



## Roost networks of northern myotis (*Myotis septentrionalis*) in a managed landscape

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### ABSTRACT

Maternity groups of many bat species conform to fission–fusion models and movements among diurnal roost trees and individual bats belonging to these groups use networks of roost trees. Forest disturbances may alter roost networks and characteristics of roost trees. Therefore, at the Fernow Experimental Forest in West Virginia, we examined roost tree networks of northern myotis (*Myotis septentrionalis*) in forest stands subjected to prescribed fire and in unmanipulated control treatments in 2008 and 2009. Northern myotis formed social groups whose roost areas and roost tree networks overlapped to some extent. Roost tree networks largely resembled scale-free network models, as 61% had a single central node roost tree. In control treatments, central node roost trees were in early stages of decay and surrounded by greater basal area than other trees within the networks. In prescribed fire treatments, central node roost trees were small in diameter, low in the forest canopy, and surrounded by low basal area compared to other trees in networks. Our results indicate that forest disturbances, including prescribed fire, can affect availability and distribution of roosts within roost tree networks.

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### 1. Introduction

Nonrandom intraspecific associations among individuals have been documented in a variety of mammals, including bats (Alexander, 1974; Kerth, 2008). From an evolutionary perspective, advantages of forming nonrandom associations mostly exceed disadvantages, and several specific mechanisms underlying advantages have been posited (Alexander, 1974). Groups may form (fusion) as a defensive mechanism, for efficient information transfer, to facilitate food sharing, and for cooperative rearing of offspring (Alexander, 1974; Kerth, 2008). Disadvantages of group formation and causes for group separation (fission) include intra-group competition for resources, increased parasite loads, and disease transmission (Kerth, 2008). Therefore, group size may be in constant flux, i.e., fission–fusion, achieving optimal size to maximize fitness of its constituents in response to varying conditions (e.g., habitat dynamics, reproductive cycle; Kummer, 1971).

Fission–fusion dynamics have been documented in a number of bat species (Barclay and Kurta, 2007), yet few studies have investigated causal mechanisms or effects of changing habitat conditions on these dynamics (O'Donnell and Sedgely, 1999). Indeed, effects of forest structure and degree and type of disturbance on fission–fusion dynamics have rarely been studied, yet the accepted para-

digm is that defined social groups of animals should be one of the focal units of conservation (Willis and Brigham, 2004; Rhodes, 2007). Bat social groups may be regarded as a management unit because females of some bat species exhibit strong natal philopatry, returning to the same areas, and even to specific roost trees, in consecutive years (Crampton and Barclay, 1998; Sedgely 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; Sedgely and O'Donnell, 1999; Kurta et al., 2002).

Roost switching patterns can be viewed as networks among trees; a 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 much more connected than other roost trees in the network (Barbási, 2002). In a scale-free network, there is an apparent “hub” or central node roost tree within the roost tree network that is more connected to other roost trees (Rhodes et al., 2006). If roost networks exist as scale-free networks, this suggests a relative importance among roost trees to bat maternity colonies. Conceptually, roost tree networks may be similar to primary (hub) and secondary roost trees as documented in Indiana myotis (*Myotis sodalis*; Barclay and Kurta, 2007). Roost networks may be specific to social groups of bats and could have implications for roost selection studies and habitat management. Although northern myotis

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(*Myotis septentrionalis*) have been shown to select for certain tree characteristics when roosting (Sasse and Pekins, 1996; Owen et al., 2002; Carter and Feldhamer, 2005), relative importance (e.g., used by more bats for more days) among trees used by social groups, primarily maternity colonies, has not been examined. Roost tree selection studies commonly give equal importance among all roost trees, comparing them to randomly located potential roost trees (Menzel et al., 2002; Miller et al., 2003). Central node roost trees may have unique characteristics that may be important in maintaining social organization.

Forest disturbances, including timber harvesting, fires, wind, and other causes, can affect availability and distribution of roost trees within roost tree networks (Chaverri et al., 2007; Perry et al., 2007). During maternity seasons, female northern myotis roost colonially in trees or snags with cavities or exfoliating bark, and roost selection may be affected by forest disturbances (Carter and Feldhamer, 2005; Garroway and Broders, 2007). Though northern myotis may use primary and secondary roost trees (Barclay and Kurta, 2007), this concept has not been well developed for northern myotis in Central Appalachian Mountains, nor in light of forest management practices.

