cm) in suitable condition (classes 2 to 6) and all conditions (classes 1 to 7) for these three tree species from the same twenty 20 m radius plots randomly located in

[1] The use of any trade, product or firm names does not imply endorsement by the US government.

the FEF burned compartment (Karp 2013). To assess final change over time, we performed a one-way ANOVA on ranked counts of trees by target species, performing an orthogonal contrast between pre-fire in 2006 and four years post fire in 2012 in the SAS 9.4 statistical software (SAS Inc., Cary, North Carolina, USA).

To describe characteristics of northern long-eared bat maternity roost networks in the burned compartment and adjacent unburned stands at the FEF, we followed the methods of Silvis *et al*. (2014) in defining a northern long-eared bat maternity colony as all female and juvenile bats connected by coincident roost use. We represented colonies graphically and analytically as two-mode networks that consisted of bats and roosts (hereafter "roost network;" Fortuna *et al*. 2009, Johnson *et al*. 2012*b*). We used these roost network representations to describe patterns of roost use by colonies and to identify roosts for our removal simulations. To reduce bias resulting from uneven tracking periods and observing only a portion of each colony, we considered relationships to be binary (i.e., presence or absence of a connection; Goodreau *et al*. 2009). We assessed roost network structure using mean degree, network degree centralization, network density, and clustering values. Within networks, degree is a count of the number of edges incident with a node (Boccaletti *et al*. 2006); high degree values indicate a higher degree of use by northern long-eared bats at a day-roost. Network degree centralization, density, and clustering all have values between 0 and 1 (0 = low, 1 = high). Network degree centralization describes the extent that a network is structured around individual day-roosts by northern long-eared bats, whereas network density and clustering describe the distribution of connections among nodes (Freeman 1978, Wasserman 1994, Borgatti and Everett 1997, Watts and Strogarz 1998, Dong and Horvarth 2007). We calculated two-mode degree centralization and density using the methods of Borgatti and Everett (1997) and clustering using the method of Opsahl (2009) for our roost network analyses. To determine whether our observed network values differed from those of random networks, we performed 999 Monte Carlo simulations and compared observed network metrics to random network metrics using two-tailed permutation tests (Hope 1969, Davison 1997); random networks (Erdos 1960) were generated with the same number of nodes as our observed networks and with a constant probability of link establishment. We then compared the relative difference from random networks between those in the burned compartment to those in the adjacent unburned stands to assess whether colony social dynamics and patterns of roost use differed. Secondly, we assessed overall changes in patterns of colony roost use by comparing burned compartment and adjacent unburned network degree centralization, density, and clustering for the roost networks. Lastly, to assess the potential effect of day-roost loss or gain on network fragmentation among networks within the burned compartment, we performed a random node (day-roost) removal simulation for our largest roost network therein. For our roost removal simulation, we randomly selected and removed an increasing proportion of day-roost nodes (up to 80%) at proportions consistent with day-roost selection for this species (Johnson *et al.* 2009), with 500 random removal simulations per number of nodes removed, and we calculated the resultant number of network fragments. These analyses were performed in the R statistical program version 3.0.2 (R Development Core Team 2014). We used the igraph (Csardi and Nepusz 2006) and tnet libraries Opsahl (2009) to visualize networks and calculate metrics. Finally, network Monte Carlo simulations were performed using a custom script with dependencies on the igraph and tnet libraries.

RESULTS

Overall, there was no significant difference in the numbers of potential black locust day-roosts across all years (F = 0.76, df = 3, 29, P = 0.53), nor was the decrease in numbers from 2006 to 2012 significant (F =1.74, df = 1, P = 0.1988; Table 1). For maple, the numbers of potential day-roosts across all years differed overall (F = 7.57, df = 3, 45, P = 0. 004) and the increase in numbers from 2006 to 2012 was significant (F = 11.00, df = 1, P = 0.002; Table 1). For oak, the numbers of potential day-roosts from 2006 to 2012 did not differ across years (F = 1.76, df = 3, 45, P = 0.163), however the increase in numbers from 2006 to 2012 approached significance (F = 3.43, df = 1, P = 0.07; Table 1).

