Day-roosting Social Ecology of the Northern Long-eared Bat (*Myotis septentrionalis*)
and the Endangered Indiana Bat (*Myotis sodalis*)

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Dissertation submitted to the faculty of the Virginia Polytechnic Institute and State
University in partial fulfillment of the requirements for the degree of

Doctor of Philosophy
In
Fish and Wildlife

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3 November 2014
Blacksburg, Virginia

Keywords: Northern long-eared bat, *Myotis septentrionalis*, social structure, fission-fusion, maternity colony, roost removal, roost selection, Indiana bat, *Myotis sodalis*

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Abstract

Day-roost use by northern long-eared bat (*Myotis septentrionalis*) maternity colonies on the Fort Knox military reservation, Kentucky, USA, resulted in formation of non-random networks of roosts that exhibited a trend toward centralization. Centralization of day-roost networks was reflected in the social structure of colonies, which were characterized by dense associations among individuals within colonies. Social structure varied among colonies and appeared to be related to reproductive condition; colonies exhibited greater cohesiveness during parturition and lactation. Northern long-eared bat maternity colonies appeared to be exclusive, occupying distinct roosting areas with one or several areas receiving intense use.

Day-roost removal simulations suggested a linear relationship between colony fragmentation and roost loss, and that loss of >20% of roosts is required to initiate colony fragmentation. Experimental hierarchical removal of day-roosts yielded results consistent with simulations, as removal of the single most-central (primary) roost had no impact on colony fragmentation, whereas removal of 24% of less-central (secondary) roosts resulted in partial network fragmentation. Patterns of colony day-roost and space use were similar pre- and post-removal treatments. Day-roost removal did not alter the number of roosts used by individual bats, but distances moved between roosts were greater in the secondary roost-removal treatment group. Day-roost characteristics largely were consistent pre-post treatment for both treatment groups.

Historical data from an Indiana bat (*Myotis sodalis*) maternity colony revealed that this species also exhibits a non-random social assorting dynamic. Non-random social assortment resulted in a closely connected centralized network of day-roosts. Individuals within the Indiana bat maternity colony exhibited close social connections with colony members, but subgroups likely existed within the colony. Indiana bat day-roosting ecology appears flexible, as patterns of roost and space use differed substantially between years.

Development of specific, but tactical, management approaches for individual colonies of both northern long-eared and Indiana bats may be possible. Such approaches would allow land managers to manage for both northern long-eared bat habitat and other objectives. However, the nature of targeted management approaches employed likely will depend on the unique forest context and dynamic within which individual colonies reside.

Dedication

This work is dedicated to my family, Tammy Silvis, Wilma Sue Tudor, Samuel Tudor, and my wife, Meryl Friedrich, all of whom always have supported me in my endeavors.

Acknowledgements

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Preface

Several chapters of this dissertation have appeared in published form, with co-authors, and appear here with permission from Hindawi Publishing, Elsevier Publishing, and PLoS ONE.

Chapter 1 appeared in the journal International Journal of Forestry Research as:

Silvis, A., W. M. Ford, E. R. Britzke, N. R. Beane, and J. B. Johnson. 2012. Forest Succession and Maternity Day Roost Selection by *Myotis septentrionalis* in a Mesophytic Hardwood Forest. International Journal of Forestry Research 2012:e148106.

Chapter 2 appeared in the journal Behavioural Processes as:

Silvis, A., W. M. Ford, E. R. Britzke, and J. B. Johnson. 2014*a*. Association, roost use and simulated disruption of *Myotis septentrionalis* maternity colonies. Behavioural Processes 103:283–290.

Chapter 5 appeared in the journal PLoS ONE as:

Silvis, A., A. B. Kniowski, S. D. Gehrt, and W. M. Ford. 2014*b*. Roosting and Foraging Social Structure of the Endangered Indiana Bat (*Myotis sodalis*). PLoS ONE 9:e96937.

Chapter 3 currently is in review with the journal PLoS ONE, under the same title, and was co-authored with W. Mark Ford and Eric R. Britzke.

Chapter 1: Forest Succession and Maternity Day-roost Selection by *Myotis septentrionalis* in a Mesophytic Hardwood Forest

Alexander Silvis

Abstract

Conservation of summer maternity roosts is considered critical for bat management in North America, yet many aspects of the physical and environmental factors that drive roost selection are poorly understood. I tracked 58 female northern long-eared bats (*Myotis septentrionalis*) to 105 roost trees of 21 species on the Fort Knox military reservation in north-central Kentucky during the summer of 2011. Sassafras (*Sassafras albidum*) was used as a day-roost more than expected based on forest stand-level availability and accounted for 48.6% of all observed day-roosts. Using logistic regression and an information theoretic approach, I was unable to reliably differentiate between sassafras and other roost species, or between day-roosts used during different maternity periods using models representative of individual tree metrics, site metrics, topographic location, or combinations of these factors. For northern long-eared bats, I suggest that day-roost selection is not a function of differences between individual tree species *per se*, but rather of forest successional patterns, stand and tree structure. Present successional trajectories may not provide this particular selected structure again without management intervention, thereby suggesting that resource managers take a relatively long retrospective view to manage current and future forest conditions for bats.

Introduction

Prior to the onset of White Nose Syndrome (WNS) in North America (Blehert et al. 2009), northern long-eared bats (*Myotis septentrionalis*) were common in most forest types in the eastern United States and southern Canada (Foster and Kurta 1999, Caceres and Barclay 2000, Lacki and Schwierjohann 2001, Menzel et al. 2002*c*, Broders et al. 2006, Perry and Thill 2007, Morris et al. 2010, Johnson et al. 2012). Northern long-eared bat foraging activity consistently has been greatest in closed-canopy forests (Jung et al. 1999, Menzel et al. 2002*c*, Owen et al. 2004, Brooks and Ford 2005, Loeb and O'Keefe 2006) and maternity roosts and roost-areas of live trees and/or snags typically are located in upland forests (Lacki and Schwierjohann 2001, Menzel et al. 2002*a*, Owen et al. 2004, Ford et al. 2006, Perry and Thill 2007).

Management for Myotine bats in North America often is based on the conservation of summer maternity roosts and winter hibernacula (Fenton 1997, Psyllakis and Brigham 2006). In particular, summer maternity roosts are widely assumed to be critical, and possibly limiting, environmental features for bats roosting in forested or formerly forested landscapes (Fenton 1997, Kunz and Lumsden 2003). Although northern long-eared bats have been the focus of several recent studies (Garroway and Broders 2007, Patriquin et al. 2010, Johnson et al. 2012), patterns of maternity roost selection at the forest stand- and landscape-scale are not well understood. There is considerable variation in forest conditions, roost tree species preference and differences (or lack thereof) between roosts and other available trees across the northern long-eared bat's distribution (Lacki and Schwierjohann 2001, Menzel et al. 2002*c*, Lausen et al. 2008). Nonetheless, consensus is that northern long-eared bat maternity colonies typically use snags or decaying live trees with cavities or loose/exfoliating bark, and that management efforts should focus on ensuring that suitable roosts are maintained on the landscape long-term (Lacki and Schwierjohann 2001, Owen et al. 2004, Perry and Thill 2007).

Although conservation of individual roosts may provide local or individual benefits, bat habitat conservation at this scale is unfeasible in the context of other forest stand and landscape management objectives. However, recent research suggests that non-random assorting social groups should be the focal point of roost conservation and that there is a need to better quantify the multi-scale habitat features necessary to preserve and maintain maternity colonies (Rhodes 2007). In the central Appalachians, Johnson et al. (2012) identified such non-random assorting social groups in female northern long-eared bats and further illustrated how these groups form scale-free networks of day-roosts on the landscape. Within this context, roost networks are the units of biological relevance that may allow management of forest bats to occur at the appropriate scales within the framework of conventional forestry (Rhodes 2007, Johnson et al. 2012). Relating forest processes such as disturbance and establishment to creation of suitable roost structure and conditions over areas relevant to social networks therefore would be useful in developing continually adaptive landscape management plans that consider bats among other resource objectives. I collected day-roost data as part of a larger long-term study on northern long-eared bat social ecology on the Fort Knox military reservation in north-central Kentucky, USA; my overall objective was to document patterns in northern long-eared bat summer maternity roost selection at Fort Knox. Because I documented strong day-roost selection of a single tree species that historically was not prevalent in pre-settlement closed canopy forests, I attempt to describe this pattern in the larger context of forest establishment and disturbance processes related to land-use history using my data and examples from previous northern long-eared bat research.

Methods

I conducted my northern long-eared bat day-roost study on the Fort Knox military reservation in Meade, Bullitt and Hardin Counties, Kentucky, USA. Fort Knox lies within the Western Pennyroyal subregion of the Mississippian portion of the Interior Low Plateau physiographic province (Arms et al. 1979). Topography in the region consists of dissected rolling plateaus, narrow valleys, and entrenched streams. Much of the area is underlain by karst formations and winter cave hibernacula are abundant. Elevations range from 116 m above sea level (asl) along the Ohio River to 323 m asl, though most uplands generally are between 180 and 275 m asl (Arms et al. 1979). Forest cover is predominantly a western mixed-mesophytic association (Braun 1950), with second- and third-growth forests dominated by white oak (*Quercus alba*), black oak (*Q. velutina*), chinkapin oak (*Q. muehlenbergii*), shagbark hickory (*Carya ovata*), yellow poplar (*Liriodendron tulipifera*), white ash (*Fraxinus americana*) and American beech *(Fagus grandifolia*) in the overstory, and sassafras (*Sassafras albidum*), redbud (*Cercis canadensis*) and sugar maple (*Acer saccharum*) in the understory (Cranfill 1991). Climate at Fort Knox is warm-temperate with an average temperature between 18 and 25°C during the growing season and an average annual precipitation of 113 cm.

I captured northern long-eared bats using mist nets erected across closed forest corridors, streams, standing water or in close proximity to previously documented trees currently being used as maternity roosts. For all northern long-eared bats netted, I determined age (by degree of epiphyseal-diaphyseal fusion [Anthony 1988]), mass, forearm length, sex and reproductive condition (Menzel et al. 2002*b*) and placed uniquely numbered lipped aluminum bands on the forearms. I also attached LB-2 radiotransmitters (0.46-0.54 g: Holohil Systems Ltd., Woodlawn, ON, Canada) between the scapulae of female northern long-eared bats using Perma-Type surgical cement (Perma-Type Company Inc., Plainville, CT, USA). I released tagged bats near net sites within a few minutes of capture. I followed the guidelines of Virginia Polytechnic Institute and State University Institutional Animal Care and Use Committee permit 11-040-FIW.

Using TRX-1000S receivers and folding three-element Yagi antennas (Wildlife Materials Inc., Carbondale, IL, USA), I located northern long-eared bat day-roosts every day for the life of the transmitter or until the unit dropped from the bat. I geo-referenced all day-roosts located using a Garmin GPSmap 60CSx global positioning system (Olathe, KS, USA). At each female northern long-eared bat day-roost, I recorded roost species, diameter at breast height (dbh), height, crown class

(Nyland 2002; i.e. 1 = suppressed, 2 = intermediate, 3 = codominant, 4 = dominant), decay class (Cline et al. 1980; 1 = live, 2 = declining, 3 = recent dead, 4 = loose bark, 5 = no bark, 6 = broken top, 7 = broken bole), and visually estimated percent remaining bark. Additionally, I measured the nearest four trees using the point-quarter system (Brower and Zar 1984); for each of these trees I determined species, measured distance to roost, dbh, decay class, and crown class. To assess canopy cover and canopy gap characteristics of day-roosts I measured gap fraction, leaf area index (LAI), and total below canopy photosynthetically-active photon flux density (PPFD) using WinSCANOPY and XLScanopy software (Régent Instruments Inc., Canada). Forest canopy photos were collected using a Nikon Coolpix 8400 camera and FC-E9 fisheye lens (Melville, NY, USA).

To calculate percent slope, elevation, and aspect at each day-roost, I input geo-referenced locations into ArcMap 9.3 (ESRI Inc., Redlands, CA, USA) and calculated position metrics with the Spatial Analyst extension. To compare distribution of used day-roost species versus availability of other potential roost species in the forest stands containing day-roosts, I recorded potential roosts (i.e., boles with loose/exfoliating bark, visible cavities or other defects) by species along randomly directed 20 x 100 m belt transects from the periphery of each point-quarter plot.