Northern myotis switch roost trees frequently (every 1–5 days), and in the Central Appalachian Mountains, exhibit selection for certain roost tree characteristics, including distinct preferences for species (Owen et al., 2002; Menzel et al., 2002). In Canada, Garroway 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. Considering forest disturbances and its potential impacts on roost selection and networks of northern myotis (Barclay and Kurta, 2007), we conducted research focusing on these aspects of the species roosting ecology and formed several predictions. Because northern myotis have been documented exhibiting nonrandom association patterns in other parts of their range (Garroway and Broders, 2007), we predicted that (1) they would exhibit these same patterns in the Central Appalachian Mountains, forming delineable social groups. Further, we predicted that (2) the roost tree topology of northern myotis social groups would exist as scale-free networks rather than random networks, with definable central node roost trees. We posited that (3) physical characteristics of central node roost trees would be similar to other roost trees in networks. Lastly, (4) central node roost trees would be physically similar between stands that were and were not subjected to prescribed fire.

## 2. Methods

### 2.1. Study area

We conducted research at the Fernow Experimental Forest (FEF) in Tucker County, West Virginia. The FEF is a 1900-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 1100 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 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 (Kochenderfer, 2006). Mean annual temperature is 9.2 °C, ranging from a mean of –18.0 °C in January to 20.6 °C in July (Kochenderfer, 2006). Vegetation at 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 undisturbed following initial harvesting in Elklick Run watershed from 1903 to 1911 (Schuler and Fajvan, 1999). Although American chestnut (*Castanea dentata*) and oak species, such as northern red oak (*Quercus rubra*), historically dominated the forest overstory, 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 (*Acer* spp.) and American beech (*Fagus grandifolia*) (Schuler and Fajvan, 1999; Schuler, 2004). Prescribed fire recently has been used to promote oak regeneration in FEF forests that are currently dominated by sugar maple (*Acer saccharum*), red maple (*Acer 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 three management compartments totaling 146 ha at FEF (121, 13, and 12 ha). Additionally, 48, 20-m radius plots were randomly located in each of the three management compartments, where all overstory or midstory trees, other than oak or hickory, were herbicided or girdled (Schuler, USDA Forest Service, personal communication).

### 2.2. Radiotelemetry

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 2008–2009. We located mist netting sites within both fire and control treatments. We considered control treatments to be any area outside fire treatments. Mist netting was conducted for 5 h following sunset, unless prevented by periods of rain, wind  $\geq 20$  kph, or temperatures  $< 10$  °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 radio-transmitted bat on a daily basis until the radio-transmitter battery completely discharged or the radio-transmitter became detached. Bat capture and handling protocols were approved by the Animal Care and Use Committee of West Virginia University (Protocol Number No. 08-0504) and followed guidelines of the American Society of Mammalogists (ACUC, 2011). 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 (Olathe, Kansas). We conducted exit counts at a random set of roost trees throughout the pregnancy and lactation periods. We commenced exit counts approximately 1 h before sunset and continued until darkness prevented us from observing emerging bats.

### 2.3. Nonrandom association patterns

To determine if northern myotis roosted nonrandomly with conspecifics, we used daily roosting location data for each radio-transmitted bat. Similar to previous research examining nonrandom association patterns of bats, we calculated a half-weight association index for each pair (dyad) of radio-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