Three northern long-eared bat maternity colonies had enough observations to construct two-mode day-roost networks: one network from adjacent unburned stands in 2008 that contained 6 females that used 13 individual day-roosts; and two networks from the burned compartment, one network in 2008 with 15 females that used 19 individual day-roosts and one network in 2009 with 13 females that used 20 day-roosts (Figure 1). Roost degree and network density of maternity colonies were similar for all three observed networks (Table 2). However, both burned networks showed higher network degree centralization and clustering than expected at random, but the unburned network did not deviate from random (Table 2). Simulations of roost-network disruption from 2008 through 2012 using these three observed northern long-eared bat networks showed that up to 40% of used day-roosts could be lost before at least one of networks would each fracture into two networks (Figure 2).

DISCUSSION

Taken in concert with the previous examinations of how northern long-eared bats on the FEF respond to prescribed burning, our study provides additional, albeit limited, data to suggest that two consecutive fires had no negative impact on the day-roost ecology of the species; positive impacts were probable at least in the short term of our limited study but remain inconclusive. Two-mode representations of roost networks from the burned compartment differed from that of the network in the adjacent unburned stand. However, network characteristics of the burned stands were similar in their relative difference from equivalent random networks to those observed by Silvis *et al*. (2014) within an oak-dominated hardwood forest in central Kentucky in that centralization and clustering were high. We believe this pattern suggests that maternity colony social structure and dynamics may have been improved by prescribed fire on the FEF. Similarly, this corresponds with larger colony size, more day-roosts used, and more probable bat-to-bat association than would be predicted by a presumable net loss of roosts in the short term. The lack of obvious negative impact in social structure is in agreement with the experimental results of Silvis *et al*. (2015*a*) that found no apparent changes in social struc-

Table 1. Mean and standard error of potential day-roost trees ha^{-1} of tree or snag condition class 2 to 6 (see text) of highly selected species (Johnson *et al.* 2009) for northern long-eared bat (*Myotis septentrionalis*) maternity colonies on the Fernow Experimental Forest, West Virginia, USA, from 2006 to 2012 in a burned forest. Prescribed fire was applied in 2007 and 2008.

Species	2006 Mean (SE)	2008 Mean (SE)	2010 Mean (SE)	2012 Mean (SE)
Black locust (*Robinia pseudoacacia*)	16.0 (3.0)	16.0 (3.5)	14.0 (2.9)	12.0 (3.0)
Maple (*Acer* spp.)[1]	14.7 (2.5)	12.6 (1.6)	28.9 (5.9)	46.8 (6.1)
Oak (*Quercus* spp.)	15.1 (2.8)	14.0 (2.0)	21.8 (3.4)	40.0 (8.5)

[1] 2006 vs. 2012 contrast significant (P < 0.05).