I used two-sample Wilcoxon tests for simple comparisons of individual day-roost metrics between day-roosts and nearest neighbor trees as well as for comparisons of live and snag day-roosts. I used chi-square goodness-of-fit tests to determine if day-roosts were distributed equitably by live/dead status and by species. Although not commonly addressed in habitat preference studies of bats, the chi-square goodness-of-fit test assumes independence of relocations among individuals and temporal independence of re-locations of individuals (Thomas and Taylor 2006). By pooling use data across individuals and counting each tree as a single location rather than each use, I assumed independence of individual trees. I used an information theoretic approach (IT) to compare day-roosts used by bats during pregnancy to those used by bats during lactation and non-lactation by examining a set of 9 candidate models representing tree-specific characteristics, topological characteristics, micro-site characteristics, combinations of those characteristics, and a null (Table 1). Although I measured canopy position, I removed it from all models due to unacceptably high standard errors. I followed Garroway and Broders (2008) in separating day-roost maternity use status (lactation or non-lactation) by date of capture of the first lactating female and volant juvenile. I used the same IT approach and candidate model set to compare the most selected day-roost species to the collective of all other species. I ranked models using Akaike's criteria (AIC), the difference between the model with the lowest AIC and the

AIC of the ith model (Δ_i) and Akaike's weights (w_i) (Burnham and Anderson 2002). I assessed significance of individual parameters within the best supported model using Wald's X^2 test and overall fit of the model using the log-likelihood ratio test against a null model, area under the curve of the receiver operating characteristic (AUC), and percent correct classification. To avoid problems of circularity when analyzing aspect, I used sine and cosine transformations of aspect for logistic analysis. All tests were performed using the R statistical program (version 2.14) (R. Development Core Team 2014) with significance for all tests accepted at $\alpha \leq 0.05$.

Results

   I mist-netted on 33 nights between 24 May and 17 July 2011 and captured 58 adult females, 2 juvenile females, and 16 adult male northern long-eared bats. Eighteen of the adult females were pregnant, 29 were lactating, 3 had ceased lactation, and 8 were non-reproductive. Transmitters were attached to all 58 adult female northern long-eared bats; mean transmitter retention time was 4.1 days. Overall, I tracked these bats to 105 day-roosts that comprised 21 tree species (Table 2) for a total of 270 re-location events. Number of tagged bats within a single day-roost ranged from 1-15, with a mean of 1.55 ± 0.16 bats/tree. The number of uses of an individual day-roost by tagged bats ranged from 1-84, with a mean of 2.55 ± 0.79, where use is defined as the sum of presences of all bats using that day-roost.

   Spatially, most day-roosts were located near ridge tops or plateaus with a mean elevation of 217.95 ± 18.26 m and a mean slope of $13.46 \pm 11.10\%$ (Table 3). Day-roosts not on plateaus tended to be located on south-facing slopes (mean aspect $= 222.90 \pm 90.84$ degrees) when topography permitted an aspect value to be meaningfully discerned. Day-roosts had a larger dbh (30.19 ± 18.59 cm; W $=$ 28443, $P < 0.001$) and were in later stages of decay (mean $= 3.53 \pm 1.59$; W $= 36504$, $P < 0.001$) than neighboring trees. Of the located trees, 71.4% were in the suppressed canopy class, 16.3% were intermediate, 5.7% were codominant, and 6.6% were dominant. Mean day-roost height was 14.56 ± 7.07 m. Day-roost sites had a mean gap fraction of $8.37 \pm 2.26\%$, a mean leaf area index of 2.55 ± 0.37 $m^2 {*} m^{-2}$, and a mean below canopy photosynthetic photon flux density of 1.65 ± 0.76 $Mol {*} m^{-2}$. Bark retention was low (64.57%) across day-roosts.

   Seventy of the day-roosts I observed were in snags whereas 35 were in live trees with visible cavities. Cavities accounted for 104 of 105 roosts. The remaining day-roost was located under exfoliating bark of a snag. Snags were used as day-roosts more than expected based on availability

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(67%; W = 19, $P < 0.001$). I detected no difference in dbh (W = 1334, $P = 0.46$), gap fraction (W = 1062, $P = 0.27$), LAI (W = 1273, $P = 0.75$) PPFD (W = 1250, $P = 0.87$), slope position (W = 1034, $P = 0.20$), aspect (W = 1175, $P = 0.74$) or elevation (W = 1312, $P = 0.55$) between snag and live day-roosts. Snags significantly were shorter (W = 1576, $P = 0.02$) and had significantly less remaining bark than live trees (W = 2205, $P < 0.001$; Table 3).

My best supported model differentiating day-roosts by maternity status was a site-specific canopy condition model containing gap fraction, LAI, and PPFD (Table 4). Under this model, probability of a day-roost being used during the lactation period increased with gap fraction and LAI, but decreased with PPFD (Table 5). This model provided a better fit than a null model (log-likelihood = -60.16, $P = 0.002$), but nonetheless had poor predictive power (71% correct classification rate, AUC = 0.72).

The most commonly observed day-roost species (sassafras, sugar maple and white oak) accounted for 48.6%, 9.5% and 7.6% of the total recorded day-roosts, whereas the remaining species each accounted for $\leq 6.0\%$ of day-roosts used (Table 2). Sassafras was the most commonly observed potential roost species (34.6%), and was used more than expected based on availability on the landscape ($\chi^2 = 6.8$, $d.f. = 1$, $P = 0.009$). Sugar maple was the second most commonly observed potential roost species (14.3%), but was used in proportion to its availability in the surrounding forest stand ($\chi^2 = 1.5$, $d.f. = 1$, $P = 0.22$). In general, the ranked order of abundance of species most used as day-roosts was equivalent to the ranking of species deemed potential roosts. My best supported model differentiating sassafras day-roosts from other species was a tree specific model containing dbh, height, decay status, and percent bark (Table 6). Within this model, probability of a roost being sassafras decreased with increasing dbh, percent bark, when decay stage was 2, or 4, but increased with height and when decay stage was 3, 5 or 6 (Table 7). This model provided a better fit than a null model (log-likelihood = -49.3, $P < 0.001$), but had a low AUC (0.84) and poor correct classification rate (72%).

Discussion

The limited day-roost documentation of northern long-eared bats mostly has shown maternity colony use of snags and live trees larger and more decadent than neighboring boles. It widely is accepted that increased solar exposure at female day-roost sites provides important thermal benefits to temperate bat species and that larger trees under open canopies receive more solar radiation and presumably provide better day-roost structures (Kunz and Lumsden 2003, Johnson et al. 2009),

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particularly during lactation. Despite this speculation, no studies have yet reported direct measures of solar radiation such as photosynthetic flux density. Similarly, measures of canopy structure/complexity such as leaf area index that may affect the amount of solar radiation reaching day-roosts are lacking (Johnson et al. 2009). Use of direct measures of solar radiation and canopy complexity, as well as more accurate measurement of gap fraction, may improve the understanding of the effects of solar radiation on roost selection and identify previously unexplored commonalities between day-roost sites across latitudinal and elevation gradients. Compared to LAI values reported for other deciduous forests (range 2-10 m^2*m^{-2}, mean = 5.41 m^2*m^{-2}), my observed LAI was low (Breuer et al. 2003). Nonetheless, my LAI value is greater than those reported for non-shrubby forest understory conditions (range 0.2-13.3 m^2*m^{-2}, mean 1.81 m^2*m^{-2}; Breuer et al. 2003), supporting the supposition that northern long-eared bats roost in relatively dense forest at Fort Knox.

Many studies have used canopy closure as a surrogate measure for solar radiation. I found that my canopy closure values calculated using hemispherical photographs were similar to those reported in the central Appalachians in both Kentucky and West Virginia by Lacki and Schwierjohann (2001) and Menzel et al (2002c) as well as to Johnson *et al.* (2009). However, canopy closures at my day-roosts were substantially greater than those reported by Garroway and Broders (2008) in Nova Scotia, Canada, and Carter and Feldhamer (2005) in southern Illinois bottomland hardwoods. Additionally, while the use of day-roosts that were larger than surrounding trees in my study generally would support the solar radiation hypothesis, the majority of day-roosts (71.4%) I observed were suppressed and under substantial canopy cover.

My analysis of day-roost selection by maternity status indicates that gap fraction and solar radiation best differentiates day-roosts used during lactation and non-lactation periods. However, the overall poor performance of the model suggests that female northern long-eared bats at my study sites did not differentiate strongly between day-roosts used during different reproductive conditions. This contrasts with Garroway and Broders (2008) who found that female northern long-eared bats selected larger day-roosts during the lactation period relative to non-lactation periods and suggest that selection of larger day-roosts is a function of increased solar radiation. Assuming solar radiation is important in roost temperature regulation and selection, latitudinal temperature gradients likely impose different restrictions on roost selection. If this is the case, greater canopy cover in my sites relative to generally cooler northern sites (Garroway and Broders 2008) is not surprising, nor is comparable canopy cover between my sites and sites along similar latitudinal gradients (Lacki and Schwierjohann 2001, Menzel

et al. 2002*c*, Johnson et al. 2009). A latitudinal temperature gradient would explain differences between my analysis of day-roost selection by maternity status and that of Garroway and Broders (2008).

I found that day-roosts consistently were located on ridge tops and plateaus primarily on south facing aspects similar to the observations of other researchers working with northern long-eared bats (Lacki and Schwierjohann 2001, Jung et al. 2004, Johnson et al. 2009). Although it may be that such positions increase solar radiation at roost sites, upper slopes and ridges also have the highest natural disturbance frequency and severity (Lorimer and White 2003). Historic cycles of repeated natural stand disturbance and increased snag presence rather than increased solar radiation might be the primary influence on northern long-eared bat selection locally. Currently, it is unclear to what extent roost solar exposure, roost availability due to increased disturbance, or some interaction of these factors plays a role in northern long-eared bat day-roost selection.

I documented a wider use of tree species by northern long-eared bats than reported elsewhere (Lacki and Schwierjohann 2001, Menzel et al. 2002*c*, Perry and Thill 2007, Johnson et al. 2009), including the first recorded use of eastern redcedar (*Juniperus virginiana*). Northern long-eared bats in my study displayed a marked preference for sassafras as day-roosts. Black locust, a preferred day-roost species by both male and female northern long-eared bats in the central Appalachians of West Virginia (Menzel et al. 2002*c*, Ford et al. 2006, Johnson et al. 2009), rarely was used at Fort Knox. Despite overwhelming selection by northern long-eared bats, my inability to reliably differentiate sassafras day-roosts from other day-roost using logistic regression was surprising. As suggested by Ford et al. (2006), and following classical use-availability theory, roost selection probably is a function of the abundance of individual species, rather than differences between species, assuming the desired physical characteristics are present. Although sassafras at my sites clearly provided appropriate roosting structure, preference for this tree species probably is ecologically novel at the scale I observed. In the context of forest succession, this fast-growing shade-intolerant species (Burns and Honkala 1984) historically would not have been a large component of closed canopy forests in my study region under small disturbance gap-phase dynamics (Trani et al. 2001, Lemenih and Teketay 2005, Albrecht and McCarthy 2006, Schweitzer and Dey 2011). Much of the extant sassafras at Fort Knox almost certainly is a product of extensive timber harvest from the late 1700s-late 1800s followed by decades of agricultural use through the early 1900s, and subsequent abandonment of agricultural areas following acquisition by the United States Army beginning in 1919 and ending in 1942. On some portions of the installation, escaped fires from weapons ranges constitute an important recurring disturbance that may mimic historic fire return intervals appropriate to the area (Frost 1998, McEwan et al. 2007).

Given the 'aberrant' nature of sassafras as a major component of forests within mixed-mesophytic forests, the wide range of tree species used as day-roosts by northern long-eared bats (Garroway and Broders 2008, Johnson et al. 2009, Lacki and Schwierjohann 2001, Menzel et al. 2002*c*, Psyllakis and Brigham 2006), and the lack of differences between tree species used as day roosts in this study, I believe that ecological processes of forests may play a greater role in bat day-roost selection than currently is recognized. Because my original intent was not to analyze the effects of forest succession on day-roost selection, I was unable to test this hypothesis directly using my data. However, I believe it is appropriate to reinterpret day-roost selection by forest bats in other studies in the context of unique forest disturbances and establishment conditions. For example, shortleaf pines (*Pinus echinata*) selected as day-roosts by northern long-eared bats in Arkansas (Perry and Thill 2007) largely were snags created following pine beetle (*Ips spp.*) outbreaks (R. Perry, personal communication). Ford et al. (2006) suggested that northern long-eared bat use of black locusts *(Robinia pseudoacacia)* as day-roosts in West Virginia was a recent ecological phenomenon directly related to disturbances from exploitative logging in the early- to mid-1900s whereby widespread landscape-level clearcutting favored regeneration and growth of black locust over historically more prevalent species. There, black locust day-roosts were in early stages of decay that were comparable to the decay stage of sassafras I observed at Fort Knox. In the absence of suppression by competitors, the observed high rates of decadence in West Virginia and at Fort Knox in black locust and sassafras, respectively, are unlikely to occur within the first several decades after establishment (Ward and Stephens 1993).