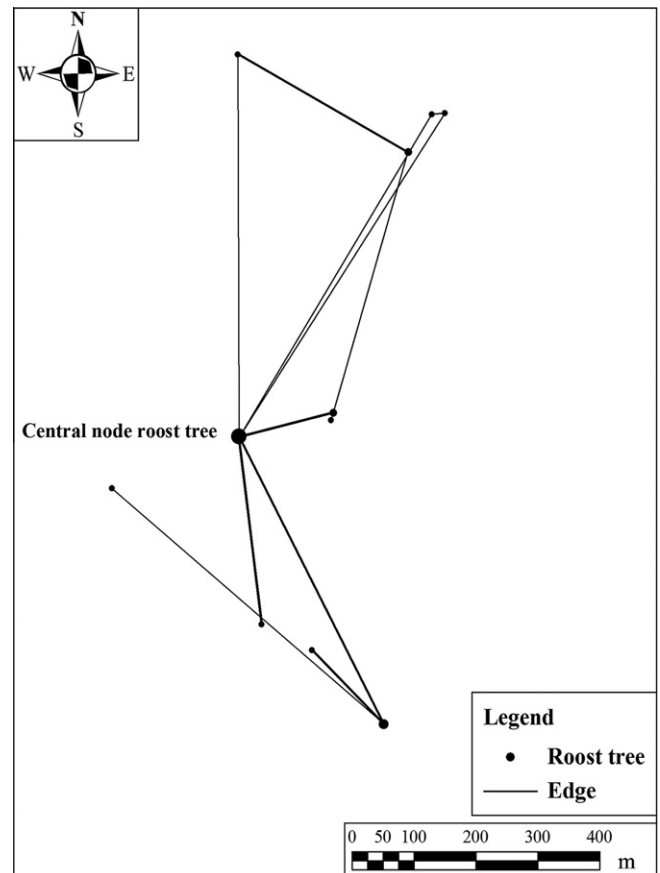
located, respectively (Bejder et al., 1998). For each year of data, we used SOCPROG 2.4 to compute HWI values for each dyad, resulting in an association matrix (Whitehead, 2009). To determine if each dyad was observed roosting together more than expected as determined by a significantly high HWI value, 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  $\geq 4$  roost trees were located (Vanhof et al., 2004). Because radio-transmitter retention time was low (mean  $\pm 1$  SE;  $5.5 \pm 0.3$  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 (Garraway and Broders, 2007).

#### 2.4. Roost network analysis

We used a graph theoretic approach to determine the relative importance of roost trees used by northern myotis social groups (Rhodes et al., 2006). 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 which it was linked (LINKS). For each social group or roost network with  $\geq 3$  roost trees, we determined which roost tree had the highest value for LINKS and denoted that tree the central node roost tree. A minimum of 3 trees was necessary to constitute a network, i.e., 1 tree in a network potentially could have more LINKS than the other 2 trees in the same network. If  $\geq 2$  roost trees had identical values, those trees were considered central node roost trees. 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). 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, degree distribution follows a Poisson distribution (Barbási, 2002; Rhodes et al., 2006). We fit power and Poisson trend lines through the degree distribution data and examined Akaike Information Criteria values adjusted for small sample sizes (AICc) and Akaike weights ( $w_i$ ) for each.

#### 2.5. 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 basal area adjacent to the roost tree 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.



**Fig. 1.** Example of roost network of a northern myotis (*Myotis septentrionalis*) social group (group T) at the Fernow Experimental Forest; West Virginia; 2009. Larger dots (roost trees or nodes) represent higher number of bat days used. Edges represent minimum bat movements between successively used roost trees.

#### 2.6. Statistical analysis

We used a Mann–Whitney *U*-test to compare exit counts (all tallied bats, including radio-tagged bats) at central node roost trees and non-central node roost trees (Proc Npar1way; SAS Institute, Inc., 2004). 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 variable pairs before subsequent analyses if their Spearman's rank (Proc Corr, SAS Institute, Inc., 2004) correlation coefficient was  $\geq 0.60$ . 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 a Mann–Whitney *U*-test, comparing central node roost tree characteristics in prescribed fire and control treatments. Due to the exploratory nature of our study, we relaxed threshold significance level for generalized additive models, chi-square tests,

and Mann–Whitney  $U$ -tests to  $P \leq 0.10$  so as not to discard potentially interesting ecological results (Robinson and Wainer, 2002).

### 3. Results

In 2008, we radio-tracked 32 female northern myotis (23 pregnant, 6 lactating, 3 non-reproductive) to 64 roost trees. Mean HWI

( $\pm 1$  SD) amongst all telemetered bats was  $0.024 (\pm 0.070)$ , 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 average linkage clustering method was 0.996, indicating strong representation of the original data. Groups (including those of 1 individual) roosted in 1 to 11 roost trees; roost areas ranged from 0.39 to