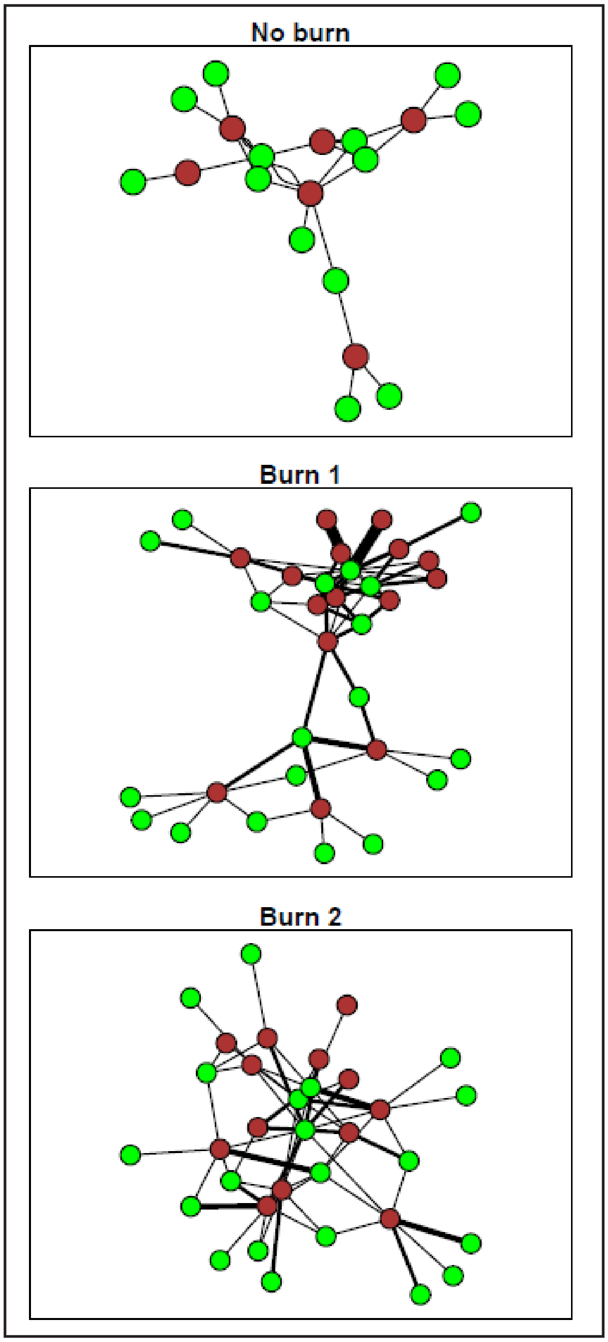

Figure 1. Two-mode graph representations of three northern long-eared bat (*Myotis septentrionalis*) maternity colony roost networks on the Fernow Experimental Forest, West Virginia, USA, from 2008 to 2009, showing the connections between bats and roosts in burned and unburned forest. Bats are shown as reddish brown nodes and roosts are shown as green nodes. Line thickness is correlated with increasing daily use of roost.

ture of northern long-eared bat maternity colonies even after targeted roost removal, lending further support to the hypothesis that northern long-eared bats are robust against the loss of limited numbers of roosts (Johnson *et al*. 2009, Silvis *et al*. 2014, Silvis *et al*. 2015*a*). The lack of difference in some metrics at our site between the unburned network and equivalent random networks likely is the result of the relatively small network sizes on the FEF. Interestingly, roost removal simulations of the unburned network indicated a higher likelihood of colony fragmentation than burned networks, suggesting that post-burn conditions provide a higher degree of day-roost redundancy. Nonetheless, an important caveat is that roost removal simulations do not include information on roost availability, and therefore may still be conservative estimates of disruption considering the increase in suitable day-roosts in the burned area. Relative to why burned networks may be more robust against roost loss, the structured nature of roost networks of this species may be in part a response to the ephemeral nature of the roosts used by this species. Unfortunately, WNS appeared within local northern long-eared bat populations in the winter of 2010 and 2011 and precipitous decreases in bat echolocation activity at the FEF were evident by 2012 (Johnson *et al*. 2013). Additional efforts to radio tag and track extant maternity colonies were unsuccessful (Karp 2013) and only one maternity colony on the FEF was documented in the summer of 2013 (J. Rodrigue, USDA Forest Service, Northern Research Station, Princeton, West Virginia, USA, unpublished data).

Johnson *et al* (2009) surmised that suitable day-roosts were not a limiting factor for northern long-eared bats in mature forests regardless of burn status, even with the strong selection for black locust that composes a relatively small amount of the overall stocking on the FEF—a hypothesis also supported by Silvis *et al*. (2012). With WNS impacts, day-roosts as a possible limiting factor are lessened even

Table 2. Roost network metrics of three northern long-eared bat (*Myotis septentrionalis*) maternity colonies on the Fernow Experimental Forest, West Virginia, USA, from 2008 to 2009 in burned and unburned forest. Network metrics were calculated directly from the two-mode network consisting of bats and day-roosts. The direction of difference between observed and equivalent random networks are given in parentheses where applicable.