In the context of day-roost spatial networks it is important to move beyond individual tree concepts and incorporate larger forest establishment conditions that create and maintain suitable long-term roosting opportunities and networks. I am aware of no comprehensive attempts to relate past land use or forest development to patterns of day-roost selection by bats, yet understanding these relationships should be invaluable for managers to relate current day-roost conditions and availability with necessary future conditions. I believe the following questions should be considered relative to understanding day-roost ecology of tree-roosting bats such as the northern long-eared bat: 1) Is current forest composition largely a result of historical or anthropogenically disturbed conditions rather than natural processes? 2) Are the species used as day-roosts typical of the regional and local forest type? 3) Are bats adapting to novel conditions related to anthropogenic or stochastic natural events that drastically have altered forest structure and composition? 4) Are the conditions in place for creation of suitable day-roosts into the future, or will the creation of suitable day-roosts be dependent on management activities?

Conclusions

Differences in establishment history and disturbance processes can lead to a myriad of alternative stable or dynamic states of forest communities that vary in their successional trajectories and long-term composition and structure (Nowacki and Abrams 2008). In the context of bats, day-roost species selection may be a function of the regional species candidate pool and successional processes. The particular anthropogenic and stochastic forest disturbance processes that shaped present forest conditions (Lorimer and White 2003, Nowacki and Abrams 2008) across the range of the northern long-eared bat feasibly may not be recreated by managers, or even desired in light of other stewardship needs. Furthermore, current conditions necessarily do not represent desired future conditions for managers. By linking forest successional and disturbance processes to bat day-roost networks, bat habitat may be managed at spatial and temporal scales compatible with larger forest management objectives for a fuller compliment of desired natural resource outcomes, however, further work directly addressing this topic across a wider range of bat species and forest types is needed.

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Table 1.1. Candidate model sets used to compare female northern long-eared bat (*Myotis septentrionalis*) day-roost species selection and day-roost selection by maternity status on the Fort Knox military reservation in Hardin, Bullitt and Meade Counties, Kentucky, USA, 2011.

Model	Parameters
1	dbh + height + decay + percent bark + percent slope + sin(aspect) + cos(aspect) + elevation + gap fraction + LAI + PPFD
2	dbh + height + decay + percent bark
3	dbh + height
4	decay + percent bark
5	decay + percent bark + gap fraction + LAI + PPFD
6	gap fraction + LAI + PPFD
7	percent + sin(aspect) + cos(aspect) + elevation + gap fraction + LAI + PPFD
8	percent slope + sin(aspect) + cos(aspect) + elevation
9	null model

Table 1.2. Female northern long-eared bat (*Myotis septentrionalis*) day-roosts by species and the number of corresponding potential day-roosts (%) in a mesophytic forest on the Fort Knox military reservation in Hardin, Bullitt and Meade Counties, Kentucky, USA, 2011. Available roosts were those trees with visible cavities or exfoliating bark found on 20 x 100 m belt transects oriented at random azimuths from each day-roost.

Species	Available (%)	Day-roosts (%)
Sassafras (*Sassafras albidum*)	847 (34.6)	51 (48.6)
Sugar maple (*Acer saccharum*)	357 (14.6)	10 (9.5)
White oak (*Quercus alba*)	132 (5.4)	8 (7.6)
White ash (*Fraxinus americana)*	166 (6.8)	6 (5.7)
Eastern redbud (*Cercis canadensis*)	99 (4.0)	4 (3.8)
Winged elm (*Ulmus alata*)	32 (1.3)	4 (3.8)
American beech (*Fagus grandifolia*)	7 (0.3)	3 (2.9)
Black locust (*Robinia pseudoacacia*)	117 (4.8)	3 (2.9)
Shagbark hickory (*Carya ovata*)	122 (5.0)	2 (1.9)
Black walnut (*Juglans nigra*)	56 (2.3)	2 (1.9)
Chinkapin oak (*Quercus muhlenbergii*)	108 (4.4)	2 (1.9)
Slippery elm (*Ulmus rubra*)	33 (1.3)	1 (1.0)
Boxelder (*Acer negundo*)	5 (0.2)	1 (1.0)
Pignut hickory (*Carya glabra*)	48 (2.0)	1 (1.0)
Hackberry (*Celtis occidentalis*)	9 (0.4)	1 (1.0)
Blue Ash (*Fraxinus quadrangulata*)	29 (1.2)	1 (1.0)
Eastern redcedar (*Juniperus virginiana*)	52 (2.1)	1 (1.0)
Blackgum (*Nyssa sylvatica*)	6 (0.2)	1 (1.0)
American sycamore (*Planatus occidentalis*)	11 (0.4)	1 (1.0)
Northern red oak (*Quercus rubra*)	64 (2.6)	1 (1.0)
Black oak (*Quercus velutina*)	44 (1.8)	1 (1.0)
American hornbeam (*Carpinus caroliniana*)	1 (0.04)	0 (0.0)
Tree of heaven (*Ailanthus altissima*)	3 (0.1)	0 (0.0)
Shellbark hickory (*Carya laciniosa*)	2 (0.1)	0 (0.0)
Flowering dogwood (*Cornus florida*)	19 (0.8)	0 (0.0)
Common persimmon (*Diospyros virginiana*)	24 (1.0)	0 (0.0)
Sweet gum (*Liquidambar styraciflua*)	5 (0.2)	0 (0.0)
Yellow poplar (*Liriodendron tulipifera*)	47 (1.9)	0 (0.0)
Red mulberry (*Morus rubra*)	2 (0.1)	0 (0.0)
Pitch pine (*Pinus rigida*)	1 (0.04)	0 (0.0)
Loblolly pine (*Pinus taeda*)	2 (0.1)	0 (0.0)

Table 1.3. Mean ± SD values of day-roost characteristics for all trees, live and snag trees, and the two tree species most commonly used by female northern long-eared bats (*Myotis septentrionalis*) in a mesophytic forest on the Fort Knox military reservation in Hardin, Bullitt, and Meade Counties, Kentucky, USA, 2011.

	All trees	Live	Snag	*Sassafras albidum*	*Acer saccharum*
N	105	35	70	51	10
dbh (cm)	30.19 ± 18.59	31.69 ± 18.06	29.44 ± 18.94	20.96 ± 7.69	26.09 ± 10.92
height (m)	14.56 ± 7.07	17.39 ± 8.14	13.15 ± 6.05	11.86 ± 4.65	13.48 ± 5.79
decay (stage)	3.53 ± 1.59	1.71 ± 0.46	4.44 ± 1.10	4.02 ± 1.48	3.6 ± 1.65
live (N)	33	NA	NA	11	4
remaining bark (%)	64.57 ± 36.11	93.00 ± 4.47	50.36 ± 36.61	52.82 ± 39.10	76.00 ± 28.36
suppressed (%)	71.4	51.4	81.4	92.2	70.0
gap fraction (%)	8.37 ± 2.26	7.98 ± 1.96	8.57 ± 2.38	8.13 ± 2.25	9.42 ± 1.81
slope (%)	13.46 ± 11.10	11.67 ± 9.42	14.35 ± 11.81	12.05 ± 10.65	16.68 ± 11.35
aspect (°)	222.90 ± 90.84	211.08 ± 93.09	227.51 ± 90.34	223.80 ± 92.15	241.91 ± 79.22
elevation (m)	217 ± 18.26	219.92 ± 16.38	216.96 ± 19.17	219.35 ± 16.96	216.92 ± 11.78
LAI ($m^2 * m^{-2}$)	2.55 ± 0.37	2.74 ± 0.34	2.71 ± 0.43	2.71 ± 0.38	2.68 ± 0.34
PPFD ($\mu mol * m^{-2} * s^{-1}$)	1.65 ± 0.76	1.68 ± 0.82	1.63 ± 0.72	1.65 ± 0.89	1.71 ± 0.59

[a] LAI = leaf area index
[b] PPFD = photosynthetic photon flux density

Table 1.4. Rankings of models used to compare female northern long-eared bat (*Myotis septentrionalis*) day-roosts used during lactation and non-lactation periods on the Fort Knox military reservation in Hardin, Bullitt and Meade Counties, Kentucky, USA, 2011. Model parameters are given as well as number of parameters (K), Akaike's information criteria (AIC) value, difference in AIC value between top model and i^th model (Δ_i) and model support (w_i).

Model	K	AIC	Δ_i	w_i
gap fraction + LAI + PPFD	5	128.33	0	0.94
percent + sin(aspect) + cos(aspect) + elevation + gap fraction + LAI + PPFD	9	135.21	6.89	0.03
null model	2	137.01	8.69	0.01
decay + percent bark + gap fraction + LAI + PPFD	11	137.95	9.62	0.01
dbh + height	4	138.95	10.63	0.00
percent slope + sin(aspect) + cos(aspect) + elevation	6	140.78	12.46	0.00
dbh + height + decay + percent bark	10	143.14	14.81	0.00
dbh + height + decay + percent bark + percent slope + sin(aspect) + cos(aspect) + elevation + gap fraction + LAI + PPFD	17	145.15	16.83	0.00
decay + percent bark	8	146.13	17.81	0.00

[a] LAI = leaf area index
[b] PPFD = photosynthetic photon flux density

Table 1.5. Parameter summary of the best supported model comparing female northern long-eared bat (*Myotis septentrionalis*) day-roosts used during lactation and non-lactation periods on the Fort Knox military reservation in Hardin, Bullitt and Meade Counties, Kentucky, USA, 2011.

Variable	Parameter Estimate	SE	Wald χ^2	*P*-value	Odds ratio
Intercept	-4.32	4.12	1.1	0.29	-
Gap fraction	0.56	0.22	6.4	0.01	1.75
Leaf area index	0.9	1.09	0.69	0.41	2.47
Photosynthetic photon flux density	-1.15	0.38	9.3	0.002	0.32

Table 1.6. Rankings of models used to compare northern long-eared bat (*Myotis septentrionalis*) sassafras day-roosts to day-roosts of other species on the Fort Knox military reservation in Hardin, Bullitt and Meade Counties, Kentucky, USA, 2011. Model parameters are given as well as number of parameters (K), Akaike's information criteria (AIC) value, difference in AIC value between top model and ith model (Δ_i) and model support (w_i).

Model	K	AIC	Δ_i	w_i
dbh + height + decay + percent bark	10	116.67	0.00	0.65
dbh + height	4	118.12	1.44	0.31
dbh + height + decay + percent bark + percent slope + sin(aspect) + cos(aspect) + elevation + gap fraction + LAI + PPFD	17	122.38	5.71	0.04
decay + percent bark + gap fraction + LAI + PPFD	11	136.32	19.65	< 0.001
decay + percent bark	8	141.22	24.55	< 0.001
gap fraction + LAI + PPFD	5	146.88	30.20	< 0.001
null model	2	147.48	30.80	< 0.001
percent + sin(aspect) + cos(aspect) + elevation + gap fraction + LAI + PPFD	9	152.20	35.53	< 0.001
percent slope + sin(aspect) + cos(aspect) + elevation	6	153.56	36.88	< 0.001

[a] LAI = leaf area index
[b] PPFD = photosynthetic photon flux density

Table 1.7. Parameter summary of the best supported model comparing northern long-eared bat (*Myotis septentrionalis*) sassafras day-roosts to day-roosts of other species on the Fort Knox military reservation in Hardin, Bullitt and Meade Counties, Kentucky, USA, 2011.

Variable	Parameter Estimate	SE	Wald χ2	*P*-value	Odds ratio
Intercept	3.31	2.13	-	-	-
dbh	-0.12	0.03	13.00	< 0.001	0.88
Height	0.06	0.06	0.97	0.32	1.06
Decay stage 2	-0.05	1.33	< 0.001	0.97	0.95
Decay stage 3	0.8	1.33	0.36	0.55	2.23
Decay stage 4	-0.01	1.43	<0.001	0.99	0.99
Decay stage 5	0.91	1.82	0.25	0.62	2.49
Decay stage 6	1.01	1.57	0.41	0.52	2.75
Percent bark	-0.02	0.01	1.70	0.20	0.98

Chapter 2: Association, Day-roost Use and Simulated Disruption of *Myotis septentrionalis* Maternity Colonies

Alexander Silvis

Abstract

How wildlife social and resource networks are distributed on the landscape and how animals respond to resource loss are important aspects of behavioral ecology. For bats, understanding these responses may improve conservation efforts and provide insights into adaptations to environmental conditions. I tracked maternity colonies of northern long-eared bats (*Myotis septentrionalis*) at Fort Knox, Kentucky, USA to evaluate their social and resource networks and space use. Day-roost and social network structure differed between maternity colonies. Overall potential day-roost availability did not appear to be related strongly to network characteristics or space use. In simulations for my two largest networks, day-roost removal was related linearly to network fragmentation; despite this, networks relatively were robust, requiring removal of > 20% of day-roosts to cause network fragmentation. Results from my analyses indicate that northern long-eared bat behavior and space use may differ among colonies and potentially across the maternity season. Simulation results suggest that colony social structure is robust to fragmentation caused by random loss of small numbers of day-roosts. Flexible social dynamics and tolerance of day-roost loss may be adaptive strategies for coping with ephemeral conditions in dynamic forest habitats.