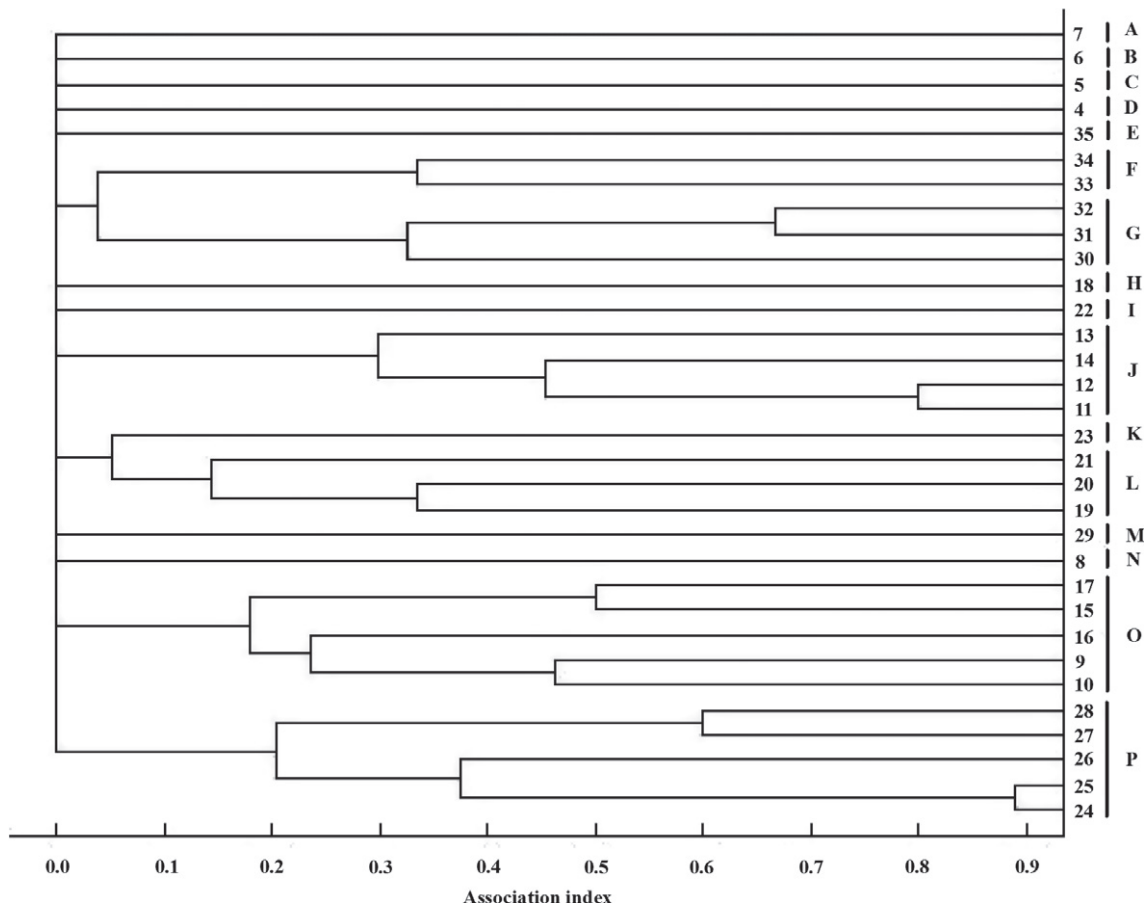
**Table 1**  
Association measures, roost area, and central node roost tree metrics for social groups of northern myotis (*Myotis septentrionalis*) maternity colonies (>1 individual) at the Fernow Experimental Forest, West Virginia, 2008–2009.

Year	Group	Bats	HWI <sup>a</sup>	Roosts	Roost area (ha)	LINKS <sup>b</sup>	CNRT <sup>c</sup>
2008	F	2	$0.28 \pm 0.23$	4	1.86	2	2
	G	3	$0.40 \pm 0.17$	11	5.65	2	7
	J	4	$0.45 \pm 0.21$	6	1.45	3	1
	L	3	$0.30 \pm 0.02$	10	13.42	4	1
	O	5	$0.31 \pm 0.12$	9	10.04	5	1
	P	5	$0.35 \pm 0.23$	7	14.77	5	1
2009		$3.7 \pm 1.2$		$7.8 \pm 2.6$	$7.9 \pm 5.8$	$3.5 \pm 1.4$	$2.2 \pm 2.4$
	Q	9	$0.32 \pm 0.17$	16	23.25	6	1
	R	2	$0.66 \pm 0.18$	5	7.97	2	2
	T	4	$0.31 \pm 0.09$	11	35.33	6	1
	V	5	$0.40 \pm 0.19$	8	8.06	5	1
	AA	12	$0.44 \pm 0.23$	8	16.78	5	1
		$6.4 \pm 4.0$		$9.6 \pm 4.2$	$18.3 \pm 11.5$	$4.8 \pm 1.6$	$1.2 \pm 0.4$