Colony	Density	Degree of centralization	Network clustering	Mean bat degree	Mean roost degree
Unburned	0.28	0.50	0.57	3.67	1.69
Burn 1	0.20	0.68 (>)	0.95 (>)	3.80	3.00
Burn 2	0.23	0.70 (>)	0.95 (>)	4.61	3.00

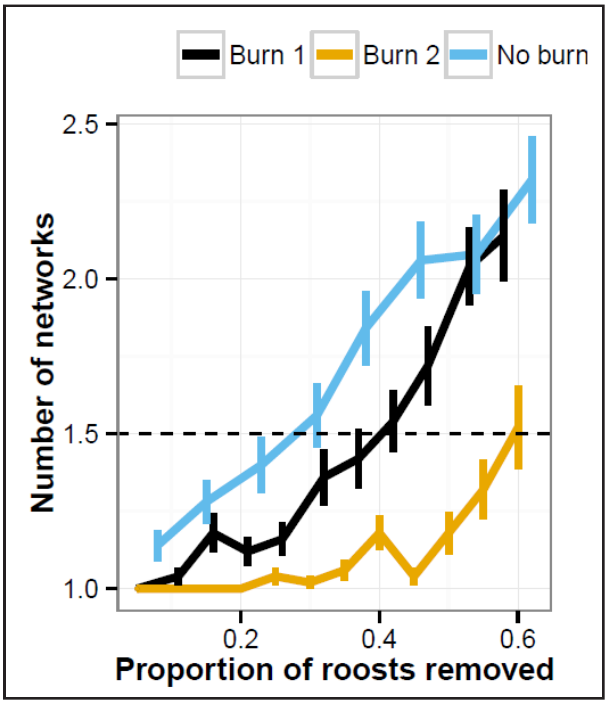

Figure 2. Simulated effect of node (day-roost) removal on the fragmentation of three northern long-eared bat (*Myotis septentrionalis*) maternity colony roost networks on the Fernow Experimental Forest, West Virginia, USA, from 2008 to 2009 in burned and unburned forest. Random node removal was performed 500 times per proportion of nodes removed; mean and standard error of the number of resultant networks per proportion of nodes removed are presented. Dashed horizontal line shows threshold for probability of number of roost networks to go from 1 to 2.

more. Our plot data suggests that, within four years following the second burn, the abundance of potential day-roosts had increased overall, although the primary roost species, black locust, showed a small non-significant decrease in availability. Because no similar tree condition and snag data exist for unburned stands, it is impossible to know if the small decrease in usable black locust was attributable to the burning or simply approximated background loss that might have occurred in similarly aged and stocked unburned stands on the FEF. Maples and oaks, on the other hand, did show increases in the number of potential day-roosts in the FEF burned stands. Long-term monitoring will be necessary to determine the fate of existing black locust potential roosts as well as the pulse of maple and oak potential roosts, particularly relative to background rates of day-roost accession of these species on unburned and unharvested FEF stands. On the FEF, northern long-eared bats primarily are a cavity-roosting species. However, Johnson *et al*. (2009) reported maternity colony use of fire-killed red maple with exfoliating bark, and northern long-eared bats readily use exfoliating bark in more southern parts of their distribution (Perry and Thill 2009). Because red maple is highly fire sensitive (Silvis 2011, Schuler 2013), many of these potential day-roosts were snags in the early stages of decay and were still retaining bark. Transition of red maple snags into late condition class 6 or 7 with a clean bole happens rapidly (Johnson *et al*. 2010), and in the absence of an accessible cavity, the stem is not a usable day-roost once remaining bark is gone unless a cavity is present. Live red maple that is fire weakened should be more susceptible to cavity formation from fungal pathogens, insect infestation, and the actions of excavators (Silvis *et al*. 2015*b*).