Introduction

Day-roost or nest site switching is a common behavior in wildlife (Hausfater and Meade 1982, Morrison and Caccamise 1990, Stouffer and Caccamise 1991, Brigham et al. 1998, Guillemain et al. 2010). Although potentially costly (Lewis 1995), day-roost switching may provide important benefits, such as predator avoidance (Kunz and Lumsden 2003), minimizing exposure to parasites (Reckardt and Kerth 2007), and maintenance of social contact (Willis and Brigham 2004). In bats, this behavior can define social structure (Willis and Brigham 2004). Some social or colonial species of bats that switch day-roosts form fission-fusion societies. Originally defined by Kummer (1971), fission-fusion societies are characterized by flexible social dynamics wherein "fusions" of individuals or small groups into larger groups are followed

by subsequent "fissions" as the larger group dissolves. In addition to bats, fission-fusion social dynamics exist in a wide range of mammalian taxa, and vary widely both within and among species (Conradt and Roper 2000, Archie et al. 2006, Ramos-Fernández et al. 2006, Lehmann et al. 2007). These societies exist under a broad range of ecological conditions and constraints, but generally occur when the benefits of sociality are transitory or temporary (Aureli et al. 2008). Day-roost switching in bat species with fission-fusion societies results in social networks of bats (J. S. Johnson et al. 2012) and in networks of day-roosts (Rhodes 2007, Fortuna et al. 2009, J. B. Johnson et al. 2012).

Analyzing day-roost switching behavior through a network approach provides a natural and informative extension to traditional day-roost switching analyses and allows group dynamics to be explored (Johnson et al. 2013). Recent research on the social and day-roost networks of maternity colonies of tree-day-roosting bats has provided important insights into patterns of how bats associate, and suggests that fission-fusion dynamics in bats are tied to the reproductive status of female bats (Garroway and Broders 2007, Patriquin et al. 2010). For these bats, the benefit of sociality is believed to be increased reproductive success, resulting from any of several possible factors. In particular, close association among female bats may minimize the physiological stress of lactation (Watkins and Shump 1981, Wilde et al. 1999) by creating more favorable day-roost thermal conditions (Willis and Brigham 2007) and may permit cooperative rearing of young (Jennions and Macdonald 1994, Kerth and Konig 1999, Kerth 2008*a*). Network analysis also has provided additional evidence that social structure in bats may be related to habitat quality and the availability of day-roosts (Chaverri 2010, J. S. Johnson et al. 2012). The study of association and networks, however, has been limited to relatively few bat species, and even for these examined species, most aspects of social dynamics largely have been unexplored. Data gaps include how maternity colonies collectively use space, whether environmental variables affect social behavior in bats in diverse habitats, and how bats respond to day-roost loss.

Tree-cavity day-roosting bats use ephemeral resources (i.e., trees and snags) that constantly are subject to attrition due to decay and disturbance processes. How bats respond to day-roost loss likely is related to numerous factors, including the degree of resource specialization, day-roost creation dynamics and subsequent availability, and association and day-roost use patterns (Chaverri 2010, Chaverri and Kunz 2011). Understanding the effects of day-

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roost loss and the distribution of maternity colonies on the landscape may provide important insights into the formation of maternity colonies on the landscape and may aid resource managers attempting to balance bat conservation with other aspects of forest stewardship. If day-roost loss reduces the ability of a colony to associate, preferentially associating individuals within maternity colonies may form new maternity colonies in adjacent areas. Given that colonies appear to follow matrilines, new colonies also may follow matrilines (Kerth 2008*b*, Patriquin et al. 2013). Or, if day-roosts provide important benefits that are not replicated elsewhere (Brigham and Fenton 1986), day-roost loss may result in the dissolution of a colony.

In this study, I focus on the day-roost and social networks of northern long-eared bat (*Myotis septentrionalis*) maternity colonies. Prior to the onset of White-nose syndrome, northern long-eared bats were common and distributed widely in forested habitats in the eastern United States and southeastern Canada. Previous research on the fission-fusion dynamics of northern long-eared bats identified presence of non-random assorting groups within maternity colonies (J. B. Johnson et al. 2012). Driven by maternity status, these groups follow a two-leveled social structure with both long-term and short-term preferred associations (Garroway and Broders 2007, Patriquin et al. 2010). Day-roost and social network characteristics of some bats with fission-fusion societies are related to day-roost availability, but this has not been assessed for the northern long-eared bat. Herein, my objectives were to: (1) describe patterns of day-roost use by and association of northern long-eared bat maternity colonies in a network context, (2) determine whether network characteristics were related to day-roost availability, (3) assess spatial patterns of day-roosting by maternity colonies, and (4) examine the potential impacts of day-roost removal on network fragmentation. Based on research by Chaverri (2010) and J. S. Johnson et al. (2012), and a review by Lewis (1995), I hypothesized that northern long-eared bat day-roost network centralization would be related inversely to day-roost availability, and that space use would be similar between colonies with similar day-roost availability. Finally, I hypothesized that removal of a moderate proportion of day-roosts in a network would result in fragmentation of the colony, but that day-roost networks should be robust to the loss of a small number, albeit unknown, of day-roosts (J. B. Johnson et al. 2012).

Materials and Methods

I conducted my study at three sites on the Fort Knox military reservation in Meade, Bullitt, and Hardin Counties, Kentucky, USA, from May through July 2011. Study sites were between 2 and 15 km apart. Forest cover at my sites is predominantly a western mixed-mesophytic deciduous association (see Silvis et al. 2012 for a complete site description). I initially captured female northern long-eared bats over small pools of standing water and attached an LB-2 radiotransmitter (0.31 g: Holohil Systems Ltd., Woodlawn, ON, Canada) between the scapulae of each female bat using Perma-Type surgical cement (Perma-Type Company Inc., Plainville, CT, USA) and applied a uniquely numbered lipped band to the forearm of each female. To maximize capture of bats within individual colonies, I erected mist nets around day-roosts I discovered by tracking individual bats; a day-roost was not netted on consecutive nights. Although I tracked bats continuously during the study period, as a result of my capture strategy I generally, but not exclusively, focused on a single day-roosting group of bats, and therefore study site, at a time. I released tagged bats near net sites within 30 minutes of capture. I located bats daily for the life of the transmitter or until the unit dropped from the bat. Additionally, I conducted a small number of day-roost exit counts to estimate minimum colony size. I tested for observation bias in day-roosting behavior by regressing the number of day-roosts used by an individual bat against the number of relocation events. I attached a marker with a unique identifier to each located day-roost tree and recorded site coordinates. I followed guidelines of Virginia Polytechnic Institute and State University Institutional Animal Care and Use Committee permit 11-040-FIW and Kentucky Department of Fish and Wildlife Resources permit SC1311170 for capturing, handling, and tracking bats.

I defined the northern long-eared bat maternity colonies as all female and juvenile bats connected by coincident day-roost use. I represented colonies graphically and analytically as two-mode networks that consisted of bats and day-roosts, hereafter roost network (Fortuna et al. 2009, J. S. Johnson et al. 2012). I used this two-mode representation to assess patterns of day-roost use by colonies. I used a single-mode projection of the bat nodes (hereafter social network) to assess colony social structure, as this provided a more generalized picture of how bats could associate than the observed patterns in the two-mode network. To reduce bias resulting from uneven tracking periods and observing only a portion of the colony in other network metrics, I removed multiple edges between nodes and did not assign edge weights; in network analysis, an

edge is the connections between two nodes. I assessed day-roost and social network structure using mean degree, network degree centralization, network density and clustering. I calculated two-mode degree centralization and density using the methods of Borgatti and Everett (1997) and clustering using the method of Opsahl (2009) for my roost network and used equivalent single-mode formulations to calculate network degree centralization (Freeman 1978), density (Wasserman and Faust 1994), and clustering (Wasserman and Faust 1994, Watts and Strogatz 1998) for the social network.

For individual nodes in a network, degree is the number of edges incident with that node (Boccaletti et al. 2006), with high degree values indicating greater connectedness within a network. For my roost networks, my mean degree value corresponds to the number of radiotracked bats that used a day-roost and provides a measure of how well day-roosts were known to bats. For the bat social network, mean degree provides a measure of how well individual bats within the network were known to each other. Network degree centralization, density, and clustering have values between 0 and 1 (0 = low, 1 = high). These measures represent the extent that a network is structured around individual nodes (network degree centralization) and the distribution of connections between nodes (clustering and density; (Freeman 1978, Wasserman and Faust 1994, Borgatti and Everett 1997, Watts and Strogatz 1998, Dong and Horvath 2007).

To determine whether my observed network values differed significantly from those of random networks, I performed 500 Monte Carlo simulations and compared observed network metrics to random network metrics using two-tailed permutation tests (Hope 1968, Davison 1997). Because network metrics are dependent upon the size of an individual network, values from networks of differing size are challenging to compare (James et al. 2009). Therefore, my random networks were generated with the same number of nodes as my observed networks and with a constant probability of link establishment. I used the *igraph* (Csardi and Nepusz 2006) and *tnet* libraries (Opsahl 2009) in the R statistical program version 2.14 (R. Development Core Team 2014) to visualize networks and calculate metrics. My permutation tests were performed in R using a custom script with dependencies on the *igraph* and *tnet* libraries.

To evaluate space use by maternity colonies, I calculated bivariate normal fixed-kernel utilization distributions with estimation of the smoothing parameter using the reference method for day-roost locations. To reflect the concentration of day-roost use (Popa-Lisseanu et al. 2008)

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I weighted day-roost locations by the number of bat-days a day-roost was used. I used utilization distributions to show core (50% utilization distribution) and whole (95% utilization distribution) network areas. I calculated utilization distributions using the *adehabitat* package (Calenge 2006) in the R statistical program.

Because previous studies suggest both bat day-roost and social network values are related to day-roost availability, I looked for trends between roost network characteristics and the availability of potential alternate day-roosts. I assessed day-roost availability by recording the number of potential day-roosts (i.e., boles with loose/exfoliating bark, visible cavities, or other defects similar to those used by radiotagged bats) by species along 20×100-m belt transects randomly emanating from day-roost locations (Ford et al. 2006). Because the number of day-roosts was not equal across networks, I standardized the number of potential day-roosts for each network by dividing the count of potential day-roosts by the number of day-roosts within the network. Therefore, my values for potential day-roost availability give the number of possible day-roosts available per located day-roost.

I assessed the potential impact of day-roost loss on colony social fragmentation using random node removal simulations for my two largest day-roost networks. I conducted these simulations using the single-mode projection of the day-roosting network to best reflect bats' knowledge of multiple day-roosts and their possible movement pathways between those day-roosts. Because my network analysis infers sociality from coincident day-roost use, fragmentation of the roost network can therefore be interpreted also as a social fragmentation of the colony. For each random removal simulation, I randomly selected and removed a set proportion of nodes. I performed simulations by iteratively removing an increasing number of nodes until only 20% remained. Because the number of nodes differed between colonies, using a removal percentage allowed me to compare the relative effects of day-roost loss between networks. I repeated removal simulations 500 times per proportion of nodes removed and calculated the mean and standard error of the number of resultant components; a component is either a network fragment or an individual node. Random removal simulations were performed in R using a custom script with dependencies on the *igraph* and *tnet* libraries.

Results

I attached radio transmitters to 58 adult female northern long-eared bats. I obtained relocation data for 54 individuals (16 gestating, 29 lactating, 3 post-lactating, 6 non-reproductive; Figure 1) representing 108 day-roosts and 271 day-roosting events. I recorded a mean (± SD) of 5.0 (± 1.9) locations per bat. Bats used an average of 3.1 (± 1.9) day-roosts and switched day-roosts every 2.4 (± 2.1) days. The number of day-roosts used by a bat was related to the total number of location events, but explained little of the variation in the number of day-roosts used ($\beta = 0.44$, 95% CI: $0.19 - 0.69$, $r^2 = 0.18$).

I identified 5 northern long-eared bat maternity colonies (A - E, Figures 2, 3) based on coincident day-roost use. I performed 15 exit counts across these 5 colonies, generating minimum estimated colony sizes of 13, 5, 18, 14 and 2 bats, respectively. Based on the proportion of radiotagged bats to minimum estimated colony size, I considered 3 of these colonies (A, C, and D) to be well represented as they contained > 60% of the minimum colony estimate (Table 1). Both of the incompletely represented colonies contained only 2 radiotagged bats. Fourteen of the 54 tracked bats did not use day-roosts visited by other bats and therefore were not assigned to any colony. Well-represented colonies contained between 4 and 33 day-roosts (Table 2). Hereafter, for network analysis, I report results from only well-represented colonies.