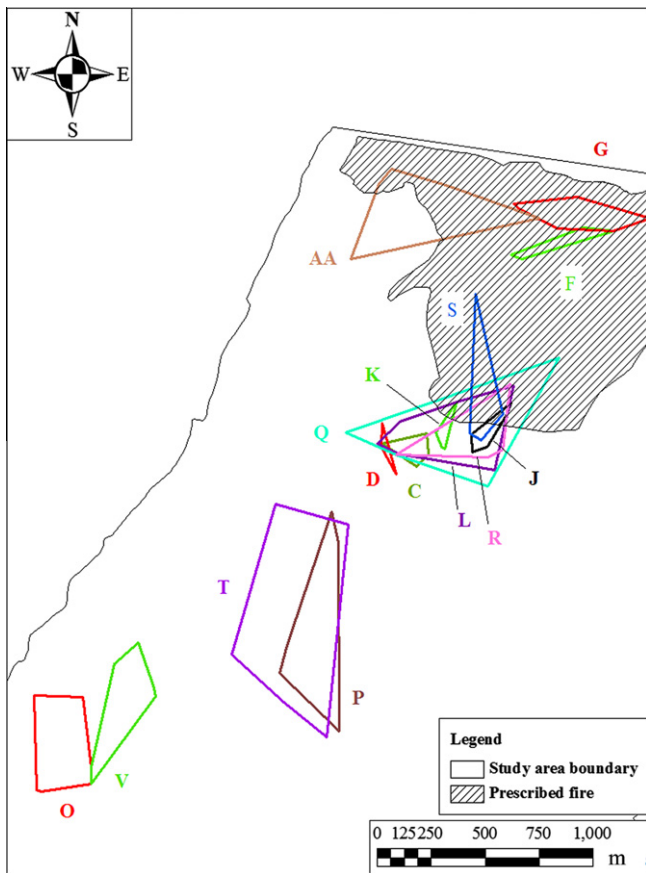
<sup>a</sup> Mean ( $\pm 1$  SD) half weight association index (HWI) of bat dyads within social groups.

<sup>b</sup> Number of roost trees that bats moved to or from the central node roost tree.

<sup>c</sup> Number of central node roost trees identified within each social group according to the maximum number of LINKS.



**Fig. 2.** Average linkage cluster analysis of non-randomly (half-weight association index  $>0.09$ ) associating groups of northern myotis (*Myotis septentrionalis*) at the Fernow Experimental Forest, West Virginia, 2008. Numbers on the y-axis denote individual bats; letters denote social groups. Higher association index numbers indicate bats roosted together more frequently.



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

14.77 ha (Table 1, Fig. 3). In 2009, we radio-tracked 38 female northern myotis (29 lactating; 6 pregnant; 3 non-reproductive) to 51 roost trees. Mean HWI ( $\pm 1$  SD) was 0.084 ( $\pm 0.120$ ), 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, indicating strong representation of the original data. Groups (including those of 1 individual) roosted in 1–16 roost trees; roost areas ranged from 5.24 to 35.33 ha (Table 1, Fig. 3). Exit counts were similar ( $U = 42$ ,  $P = 0.792$ ) between central node roost trees ( $n = 12$ ;  $19.2 \pm 4.5$  bats; range = 1–47) and non-central node roost trees ( $n = 5$ ;  $17.6 \pm 8.0$  bats; range = 4–48).

We were able to determine roost networks for 18 social groups; 11 (61%) had a single central node roost tree according to the LINKS metric. Central node roost trees (including those in networks used by social groups of 1 individual) 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  $P(k) \approx k^{-1.84}$ , ( $AICc = 31.11$ ,  $w_i = 0.748$ , more closely than Poisson ( $AICc = 33.28$ ,  $w_i = 0.252$ )). The number of bat days (number of bats  $\times$  number of days) spent roosting in central node roost 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 ( $\rho = -0.652$ ). We retained CROWN and BARK in the models. Central node roost trees were in early stages of decay (BARK;  $P = 0.011$ ) and were surrounded by more basal area (BASAL;  $P = 0.064$ ; Fig. 5) than other roost trees in