Some aspects of day-roost ecology did differ between the burned compartment and unburned stands. Northern long-eared bats in the burned compartment selected roosts that often were smaller and located in larger canopy gaps, conditions that were created by the two fires (Johnson *et al*. 2009). Roost area overlap among defined maternity colonies also was less in the burned compartment than in unburned stands, suggesting that day-roost resources may have been greater in the recently burned forest than in the unburned area (Johnson *et al*. 2012). Moreover, exclusivity of roost area among colonies may have an added benefit of minimizing disease and parasite transmission within the local northern long-eared bat population (Johnson *et al*. 2012). Burning also reduced intra-stand clutter, which has been attributed to increased foraging activity for other species of bats in other regions (Boyles and Aubrey 2006, Ford *et al*. 2006*a,* Loeb and Waldrop 2008). In the Appalachians, insect prey abundance in the first few years following burning has been shown to increase (Lacki *et al.* 2009). Whether or not foraging activity by northern long-eared bats in the burned compartment was greater than in unburned stands on the FEF is unknown. Still, Johnson *et al*. (2012) noted that echolocation activity patterns around day-roosts was slightly greater in unburned rather than burned stands despite similar maternity colony sizes, as ascertained by physical exit counts. Northern long-eared bats at the FEF in burned stands may have simply dispersed more quickly to take advantage of the surrounding reduced clutter and increased number of small canopy gaps that presumably would offer more optimal foraging conditions. Conversely, higher levels of solar radiation in the burn stands may have increased bats' metabolic condition during the day, increasing the need to quickly exit day-roosts for available water (Johnson *et al*. 2012) that was present only in a small first-order stream bisecting the burned compartment and one small (0.001 ha) vernal pool in the southeast portion of the compartment.

With the knowledge that day-roosts are not limiting factors for northern long-eared bats on the FEF or throughout much of the central Appalachians, and with the reality that white-nose syndrome has decreased extant populations of the bat by 90% or more (Frick *et al*. 2015, Powers *et al*. 2015), we suggest that managers seeking reasons to justify the reintroduction of fire on central Appalachian landscapes choose stewardship goals other than bats. In the near-term, resumption of burning in stands that have been fire suppressed for decades appears to have no readily discernible negative impacts to northern long-eared bat habitat and may improve forest stand structure and tree condition for day-roosting. Long-term impacts will need to be assessed by tracking the fate of currently available potential roosts and by monitoring the suitability of regeneration of fire-tolerant, shade-intolerant species such as oaks, hickories (*Carya* spp. Nutt.), and black locust, and the reduction of fire-intolerant, shade-tolerant species such as red maple or American beech in the future. Shorter fire-return intervals or successive fires used as a "reset" in oak-dominated stands in the central Appalachians where fire suppression has occurred over several previous decades could conceivably reduce stem densities and snag availability, whereby day-roost habitat for northern long-eared bats would be reduced. However, with extant bat populations so reduced, and with little prospect of near-term recovery (Frick *et al*. 2015), and with burn-windows so temporally narrow in the late-dormant season on the FEF and the surrounding Allegheny landscape, we think the prospect of this occurrence is low.

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LITERATURE CITED

Bender, M.J., S.B. Castleberry, D.A. Miller, and T.B. Wigley. 2015. Site occupancy of foraging bats on landscapes of managed pine forest. Forest Ecology and Management 336: 1–10. doi: 10.1016/j.foreco.2014.10.004

Boccaletti, S., V. Latora, Y. Moreno, M. Chavez, and D-U Hwang. 2006. Complex networks: structure and dynamics. Physiological Response 424: 175–308. doi: 10.1016/j.physrep.2005.10.009

Borgatti, S.P., and M.G. Everett. 1997. Network analysis of 2-mode data. Social Networks 19: 243–269. doi: 10.1016/S0378-8733(96)00301-2

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. doi: 10.1016/j.foreco.2005.09.024

Brack, V., C.W. Stihler, R.J. Reynolds, C. Butchkoski, and C.S. Hobson. 2002. Effect of climate and elevation on distribution and abundance in the mideastern United States. Pages 21–28 in: A. Kurta and J. Kennedy, editors. The Indiana bat: biology and management of an endangered species. Bat Conservation International, Austin, Texas, USA.