Neither roost network nor social network metrics for colony A were significantly different than those of random networks ($P > 0.05$) (Tables 1, 2). Roost networks for colonies C and D were both more centralized than my random network values ($P \leq 0.006$), though density was no different ($P \geq 0.06$) for either colony. Roost network clustering for colony D was no different than that of random networks. Colony C bat social network clustering and density values were significantly greater than those of random networks ($P < 0.05$), whereas degree centralization was significantly less ($P = 0.002$). Bat social network degree centralization and density were no different than random networks ($P > 0.05$) in colony D, but clustering was significantly greater ($P = 0.002$).

Colony core day-roosting areas were between 0.2 and 10.8 ha, and whole day-roosting areas were between and 1.3 and 59.5 ha (Figure 4). The minimum distance between two day-roosts assigned to different colonies was 322 meters, while the maximum distance (at a single site) between two colonies was 1,034 meters. I measured day-roost availability using 58

transects; the number of transects per colony corresponded with the number of located day-roosts. Overall relative availability of day-roosts was similar among networks, with between 20.5 and 26.5 possible day-roosts available for each used day-roost (Table 3).

In my simulations of the effect of day-roost removal on network fragmentation, number of network fragments in both colonies A and D increased linearly until approximately 65 - 70% of day-roosts had been removed (Figure 5). After removal of 65 - 70% of day-roosts, network fragmentation decreased but the network dissolved. Roost network division into two fragments required the simulated removal of > 20% of day-roosts.

Discussion

Using two-mode networks to represent the connections between bats and day-roosts, I identified what appeared to be multiple distinct northern long-eared bat maternity colonies. Two of the maternity colonies I identified existed in close proximity but did not overlap. Similar patterns of maternity colony day-roosting areas existing in close, but distinct, areas with minimal overlap have been observed elsewhere for the northern long-eared bat (J. B. Johnson et al. 2012) and for other species (Fortuna et al. 2009). Because my tracking periods for individual bats were short relative to the length of the maternity season, it is possible that I artificially may have represented a single colony as two distinct colonies. Indeed, my minimum distance between day-roosts in different colonies was short relative to the distances that northern long-eared bats can travel in a single night (Owen et al. 2003, Henderson and Broders 2008), but two separate lines of evidence suggest that I did not split a single colony artificially. First, movements of the 14 bats that were not assigned to a colony were almost exclusively within the day-roosting area of a single colony, and never crossed between day-roosting areas. Second, I captured the majority of my bats at day-roost trees, and captured > 60% of the bats in three of my colonies. Given the high proportion of bats within colonies that I captured, it seems unlikely that I would not have captured at least one previously banded bat if the colonies were not distinct entities at the time of observation.

Although social and roost network characteristics of some other bat species are related to total availability of day-roosts (Chaverri 2010, J. S. Johnson et al. 2012), this did not appear to be the case in my study as the total availability of potential day-roosts was similar across networks.

Relative availability of individual potential day-roost tree species, in particular sassafras (*Sassafras albidum*), could be influencing network structure as availability of potential day-roosts was inversely related to roost network centralization. In a concurrent study, Silvis et al. (2012) found that northern long-eared bats demonstrated a day-roost selection preference for sassafras over other tree species at Fort Knox. Given that the maximum distance between day-roosts in adjacent networks was only 1,034 m, well within the flight distance of a northern long-eared bat (Owen et al. 2003, Henderson and Broders 2008), if day-roost limitations were a factor determining social structure it is unclear why colonies would not take advantage of more abundant day-roosts in adjacent areas.

Reproductive status can affect association (Garroway and Broders 2007, Patriquin et al. 2010), and in some cases day-roost preferences (Garroway and Broders 2008, Silvis et al. 2012) of northern long-eared bats. Because I focused on tracking only a single colony at any given time, my colonies generally, but not exclusively, were followed during different reproductive time periods. Colony A contained primarily gestating bats, colony C contained both gestating and lactating individuals, and colony D only lactating individuals. Presence of both pregnant and lactating bats in colony C suggests that I began tracking this colony at the time of parturition. Due to my generally non-concurrent tracking periods among colonies, I cannot directly relate reproductive condition to colony social structure. I note however, that the differences in network structure that I observed among my colonies broadly are consistent with association patterns documented by Garroway and Broders (2007) and Patriquin et al. (2010) for the northern long-eared bat relative to reproductive condition. Specifically, close association around a small number of day-roosts by colony C is consistent with the closer association during this period documented by Garroway and Broders (2007). Similarly, the day-roosting social patterns that I observed are consistent with patterns previously documented for northern long-eared bats (Garroway and Broders 2007, J. B. Johnson et al. 2012) and other colonial-day-roosting bat species (Kerth and Konig 1999, Rhodes 2007, Popa-Lisseanu et al. 2008).

Social index analysis can reveal presence of preferred social groups within bat maternity colonies (Garroway and Broders 2007, Patriquin et al. 2010, J. B. Johnson et al. 2012). Because I did not conduct a social index analysis due to my relatively short tracking periods, I cannot report on the strength of association between individuals or assess temporal patterns of association. However, clustering in social networks also can be used to identify the presence of

preferentially associating groups (Watts and Strogatz 1998). In my study, higher than expected clustering values for social networks of colonies C and D suggest preferential groups, but, based on network graphs for these colonies, I only can conclude definitively that all of the bats within the colonies were closely associated at the time of observation.

Why some network metrics for some colonies differed significantly from random networks while others did not is unclear, but may be due to my short tracking periods, natural variability, or ecological factors that I did not measure. Although day-roost availability did not appear to influence network structure, my classification of day-roosts as potentially available does not necessarily capture all characteristics of a day-roost that are relevant to selection by bats. In particular, cavity characteristics of roosts may be an important factor in selection that I did not quantify.

Day-roosting areas for my two largest colonies (A and D) at both the 50% and 95% home range level were similar, despite considerable differences in the number of day-roosts used and the number of bat-days per network. Surprisingly, the centralized nature of the roost network of colony D indicated concentrated use of an individual day-roost, but relative to colony A, this did not result in a smaller day-roosting area. Concentrated use of a single day-roost did result in a substantially smaller estimate of the day-roosting area used by colony C, as would be expected given the high level of centralization in that roost network. Despite differences in patterns of day-roosting behavior, use of space within day-roosting areas was similar between colonies, with all colonies exhibiting a distinct core day-roosting area with infrequently used day-roosts distant from the core area. Interestingly, day-roosts outside core areas were not concentric around the core. Popa-Lisseanu et al. (2008) documented similar use of space within maternity colonies of giant noctule bats (*Nyctalus lasiopterus*) in a Mediterranean forest type in Spain. As they suggested, spatial concentration of day-roost use may be related to the distribution of preferred day-roosting resources. Although I did not quantify the overall distribution and density of tree species at my study sites, core day-roosting areas of colonies A and D appeared to coincide with dense clusters of sassafras.

Although my colonies appeared to be unique entities, occasional movement of individuals between colonies and day-roost sharing is probable. It is unclear whether day-roost sharing among colonies is most likely to occur at infrequently used day-roosts at the periphery of the colony day-roosting area or within the core area, but sharing day-roosts in these different

areas may have different functional value. Day-roost sharing may be inconsequential and coincidental at the periphery of day-roosting areas where day-roosts receive relatively little use. In core areas, however, day-roost sharing may serve as an important pathway for transfer of social information and disease between colonies (Fortuna et al. 2009), as the likelihood of sharing a day-roost with a bat in a different colony is expected to be greater. Fidelity to a core day-roosting area may provide social benefits by increasing ability of colonies to maintain day-roost group cohesion through social contact (Wilkinson 1992, Kerth and Reckardt 2003, Russo et al. 2005, Kerth et al. 2006). Low sample sizes and the reference method of bandwidth selection increase variance and error in utilization distributions, thereby inflating area estimates (Seaman et al. 1999, Börger et al. 2006, Gitzen et al. 2006). Here, inflated area estimates allowed me to make a liberal estimate of the extent of maternity colony day-roosting areas.

My day-roost removal simulations suggest that removal of a single random day-roost will not reduce substantially the ability of northern long-eared bats to assemble in social groups or to interact. However, removal of multiple day-roosts quickly resulted in network fragmentation, with fragmentation increasing linearly with the proportion of day-roosts removed. It is unclear whether northern long-eared bats would be able to re-establish social connections, and therefore reconstitute the network, if day-roosts are removed. Other bat species communicate day-roost and feeding sites (Wilkinson 1992, Jonker et al. 2010) and recognize familiar conspecifics (Mann et al. 2011) during flight, and overlap in foraging and day-roosting areas corresponds to association patterns in at least one species (Chaverri et al. 2007). Given the ability of other bat species to communicate in flight, and the multi-year site fidelity and association preferences documented for the northern long-eared bat (Patriquin et al. 2010, Perry 2011), it seems plausible that social connections could be re-established even if a substantial proportion of day-roosts are removed. Nonetheless, if bats are unable to re-establish social connections, day-roost loss may be a mechanism for creation or dissolution of maternity colonies on the landscape.

Removal of day-roosts may have consequences beyond fragmentation that are not modeled easily. In particular, changes in space use or resource selection may occur if individual day-roosts serve specific functions that are not replicated in other day-roosts or if a high degree of resource selection is prevalent (Brigham and Fenton 1986, Chaverri and Kunz 2011). Presumably, functional consequences of day-roost loss on space use or resource selection would be related to the magnitude of the disturbance, degree of resource specialization, and social

system of individual species. For the northern long-eared bat, robustness to day-roost loss is consistent with the ephemeral nature of snags as a forest habitat resource.

Conclusions

My results should be interpreted in the appropriate context– my study was conducted in a warm-temperate, contiguous, closed-canopy forest, where day-roosts do not appear to be limited and temperature restrictions on day-roosting social patterns may be less than those prevalent at more northern latitudes. Under these conditions, day-roost and social structure of northern long-eared bats do not appear to be related to day-roost availability. In other habitats, ecological conditions may play a greater role in social and day-roosting behavior, particularly if day-roost availability is limited (Chaverri and Kunz 2010). Additionally, my results represent only a subset of the bats within the colonies I studied from short time windows relative to the length of the maternity season. Although my different network characteristics are consistent with observations of association based on reproductive condition by Garroway and Broders (2007), my sampling design precludes me from identifying this as the cause of the network structures that I observed. My results do suggest, however, that northern long-eared bat maternity colony social structure and day-roost use patterns can vary substantially among colonies.

The degree of resource sharing by separate social groups of bats likely varies among species, but my results, as well as those of Fortuna et al. (2009) and J. S. Johnson et al. (2012), suggest that maternity colonies of tree-day-roosting bats may be unique entities on the landscape. As such, maternity colonies should be amenable to targeted management approaches, such as creation of day-roosts or scalable levels of natural forest disturbance processes or forest harvesting. Through my day-roost removal simulations, I found that maternity colony fragmentation is unlikely to occur with removals of small proportions of day-roosts, further suggesting that northern long-eared bats may respond well to direct management, or at least tolerate forest disturbance. Given that bats may be able to re-establish social connections during flight (Vonhof et al. 2004), and that individual day-roosts may serve important social functions (Brigham and Fenton 1986) or not be replaced easily (Chaverri and Kunz 2011), field experiments on day-roost removal, where day-roosts and day-roost abundance vary across

spatio-temporal scales and disturbance or successional-trajectory regimes, are needed to assess the effect of day-roost loss on the social dynamics of bats.

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Table 2.1. Social network metrics of 3 northern long-eared bat (*Myotis septentrionalis*) maternity colonies (A, C, D) on the Fort Knox military reservation, Kentucky, USA, 2011. Network metrics were calculated from the single-mode projection of the 2-mode network consisting of bats and day-roosts. *P*-values from Monte Carlo simulations and the direction of difference relative to the random networks are given in parentheses.

	A	C	D
Number of bats	8	15	13
Mean bat degree	3.5	14	4.61
Degree centralization	0.35 (0.89)	0.00 (<, 0.002)	0.28 (0.09)
Clustering coefficient	0.64 (0.25)	1.00 (>, 0.002)	0.74 (>, 0.002)
Density	0.50 (0.36)	1.00 (>, 0.002)	0.38 (0.23)

Table 2.2. Day-roost network metrics of 3 northern long-eared bat (*Myotis septentrionalis*) maternity colonies (A, C, D) on the Fort Knox military reservation, Kentucky, USA, 2011. Network metrics were calculated directly from the two-mode network consisting of bats and day-roosts. *P*-values from Monte Carlo simulations and the direction of difference relative to the random networks are given in parentheses.