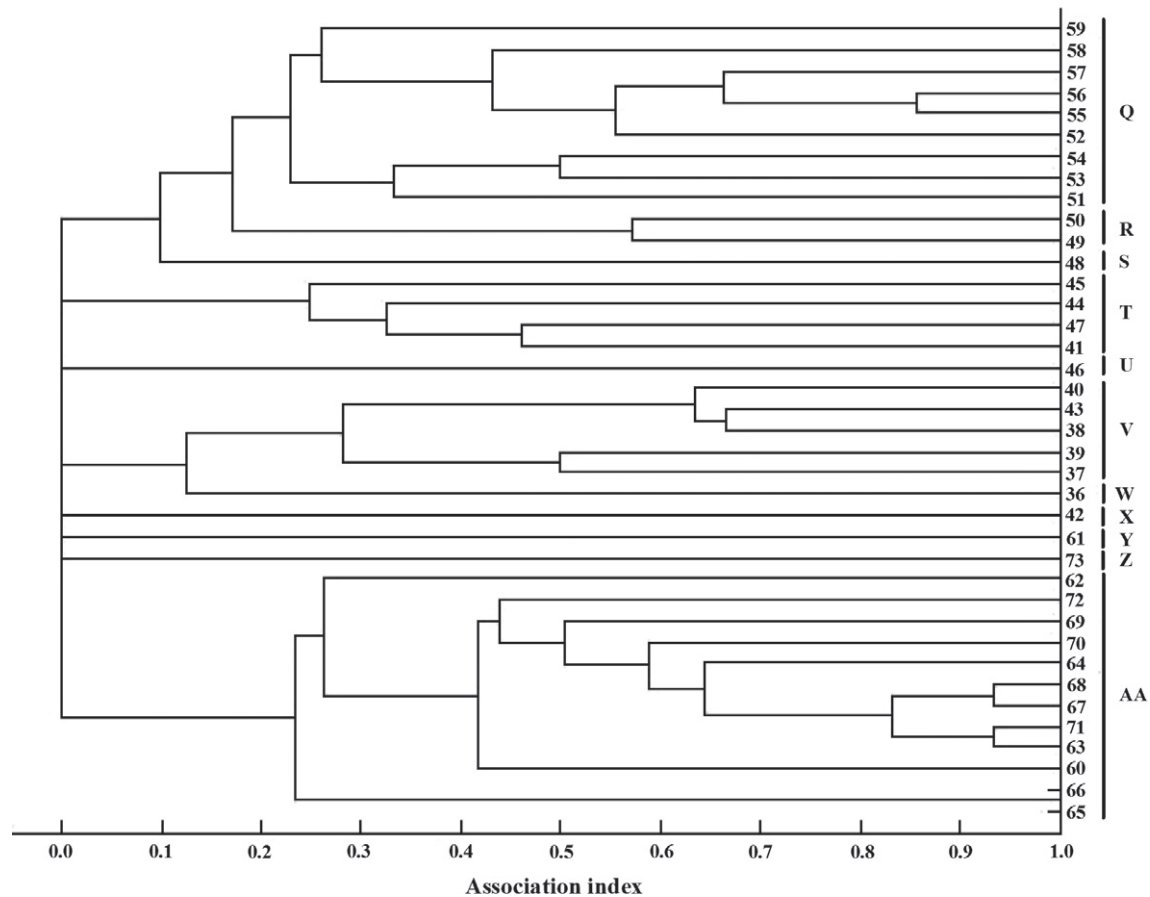
networks. Variables CROWN ( $P = 0.729$ ) and DBH ( $P = 0.875$ ) were not predictive characteristics of central node roost trees. Non-central node roost trees were disproportionately cavity trees ( $\chi^2 = 3.214$ ,  $P = 0.073$ ).

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 (DBH;  $P = 0.021$ ), in lower crown classes (CROWN;  $P = 0.075$ ), and in stands of lower basal area (BASAL;  $P = 0.014$ ; Fig. 5). Variable BARK ( $P = 0.558$ ) was not a predictive characteristic. 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 2).

#### 4. Discussion

Northern myotis exhibited nonrandom association patterns, forming social groups nested within networks of roost trees across the landscape. Previous studies have shown that northern myotis roost nonrandomly 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. 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 return to the same summer ranges yearly, a phenomenon that may or may not partially drive association patterns (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 affects group size, roosting associations, and roost tree selection (Garroway and Broders, 2007, 2008), but relatively short sampling effort, i.e., radiotransmitter retention time, per bat in our study prevented us from determining trends. Moreover, short radiotransmitter retention time affected our ability to confidently determine network degree distribution, which generally fit a power curve, but undoubtedly was confounded by smaller roost networks consisting of few trees, as opposed to perfect scale-free networks as observed in *Tadarida australis* in Queensland, Australia (Rhodes et al., 2006). Colony sizes of northern myotis typically are larger early in the summer and decline as they form groups of smaller numbers of individuals (Sasse and Pekins, 1996; Foster and Kurta, 1999; Garroway and Broders, 2007). As a consequence, perceived roost selection and roost networks observed in our study may have been influenced by our short sample period that did not track individual bats throughout the summer maternity period. 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.