Brooks, R.T., and W.M. Ford. 2006. Bat activity in a working forest landscape of central Massachusetts. Northeastern Naturalist 12: 447–462 doi: 10.1656/1092-6194(2005)012[0447:BAIAFL]2.0.CO;2

Carter, T.C. 2006. Indiana bats in the Midwest: the importance of hydric habitats. Journal of Wildlife Management 70: 1185–1190. doi: 10.2193/0022-541X(2006)70[1185:IBITMT]2.0.CO;2

Carter, T.C., W.M. Ford, and M.A. Menzel. 2002. Fire and bats in the southeast and mid-Atlantic: more questions than answers? Pages 139–143 in: W.M. Ford, K.R. Russell, and C.E. Moorman, editors. The role of fire in nongame wildlife: traditional uses and new directions. USDA Forest Service General Technical Report NE-288, Northern Research Station, Newtown Square, Pennsylvania, USA.

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. doi: 10.2307/3808305

Csardi, G., and T. Nepusz. 2006. The igraph software package for complex network research. International Journal of Complex Systems: 1695.

Davison, A.C. 1997. Bootstrap methods and their application. Cambridge University Press, Cambridge, New York, USA. doi: 10.1017/CBO9780511802843

Dickenson, M.B., J.C. Norris, A.S. Bova, R.L. Kremens, V. Young, and M.J. Lacki. 2010. Effects of wildland fire smoke on a tree-roosting bat: integrating a plume model, field measurements, and mammalian dose-response relationships. Canadian Journal of Forest Research 40: 2187–2203. doi: 10.1139/X10-148

Dong J., and S. Horvath. 2007. Understanding network concepts in modules. BMC Systems Biology 1: 24. doi: 10.1186/1752-0509-1-24

Erdős P., and A. Rényi. 1960. On the evolution of random graphs. Mathematical Institute of the Hungarian Academy of Science 5: 17–61.

Ford, W.M., J.M. Menzel, M.A. Menzel, J.W. Edwards, and J.C. Kilgo. 2006*a*. Presence and absence of bats across habitat scales in the upper Coastal Plain of South Carolina. Journal of Wildlife Management 70: 1174–1184. doi: 10.2193/0022-541X(2006)70[1200:PAAOBA]2.0.CO;2

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. doi: 10.1016/j.biocon.2005.07.003

Ford, W.M., S.F. Owen, J.W. Edwards, and J.L. Rodrigue. 2006*b*. Black locust (*Robinia pseudoacacia*) as day-roosts of male Northern bats (*Myotis septenetrionalis*) on the Fernow Experimental Forest, West Virginia. Northeastern Naturalist 13: 15–24. doi: 10.1656/1092-6194(2006)13[15:RPBLAD]2.0.CO;2

Fortuna, M.A., A.G. Popa-Lisseanu, C. Ibáñez, and J. Bascompte. 2009. The roosting spatial network of a bird-predator bat. Ecology 90: 934–944. doi: 10.1890/08-0174.1

Francl, K.E., W.M. Ford, D.W. Sparks, and V. Brack. 2012. Capture and reproductive trends of summer bat communities in West Virginia: assessing the impacts of white-nose syndrome. Journal of Fish and Wildlife Management 3: 33–42.

Freeman, L.C. 1978. Centrality in social networks conceptual clarification. Social Networks 1: 215–239. doi: 10.1016/0378-8733(78)90021-7

Frick, W.F., S.J. Puechmaille, J.R. Hoyt, B.A. Nickel, K.E. Langwig, J.T. Foster, K.E. Barlow, T. Bartonicak, D. Feller, A-J Haarsma, C. Herzog, I. Horacek, J. van der Kooij, B. Mulkens, B. Petrov, R. Reynolds, L. Rodrigues, C.W. Stihler, G.G. Turner, and A.M. Kilpatrick. 2015. Disease alters macroecological patterns of North American bats. Global Ecology and Biogeography 24(7): 741–749. doi: 10.1111/geb.12290

Goodreau, S.M., J.A. Kitts, and M. Morris. 2009. Birds of a feather, or friend of a friend? Using exponential random graph models to investigate adolescent social networks. Demography 46: 103–125. doi: 10.1353/dem.0.0045

Hope, A.C.A. 1968. A simplified Monte Carlo significance test procedure. Journal of Research Statistics Methodology 30: 582–598.