	A	C	D
Number day-roosts	21	4	33
Total relocations	41	88	75
Mean day-roost use	1.95	22.00	2.27
Network degree centralization	0.30 (0.50)	0.99 (>, 0.002)	0.44 (>, 0.006)
Network clustering	0.57 (0.22)	0.00 (NA)	0.57 (0.07)
Network density	0.19 (0.11)	0.30 (0.06)	0.14 (0.14)
Core (50%) day-roosting area (ha)	10.04	0.22	12.11
Whole (95%) day-roosting area (ha)	45.26	1.30	50.00

Table 2.3. Relative availability day-roosts by species and colony (A, C, D) for the 10 most relatively potentially available tree species on the Fort Knox military reservation, Kentucky, USA, 2011. Potentially available day-roosts were those trees with visible cavities or exfoliating bark found on 20 × 100-m belt transects oriented at random azimuths from each day-roost. Counts were standardized by the number of day-roosts used in each group; counts of used day-roosts for each group are presented in Table 1.

	A	C	D	Standardized Total
Sassafras (*Sassafras albidum*)	12.60	3.50	5.45	38.58
Sugar Maple (*Acer saccharum*)	4.00	7.25	3.30	19.28
White Ash (*Fraxinus americana*)	0.45	2.25	2.12	7.40
Black Locust (*Robinia pseudoacacia*)	2.20	1.75	0.67	6.19
Shagbark Hickory (*Carya ovata*)	0.55	0.25	1.64	5.51
White Oak (*Quercus alba*)	0.95	0.75	1.21	3.99
Chinkapin Oak (*Quercus muhlenbergii*)	0.00	0.75	1.94	3.86
Eastern Redbud (*Cercis canadensis*)	0.95	0.50	1.27	3.47
Northern Red Oak (*Quercus rubra*)	0.55	0.75	0.88	2.75
Yellow poplar (*Liriodendron tulipifera*)	0.75	0.50	0.18	2.26
…	…	…	…	…
Standardized Total	26.05	20.50	22.58	107.73
Count Total	521.00	82.00	745.00	1607.00
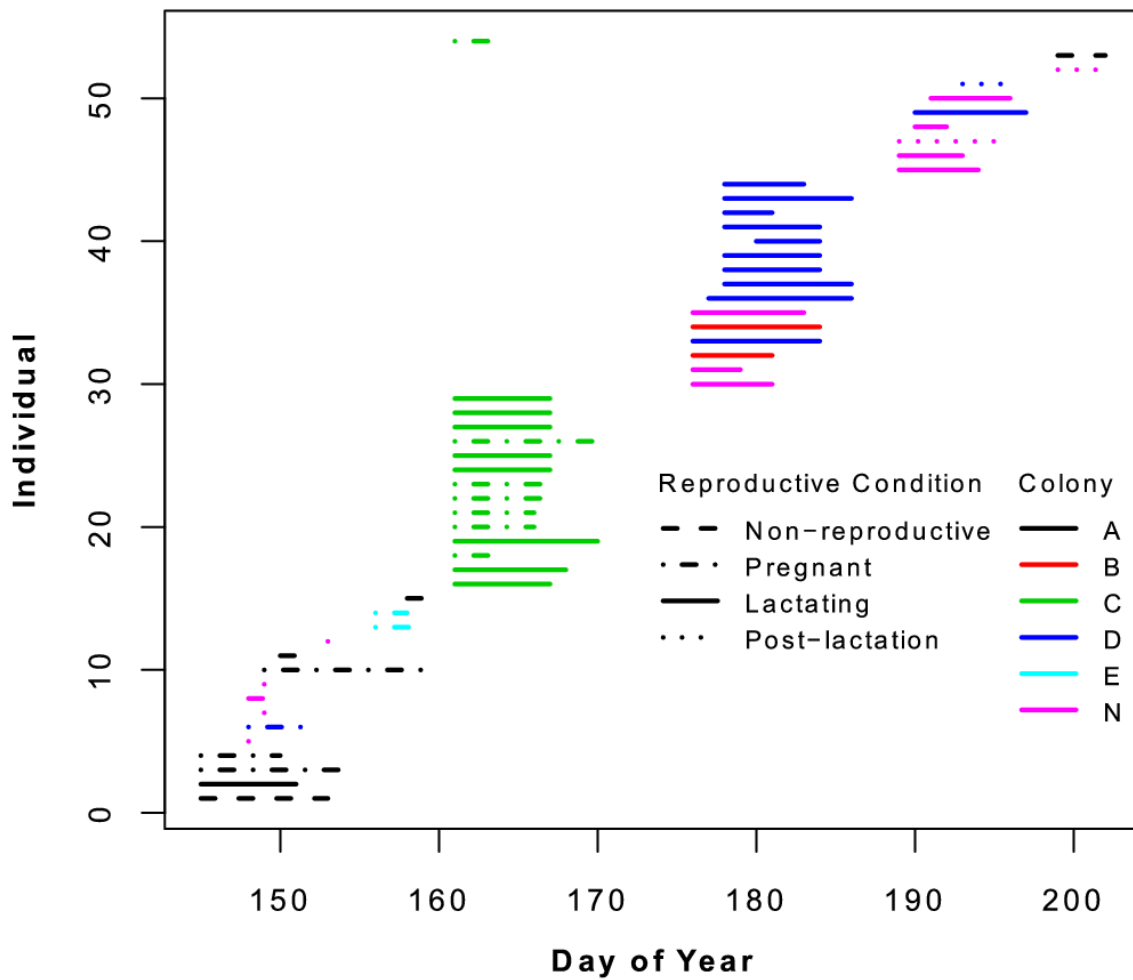
Figure 2.1. Observation windows of female northern long-eared bats (*Myotis septentrionalis*) tracked on the Fort Knox military reservation, Kentucky, USA, 2011. Each line represents the time window that an individual bat was tracked. Date is presented as day of year; colony identification and reproductive status are given; bats in colony "N" were those that never shared a day-roost with another bat.
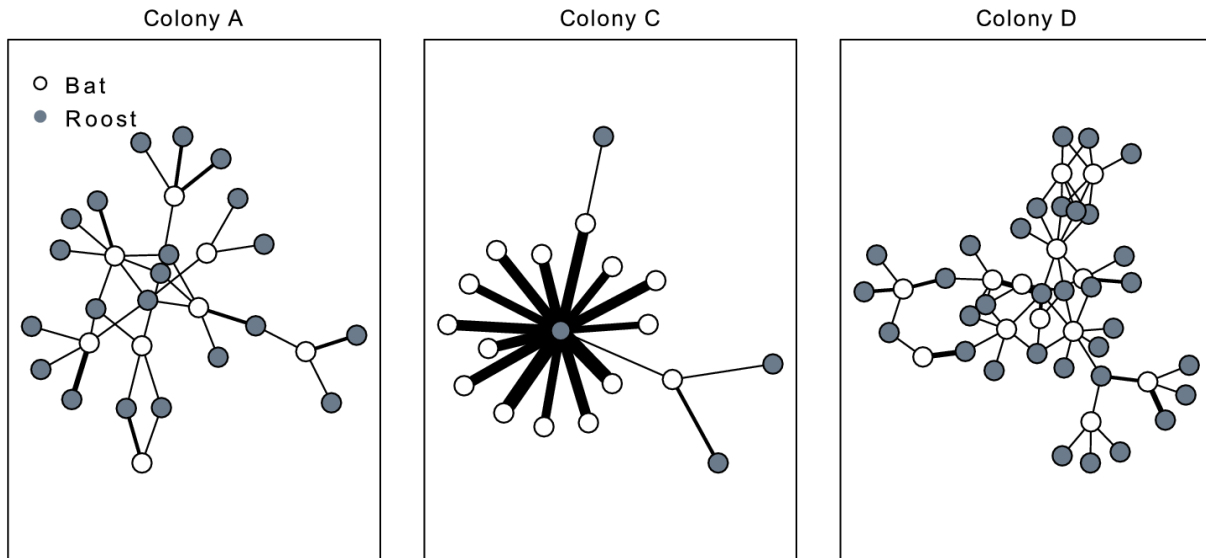
Figure 2.2. Two-mode graph representations of 3 northern long-eared bat (*Myotis septentrionalis*) maternity colony roost networks (A, C, D) on the Fort Knox military reservation, Kentucky, USA, 2011 showing the connections between bats and day-roosts. Bats are shown as white nodes and day-roosts are shown as grey nodes. Edge width is scaled by the number of connections between a bat and an individual day-roost.
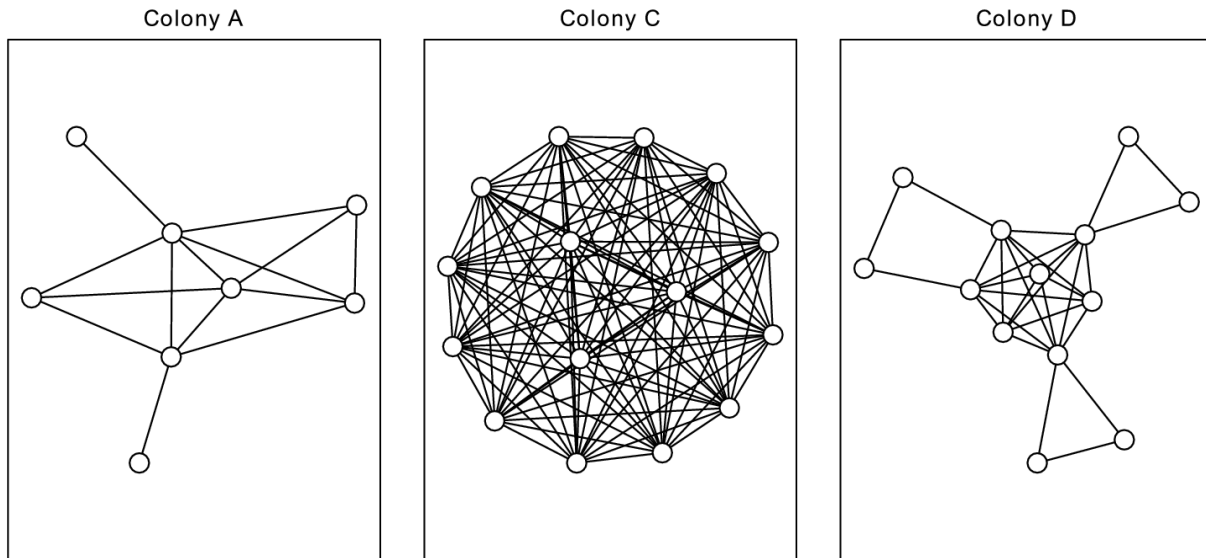
Figure 2.3. Single-mode graph representation of the social networks of 3 female northern long-eared bat (*Myotis septentrionalis*) maternity colonies (A, C, D) on the Fort Knox military reservation, Kentucky, USA, 2011. Association was attributed to a dyad when day-roost use was coincident between the two.
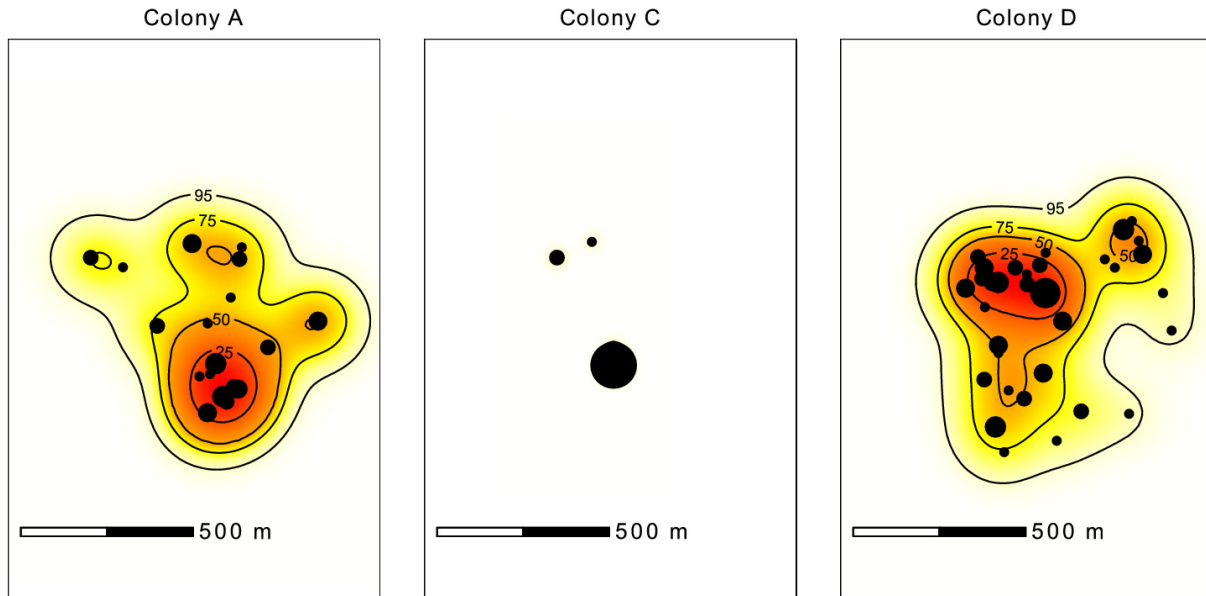
Figure 2.4. Bivariate fixed-kernel density utilization distributions and day-roost locations for 5 female northern long-eared bat (*Myotis septentrionalis*) maternity colonies (A, C, D) on the Fort Knox military reservation, Kentucky, USA, 2011. Day-roost sizes are scaled by ln(Degree + 1) to show the relative contribution of each day-roost in calculation of the utilization distribution. See table 2 for complete network values and area estimates for the 50 and 95% utilization distributions.
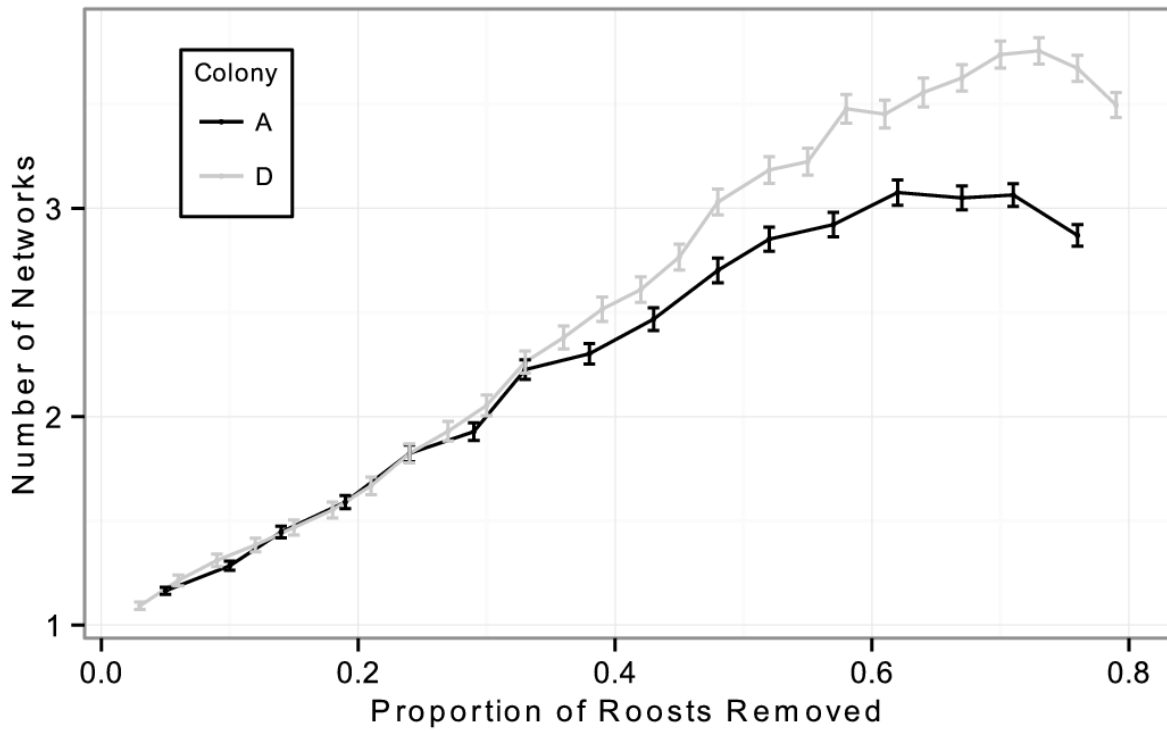
Figure 2.5. Simulated effect of node removal on the fragmentation of two female northern long-eared bat (*Myotis septentrionalis*) roost networks (colonies A, D) on the Fort Knox military reservation, Kentucky, USA, 2011. Random node removal was performed 500 times per proportion of nodes removed; mean and standard error of the number of resultant networks per proportion of nodes removed are presented.