Likewise, we observed that roosting areas of northern myotis social groups were similar to those found in Nova Scotia, Canada (0.3–31.1 ha; Henderson and Broders, 2008). Largely confined to ridgetops, roosting areas of many northern myotis social groups in our study overlapped, with some being entirely enveloped by others. However, roosting networks of social groups on separate ridges never overlapped. Although there was some overlap among



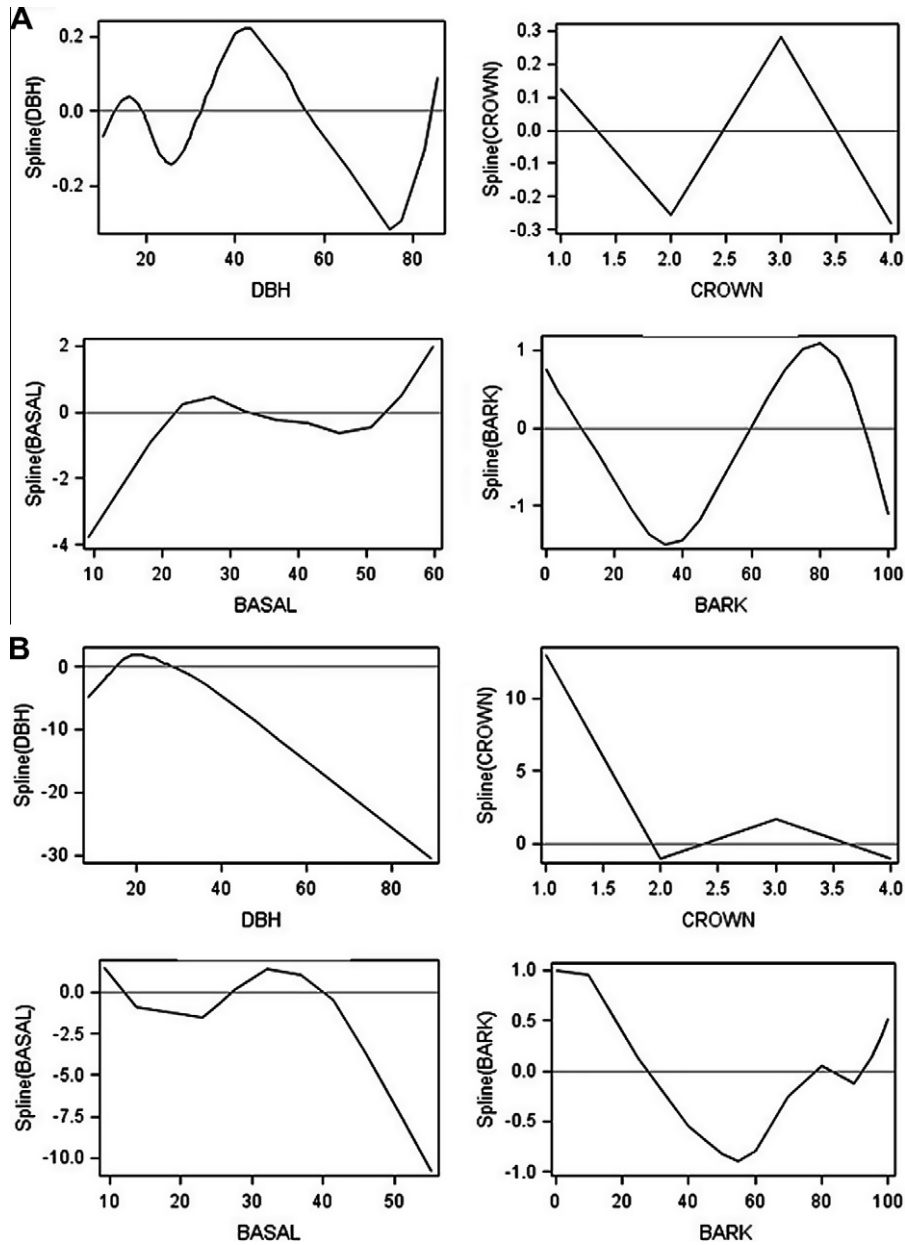
**Fig. 4.** Average linkage cluster analysis of non-randomly (half-weight association index  $>0.20$ ) associating groups of northern myotis (*Myotis septentrionalis*) at the Fernow Experimental Forest, West Virginia, 2009. Numbers on the y-axis denote individual bats; letters denote social groups. Higher association index numbers indicate bats roosted together more frequently.