Johnson, J.B., J.W. Edwards, W.M. Ford, and J.E. Gates. 2009. Roost tree selection by Northern *Myotis* (*Myotis septentrionalis*) in a central Appalachian Mountains hardwood forest subjected to prescribed fire. Forest Ecology and Management 258: 233–242. doi: 10.1016/j.foreco.2009.04.008

Johnson, J.B., J.W. Edwards, and W.M. Ford. 2012*a*. Nocturnal activity patterns of Northern *Myotis* (*Myotis septentrionalis*) during the maternity season in West Virginia (USA). Acta Chiropterologica 13: 391–397. doi: 10.3161/150811011X624866

Johnson, J.B., W.M. Ford, and J.W. Edwards. 2012*b*. Roost networks of Northern *Myotis* (*Myotis septentrionalis*) in a managed landscape. Forest Ecology and Management 266: 223–231. doi: 10.1016/j.foreco.2011.11.032

Johnson, J.B., W.M. Ford, J.W. Edwards, J.L. Rodrigue, and C.L. Johnson. 2010. Roost selection by male Indiana *Myotis* following forest fires in central Appalachian hardwoods forests. Journal of Fish and Wildlife Management 1: 111–121. doi: 10.3996/042010-JFWM-007

Johnson, J.B., J.L. Rodrigue, and W.M. Ford. 2013. Nightly and yearly bat activity before and after white-nose syndrome on the Fernow Experimental Forest in West Virginia, Tucker County, USA. USDA Forest Service Research Paper NRS-Research Paper 24, Northern Research Station, Newtown Square, Pennsylvania, USA.

Johnson J.S., J.N. Kropczynski, M.J. Lacki, and G.D. Langlois. 2012*b*. Social networks of Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) in bottomland hardwood forests. Journal of Mammalogy 93: 1545–1558. doi: 10.1644/12-MAMM-A-097.1

Karp, M. 2013. Northern *Myotis* roosting ecology and use of prescribed fire and herbicide treatment to enhance roost availability in hardwood forests. Thesis, West Virginia University, Morgantown, USA.

Keyser, P.D., and W.M. Ford. 2006. Influence of fire on mammals in Eastern oak forests. Pages 180–190 in: M.B. Dickinson, editor. Proceedings of a conference—fire in Eastern oak forests: delivering science to land managers. USDA Forest Service General Technical Report NRS-P-1, Northern Research Station, Newtown Square, Pennsylvania, USA.

Lacki, M.J., D.R. Cox, L.E. Dodd, and M.B. Dickenson. 2009. Response of Northern bats (*Myotis septentrionalis*) to prescribed fires in eastern Kentucky. Journal of Mammalogy 90: 1165–1175. doi: 10.1644/08-MAMM-A-349.1

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. doi: 10.1016/j.foreco.2007.10.060

Menzel, M.A., S.F. Owen, W.M. Ford, B.R. Chapman, K.V. Miller, J.E. Edwards, and P.B. Wood. 2002. Roost tree selection by maternity colonies of northern long-eared bats (*Myotis septentrionalis*) in an industrial forest of the central Appalachian Mountains. Forest Ecology and Management 155: 107–114. doi: 10.1016/S0378-1127(01)00551-5

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 NE-291, Northern Research Station, Newtown Square, Pennsylvania, USA.

Nowacki, G.J., and M.D. Abrams. 2008. The demise of fire and the "mesophication" of forest in the eastern United States. BioScience 58: 123–138. doi: 10.1641/B580207

Nyland, R.D. 1996. Silviculture: concepts and applications. McGraw-Hill, New York, New York, USA.

Opsahl, T. 2009. Structure and evolution of weighted networks. Dissertation, Queen Mary University of London, England, United Kingdom. <http://ethos.bl.uk/OrderDetails.do?uin=uk.bl.ethos.507253>. Accessed 1 April 2013.