Chapter 3: Effects of Hierarchical Day-roost Removal on *Myotis septentrionalis* Maternity Colonies

Alexander Silvis

Abstract

Forest roosting bats use a variety of day-roost types, including snags and declining live trees that are considered ephemeral. Although conservation of summer maternity habitat is considered critical for forest-roosting bats, bat response to day-roost loss still is poorly understood. To address this, I monitored 3 northern long-eared bat (*Myotis septentrionalis*) maternity colonies on Fort Knox Military Reservation, Kentucky, USA, before and after targeted day-roost removal during the dormant season when bats were hibernating in caves. I used 2 treatments: removal of a single highly used (primary) day-roost and removal of a quarter of less used (secondary) roosts, and an un-manipulated control. Day-roost removal did not alter the number of roosts used by individual bats, but secondary day-roost removal doubled the distances moved between sequentially used roosts. Overall space use by and location of colonies was similar pre- and post-treatment. Patterns of day-roost use before and after removal treatments also were similar; bats maintained closer social connections after my treatments. Day-roost diameter at breast height, height, percent canopy openness at roosts, and day-roost species composition were similar pre- and post-treatment. I detected differences in the distribution of roosts among decay stages and canopy positions pre- and post-day-roost removal, but this may have been a result of temperature differences between treatment years. My results suggest that loss of limited numbers of roosts in the dormant season may not cause northern long-eared bats to abandon roosting areas or substantially alter roosting behavior in the following active season when tree-roosts are used. Increased understanding of the response of northern long-eared bats to day-roost loss can be used to improve future conservation efforts by placing focus on determining thresholds for response to forest management or disturbance and other major stressors.

Introduction

Roosts provide bats with sites for day-time sheltering as protection from weather and predators, mating, and social interaction. For species in temperate areas that form maternity groups in forested landscapes, roosts also provide thermal benefits for successful juvenile

development (Grindal et al. 1992, Willis et al. 2005, Speakman 2008, Frick et al. 2010). Because of their importance in both survival and recruitment, roosts long have been considered a critical habitat feature for bats (Fenton 1997, Kunz and Lumsden 2003). Approximately half of all known bat species use plants as roosts (Kunz and Lumsden 2003); in North America, roosts most commonly are found in snags or live trees with cavities or defects. Roosts such as snags in forests are ephemeral (Moorman et al. 1999, Wisdom and Bate 2008); bats therefore must be adaptive to day-roost loss. This plasticity often is ignored as many managers tasked with bat conservation often view roosts and roosting areas as fixed landscape elements that are decoupled from stochastic environmental processes (Dixon et al. 2013, Stone et al. 2013).

Bat conservation in forested landscapes often involves identification of day-roost sites with subsequent limitations on management activities (e.g., forestry) within these areas. Conservative approaches to day-roost habitat management may seem warranted, but this strategy may interrupt natural processes or anthropogenic management actions that are vital to create suitable roosts in the present or provide roosts in the future. However, impact of management actions that result in day-roost loss are unknown as few studies directly have assessed the effect of day-roost loss on bat roosting behavior in controlled, manipulative studies. Evidence from day-roost exclusion studies suggests that exclusion from permanent structures can decrease site fidelity, alter home range size, lower reproductive recruitment, and reduce colony size and the strength of association among individuals (Brigham and Fenton 1986, Neilson and Fenton 1994, Borkin et al. 2011, Chaverri and Kunz 2011). However, several lines of evidence suggest that forest roosting bats may be tolerant of day-roost loss up to some threshold point. For example, prescribed fires in forests can result in rapid, increased snag recruitment, offsetting the loss of existing snags (Signell et al. 2005, Bagne et al. 2008, Hutchinson et al. 2008) with bats sometimes showing a positive roosting response thereafter at short-term and long-term temporal scales (Boyles and Aubrey 2006, Johnson et al. 2009, 2010, Lacki et al. 2009, Womack et al. 2013). Clearly, natural forest disturbance processes can remove but also create bat roosts. This is in contrast to many types of forest harvest that remove potential and available roosts without creating new roosts in the short-term. However, if applied on the landscape properly, it is possible that harvesting may mimic natural processes that also create suitable roosting areas. As such, ephemerality of the day-roost resource strongly suggests that bats experience day-roost loss at some low constant background level, with periodic pulses of increased day-roost loss after

intense disturbances from fire, wind throw, ice damage, insect outbreak, or certain types of forest management actions (McShea and Healy 2002, Menzel et al. 2002*a*, Lorimer and White 2003, Copenheaver et al. 2006).

Tolerance limits to day-roost loss are unclear and probably highly variable among species and the forest systems wherein they reside (Brigham and Fenton 1986, Neilson and Fenton 1994, Borkin et al. 2011, Chaverri and Kunz 2011, Silvis et al. 2014*a, b*). For colonial species, insight into the impacts of day-roost loss will require understanding both of individual and colony level factors (Rhodes et al. 2006). Responses to day-roost loss may be apparent in demographics, survival, day-roost use, space use, and sociality. Assessment of demographic changes may be exceedingly difficult for bats that day-roost-switch frequently and exhibit fission-fusion behavior. Within the context of day-roost use, resilience to day-roost loss generally may be visible as either a shift in overall uses of individual roosts without a change in overall space use or social structure, or as a shift in roosting area and roosts without a change in social structure. Conversely, if colonies are not robust to disturbance, the colony may either dissolve such that social structure at the site is not maintained, or dissolve to the point where no bats are present on the site (Silvis et al. 2014*a*). Within the network of roosts used by colonies of bats, individual roosts frequently are used differentially, with some receiving intense use (primary roosts) and others limited use (secondary roosts) (Rhodes et al. 2006, Fortuna et al. 2009, J. S. Johnson et al. 2012). Day-roost switching studies have provided insight on why bats may switch roosts, but the underlying causes for differences in the relative level of day-roost use have not been investigated widely. Regardless, differential day-roost use suggests that individual roosts may either serve different functions for colonies and individual bats therein or vary in value. If so, loss of heavily used or primary roosts may impact colonies more strongly than loss of less frequently used roosts (Rhodes et al. 2006, Silvis et al. 2014*b*).

My objective was to experimentally examine how hierarchical loss of roosts affects roosting social structure and day-roost and space use by female northern long-eared bats (*Myotis septentrionalis*), a proposed endangered species currently of very high conservation concern in North America (*Federal Register* § 78:61045-61080) due to severe population declines following White-nose Syndrome, during the maternity season at both the colony and individual level. Northern long-eared bats occur in forests throughout the eastern United States and southern Canada (Foster and Kurta 1999, Lacki and Schwierjohann 2001, Menzel et al. 2002*b*,

Broders et al. 2006, Perry and Thill 2007, Morris et al. 2010, J. B. Johnson et al. 2012), but foraging activity consistently is greatest in closed-canopy forests (Jung et al. 1999, Menzel et al. 2002b, Owen et al. 2004, Brooks and Ford 2005, Ford et al. 2005, 2006a, Loeb and O'Keefe 2006). During the maternity season (May-July), female northern long-eared bats form non-random assorting colonies in upland forests under the exfoliating bark or within cavities of snags or declining live trees (Lacki and Schwierjohann 2001, Menzel et al. 2002a, Owen et al. 2004, Perry and Thill 2007). I assessed changes in colony day-roost and space use, day-roost selection, and social structure, as well as changes in individual behaviors related to day-roost switching. I specified several *a priori* hypotheses related to the differing levels of day-roost site disturbance. For primary day-roost tree removal, I proposed 2 hypotheses:

1. H_1: At the colony level, loss of the primary day-roost will result in an alternate tree receiving increased use, subsequently causing a previously less-used day-roost to become the primary day-roost; bats will not display evidence of day-roost seeking behavior. Bats will display an affinity for the same roosting area, but the core use area would re-center around the new primary day-roost, and day-roost selection would be consistent. At the individual level, loss of the primary day-roost will not impact day-roost switching behavior or distances moved between sequentially used roosts. Day-roost characteristics will not differ.

2. H_2: At the colony level, loss of the primary day-roost will result in dissolution of the colony. Space use will either be random across the former roosting area or will be nonexistent. Bats will display characteristics of day-roost searching, and the characteristics of selected roosts will differ. At the individual level, loss of the primary day-roost will increase day-roost switching frequency and the distances moved between sequentially used roosts. Day-roost characteristics will differ.

For secondary day-roost loss, I proposed three hypotheses:

1. H_1: At the colony level, loss of multiple secondary roosts will not impact roosting behavior, social structure, space use, or day-roost selection by northern long-eared bat maternity colonies. At the individual level, loss of multiple secondary roosts will not impact day-roost switching behavior or distances moved between sequentially used roosts. Day-roost characteristics will not differ.