networks between years, potentially indicating we tracked the same individuals, preliminary genetic analysis show that all individuals we tracked were unique (Johnson, unpublished data). 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. Temporal differences in roost tree use have implications for 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 (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 (WNS; *Geomyces destructans*; Lorch et al., 2011). It may be possible that spores and parasite eggs or pupae may persist in roost trees in the absence of roosting bats (Kerth, 2008). 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.

Central node roost trees may be conceptually and functionally similar to primary roost trees used by Indiana myotis in that they may serve as sites for information exchange and thermal buffering by large numbers of bats (Callahan et al., 1997). Although our sample size for exit counts was small and should be interpreted with caution, our results indicate that central node roost trees are not reliably identified by number of individuals using the trees, but rather by the degree of connectivity with other roost trees used by the colony. Callahan et al. (1997) indicated that primary roost

trees used by Indiana myotis were those used by colonies of  $>30$  individuals on  $>1$  occasion. Similar to findings of Callahan et al. (1997) that Indiana myotis colonies each used 1–3 primary roost trees, we identified 1–2 central node roost trees for all but 1 colony.

Across the FEF landscape, some physical characteristics of central node roost trees and surrounding stands differed from other roost trees within networks. Within control treatments, central node roost trees were in early stages of decay, based on high amounts of bark coverage, and were surrounded by trees of greater basal area. Northern myotis maternity colonies selected large cavity trees in early stages of decay, compared to randomly-located potential roost trees (Johnson et al., 2009). Characteristics of central node roost trees in control treatments were similar to those of primary roost trees observed in New Hampshire, where northern myotis roosted in large-diameter snags with high amounts of remaining bark and were surrounded by high basal area (Sasse and Pekins, 1996). 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, similar to overall roost selection by northern myotis (Foster and Kurta, 1999; Carter and Feldhamer, 2005). 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 roost networks. Trees in later stages of decay were connected to fewer trees in networks, possibly because these trees imminently would either decay to the point of unsuitability or collapse, rendering them less reliable nodes within networks (Callahan et al., 1997). Whereas central



**Fig. 5.** Relations of roost tree characteristics [diameter at breast height (DBH), crown class (Nyland, 1996; CROWN), visual estimate of percent bark remaining on the tree (BARK), and basal area adjacent to the roost tree (BASAL)] and central node roost trees of northern myotis (*Myotis septentrionalis*) maternity colonies in control (A) and prescribed fire (B) treatments at the Fernow Experimental Forest, West Virginia, 2008 and 2009. Splines outside  $\pm 1$  indicate significant relations.

**Table 2**  
Characteristics of central node roost trees used by northern myotis (*Myotis septentrionalis*) maternity colonies in prescribed fire ( $n = 14$ ) and control treatments ( $n = 17$ ) at the Fernow Experimental Forest, West Virginia, 2008–2009.

Variable	Fire treatment		Control treatment		P
	Mean <sup>a</sup>	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 <sup>2</sup> /ha)	29.84	2.66	34.02	2.43	0.546

<sup>a</sup> Actual values presented. Mann–Whitney tests performed on ranked values.

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 trends observed among available and used roost trees across control and fire treatments (Johnson et al., 2009; Lacki et al., 2009).

Within stands that were subjected to prescribed fire, compared to other roost trees in networks, 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 (Johnson et al., 2009; Lacki 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. Persistence of black locust in forest stands likely promotes establishment of roost networks that remain relatively unchanged 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 using 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. Canopy gaps allowed solar exposure to reach central node roost trees that were 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. In Kentucky, Lacki et al. (2009) documented northern myotis roost tree use before and after prescribed fire treatments, but it is unclear if bats roosted in the same trees after treatment.

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., 2009). Disturbances to roost networks resembling random networks should have minimal effects on social organization because trees in the network are more similar in terms of use and connectivity compared to trees in scale-free networks. Social organization may be reordered to adapt to new networks depending on 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 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. Additionally, 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, disease, and parasite exchange. Removal of these trees from networks may cause bats to establish their central node roost trees in other trees within networks. 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 (Fortuna et al., 2009; Lorch et al., 2011).

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