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. USDA Forest Service General Technical Report NE-292, Northern Research Station, Newtown Square, Pennsylvania, USA.

Owen, S.F., M.A. Menzel, W.M. Ford, B.R. Chapman, K.V. Miller, J.W. Edwards, and P.B. Wood. 2003. Home-range size and habitat used by the Northern *Myotis* (*Myotis septentrionalis*). American Midland Naturalist. 150: 352–359. doi: 10.1674/0003-0031(2003)150[0352:HSAHUB]2.0.CO;2

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. 2012. A review of fire effects on bats and bat habitat in the Eastern oak region. Pages 170–191 in: D.C. Day, M.C. Stambaugh, S. Clark, and L. Schweitzer, editors. Proceedings of the 4th fire in Eastern oak forests conference. USDA Forest Service General Technical Report NRS-P-102, Northern Research Station, Newtown Square, Pennsylvania, USA.

Perry, R.W., and R.E. Thill. 2009. Roost selection by male and female northern long-eared bats in a pine-dominated landscape. Forest Ecology and Management 247: 220–226. doi: 10.1016/j.foreco.2007.04.041

Powers, K.E., R.J. Reynolds, W. Orndorff, W.M. Ford, and C.S. Hobson. 2015. Post-white-nose syndrome trends in Virginia's cave bats, 2008–2013. Journal of Ecology and the Natural Environment 6: 56–64.

R Development Core Team. 2014. R: a language and environment for statistical computing. <http://www.R-project.org/>. Accessed 13 May 2014.

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

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. doi: 10.1139/x03-262

Schuler, T.M., M. Thomas-Van Gundy, M.B. Adams, and W.M. Ford. 2013. Analysis of two pre-shelterwood prescribed fires in a mesic mixed oak forest in West Virginia. Pages 430–446 in: G.W. Miller, T.M. Schuler, K.W. Gottschalk, J.R. Brooks, S.T. Grushecky, B.D. Spong, and J.S. Rentch, editors. Proceedings of the 18th central hardwood conference. USDA Forest Service General Technical Report NRS-P-117, Northern Research Station, Newtown Square, Pennsylvania, USA.

Silvis, A. 2011. The response of bats to shelterwood harvest and prescribed fire. Thesis, Ohio State University, Columbus, USA.

Silvis, A., W.M. Ford, and E.R. Britzke. 2015*a*. Effects of hierarchical roost removal on northern long-eared bat (*Myotis septentrionalis*) maternity colonies. PLoS ONE 10(1): e0116356. doi: 10.1371/journal.pone.0116356

Silvis, A., W.M. Ford, E.R. Britzke, N.R. Beane, and J.B. Johnson. 2012. Forest succession and maternity roost selection by *Myotis septentrionalis* in a mesophytic hardwood forest. International Journal of Forestry 2012(2012): Article ID 148106. doi: 10.1155/2012/148106

Silvis, A., W.M. Ford, E.R. Britzke, and J.B. Johnson. 2014. Association, roost and social networks of *Myotis septentrionalis* maternity colonies. Behavioral Processes 103: 283–290. doi: 10.1016/j.beproc.2014.01.016

Silvis, A., E.R. Thomas, W.M. Ford, E.R. Britzke, and M.J. Friedrich. 2015*b*. Cavity characteristics of northern long-eared bat (*Myotis septentrionalis*) maternity day-roosts. USDA Forest Service Research Paper NRS-27, Northern Research Station, Newtown Square, Pennsylvania, USA.

Swengel, A.B. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. Biodiversity and Conservation 10: 1141–1169. doi: 10.1023/A:1016683807033

Wasserman, S., and K. Faust. 1994. Social network analysis: methods and applications. Cambridge University Press, New York, New York, USA. doi: 10.1017/CBO9780511815478

Watts, D.J., and S.H. Strogatz. 1998. Collective dynamics of "small-world" networks. Nature 393: 440–442. doi: 10.1038/30918