2. H_2: At the colony level, loss of multiple secondary roosts will result in dissolution of the colony. Space use will either be random across the former roosting area or will be nonexistent. Bats will display characteristics of day-roost searching and day-roost characteristics will differ. At the individual level, loss of multiple secondary roosts will increase day-roost switching frequency and the distances moved between sequentially used roosts.

3. H_3: At the colony level, loss of multiple secondary roosts will result in increased social cohesion and increased use of the primary day-roost, and roosting area will decrease. Day-roost characteristics will not differ. At the individual level, loss of multiple secondary roosts will decrease the number of roosts used by individual bats and the distances moved between roosts.

Methods

I conducted my study at 3 sites on the Fort Knox military reservation in Meade, Bullitt, and Hardin Counties, Kentucky, USA (37.9°N, -85.9°E, WGS84) from May through July 2011 (pre-day-roost removal) and 2012 (post-day-roost removal). My sites are predominantly western mixed-mesophytic deciduous forest and lie in the Western Pennyroyal subregion of the Mississippian portion of the Interior Low Plateau physiographic province of the upper South and lower Midwest portion of the USA (Arms et al. 1979). Forest cover is predominantly a western mixed-mesophytic association (Braun 1950), with second- and third-growth forests dominated by white oak (*Quercus alba*), black oak (*Q. velutina*), chinkapin oak (*Q. muehlenbergii*), shagbark hickory (*Carya ovata*), yellow poplar (*Liriodendron tulipifera*), white ash (*Fraxinus americana*), and American beech *(Fagus grandifolia*) in the overstory, and sassafras (*Sassafras albidum*), redbud (*Cercis canadensis*), and sugar maple (*Acer saccharum*) in the understory (Cranfill 1991).

I initially captured northern long-eared bats over small woodland pools and attached a radiotransmitter (LB-2, 0.31 g: Holohil Systems Ltd., Woodlawn, ON, Canada) between the scapulae of each female bat using Perma-Type surgical cement (Perma-Type Company Inc., Plainville, CT, USA). A uniquely numbered lipped band was attached to the forearm of all captured bats. I maximized number of bats captured by erecting mist nets around roosts located while radiotracking bats. Captured bats were released within 30 minutes of capture at the net site.

I attempted to locate radiotagged bats daily for the life of the transmitter or until the unit dropped from the bat. For each located day-roost, I recorded tree species, diameter at breast height (dbh; cm), height (m), canopy openness (%), decay class (Cline et al. 1980; live [1], declining [2], recent dead [3], loose bark [4], no bark [4], broken top [6], broken bole [7]) and crown class ((Nyland 2002); i.e., suppressed [S], intermediate [I], codominant [CO], dominant [D]). I estimated size of individual colonies by performing 5 exit counts per colony at day-roosts used by radiotracked bats.

I followed the methods of Silvis et al. (2014*a*) in defining a northern long-eared bat maternity colony as all female and juvenile bats connected by coincident day-roost use. I represented colonies graphically and analytically as two-mode networks that consisted of bats and roosts (hereafter "day-roost network") (Fortuna et al. 2009, J. S. Johnson et al. 2012). I used these day-roost network representations to describe patterns of day-roost use by colonies and to identify roosts for my removal treatments. To reduce bias resulting from uneven tracking periods and observing only a portion of each colony, I considered relationships to be binary (i.e., presence or absence of a connection) (Goodreau et al. 2009). I assessed day-roost network structure using mean degree, network degree centralization, network density, and clustering. Within networks, degree is a count of the number of edges incident with a node (Boccaletti et al. 2006); high degree values indicate a large number of connections to a node. 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 nodes, whereas network density and clustering describe the distribution of connections among nodes (Freeman 1978, Wasserman and Faust 1994, Borgatti and Everett 1997, Watts and Strogatz 1998, Dong and Horvath 2007). I calculated two-mode degree centralization and density using the methods of Borgatti and Everett (1997) and clustering using the method of Opsahl (2009) for my day-roost network. To determine whether my observed network values differed from those of random networks I performed 999 Monte Carlo simulations and compared observed network metrics to random network metrics using two-tailed permutation tests (Hope 1968, Davison 1997); random networks (Erdős and Rényi 1960) were generated with the same number of nodes as my observed networks and with a constant probability of link establishment. I then compared the relative difference from random networks pre-post treatment to assess whether colony social dynamics and day-roost use patterns were disrupted.

I designated 2 treatment groups and 1 control following identification and analysis of day-roost use by colonies tracked in 2011. For my primary day-roost removal treatment, I felled via chainsaw the single day-roost with the highest degree centralization value. I felled 5 roosts with degree centralization values less than the colony maximum, but greater than the colony minimum in my secondary day-roost removal treatment group, to specifically test the simulation-based predictions of Silvis *et al*. (2014*a*) that colonies may fragment with loss of ~20% of roosts. Secondary roosts were selected randomly among all that met these day-roost-use characteristics. I removed all roosts during the winter of 2012 when bats were hibernating and were not occupants of trees and snags.

I used conditional Wilcoxon 2-sample tests and conditional Chi-squared tests to compare continuous and categorical day-roost characteristics (respectively) pre- and post-treatment and among groups; I corrected for multiple comparisons using the Bonferroni method. Conditional tests were performed using Monte Carlo simulations with 999 permutations. I examined the day-roost switching behavior of individual bats by creating a Poisson regression model describing the number of roosts used by a bat relative to the total number of relocations, reproductive condition, and treatment identity with a multiplicative interaction. I used this Poisson model to conduct general linear hypothesis tests with Tukey's adjustment for multiple comparisons to determine whether the number of roosts used by bats differed within or among treatment areas. I evaluated the fit of my Poisson model using maximum-adjusted D^2 (Guisan and Zimmermann 2000). I assessed the spatial component of day-roost switching behavior by individual bats by comparing the distances that bats within treatment areas moved between sequentially used roosts with general linear hypothesis tests with Tukey's adjustment for multiple comparisons. I performed my general linear hypothesis tests on a linear mixed model containing year, group, their interaction term, and reproductive condition as fixed effects, and bat identity as a random effect; I used a log transformation to normalize distance data. I assessed the fit of my linear mixed model using the conditional (R^{2c}) and marginal (R^{2m}) coefficients of determination (Nakagawa and Schielzeth 2013).

I evaluated day-roost removal impacts on colony roosting area space use for each treatment group using Bhattacharya's affinity (BA) (Fieberg and Kochanny 2005) and the difference in roosting area centroids between years. BA uses the joint distribution of 2 utilization distributions to quantify similarity between utilization distributions and is appropriate for

comparisons of utilization distributions for the same individual or group (Fieberg and Kochanny 2005). These values range from 0 to 1, with values close to 1 indicating highly similar utilization distributions (Fieberg and Kochanny 2005). I calculated 95% utilization distributions from the pooled locations of all bats within a colony using bivariate normal fixed kernel methodology. To reflect the concentration of day-roost use, I weighted day-roost locations by the number of times a day-roost was used by radio-tagged bats (Popa-Lisseanu et al. 2008). I used the reference method for smoothing parameter estimation as appropriate for weighted locations (Gitzen et al. 2006), that also allowed us to consider my estimates of colony space use as liberal. In cases where roosting areas of separate colonies overlapped to a large extent, I calculated the utilization distribution overlap index (UDOI) to determine if space use was independent; UDOI values range from 0 to infinity, with values <1 indicating independent space use, and values >1 indicating non-independence (Fieberg and Kochanny 2005).

I assessed overall changes in colony day-roost use patterns by comparing pre- and post-day-roost removal network degree centralization, density, and clustering for the day-roost networks. I used this same comparative network approach to assess changes in colony roosting social structure as given by the single mode projections of my 2-mode day-roost networks. Because comparing values from networks of differing size may yield inappropriate inferences (James et al. 2009), I used indirect comparisons of network characteristics. In these, I compared the relative difference between a day-roost or social network and its equivalent random network pre- and post-treatment. All analyses were performed in the R statistical program version 3.0.2 (R. Development Core Team 2014). I calculated conditional tests using the *coin* package (Hothorn et al. 2006), linear mixed models using *lme4* (Bates et al. 2014), and utilization distributions, BA, and UDOI values using the *adehabitatHR* package (Calenge 2006). I used the *igraph* (Csardi and Nepusz 2006) and *tnet* libraries (Opsahl 2009) to visualize networks and calculate metrics. Network Monte Carlo simulations were performed using a custom script with dependencies on the *igraph* and *tnet* libraries. I used an $\alpha = 0.05$ for all tests of statistical significance.

Results

I captured 58 female northern long-eared bats in 2011. Based on patterns of coincident day-roost use, I assigned 36 of these bats (11 gestating, 20 lactating, 1 post lactation, and 4 non-

reproductive) to 3 colonies. Exit counts for these 3 colonies generated minimum estimated colony sizes of 13, 18, and 14 bats, respectively. I captured 67 bats in 2012, 62 of which (4 gestating, 45 lactating, 10 post lactation, and 3 non-reproductive) I was able to assign to the 3 colonies identified in 2011. I recaptured only 3 individuals banded in 2011 during 2012. Exit counts indicated that the 2012 colonies contained a minimum of 24, 20 and 25 bats, respectively. I located 58 roosts over 204 relocation events for the 3 colonies identified in 2011 and 100 roosts (7 of which were used in 2011) over 324 relocation events in 2012. I recorded a mean (± SD) of 5.7 (± 1.5) locations per bat in 2011 and 5.2 (± 2.9) in 2012.

I identified between 4 and 33 roosts per colony pre-day-roost removal, and between 23 and 42 roosts per colony post-removal (Table 1). When controlling for the total number of relocations of an individual bat and reproductive condition, the number of roosts used by individual bats was similar between pre- and post-treatment and among colonies, with the exception of the control colony, pre-removal, that differed from all other groups (model D^2 = 0.74; Tables 1, 2).

Neither day-roost dbh nor height differed between treatments or among colonies (Table 3). Canopy openness was similar between pre- and post-treatment, but some individual colonies differed from one another (Table 3). Distribution of roosts among decay stages differed pre- and post-treatment within the primary removal colony but not in the control colony or the secondary removal colony (Table 3). Distribution of roosts among canopy positions differed pre- and post-treatment for the primary removal colony but not in the control or secondary removal colony (Table 3). Distribution of roosts among decay stage and canopy positions did differ among colonies in some cases (Table 3). I found no difference in day-roost species composition between pre- and post-treatment or among any of my groups (Table 3). Sassafras (*Sassafras albidum*) was the most commonly used day-roost species, accounting for between 43 and 57% of roosts used in each group.

Distances moved between sequentially used roosts were non-normally distributed with right skew; median distances were between 111.1 and 219.4 m (Table 1). Distances between sequentially used roosts differed only pre- and post-day-roost removal in my secondary day-roost removal treatment group (model R^{2c} = 0.18, R^{2m} = 0.08; Tables 1, 4). Overall colony roosting areas were between 1.3 and 58.5 ha (Table 1). Patterns of roosting area space use largely were consistent between pre- and post-treatment in my primary and secondary day-roost removal

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treatment groups, particularly evident in the distances between weighted colony roosting area centroids (Table 1, Figure 1). However, space use by and roosting area centroids of my control colony differed substantially between years (Table 1).

Day-roost network degree centralization significantly was greater than random for all groups except the secondary day-roost removal colony pre-treatment (Table 1). Day-roost network clustering differed from random networks in both the primary and day-roost removal colonies post-treatment, but, for all other colonies, there was no difference from random networks (Table 1). Day-roost network density did not significantly differ from random networks for any group (Table 1). As represented in the social networks, bats shared between 3.5 and 15.9 social connections with other bats within colonies (Table 5). Social network degree centralization differed from random networks only for the control colony pre-treatment and the primary day-roost removal treatment post-treatment; the former was significantly less than and the latter significantly greater than equivalent random networks (Table 5). Social network clustering significantly was greater than that of random networks for all groups except the secondary day-roost removal treatment group pre-treatment (Table 5). Social network density did not differ from random networks pre-treatment, but was greater in all other cases (Table 5).

Visual inspection of the day-roost network maps indicated that the secondary day-roost removal colony was split into 2 groups connected by a single day-roost post-treatment (Figure 2). Because these 2 halves possibly represented 2 separate colonies connected by a single 'chance' day-roost use, I conducted a *post-hoc* analysis wherein I removed the day-roost connecting the 2 network sections (Subcolony 1 and Subcolony 2) and re-calculated spatial metrics. Roosting area was 46.37 ha for Subcolony 1 and 27.43 ha for Subcolony 2. Roosting areas of these 2 sections overlapped substantially (UDOI = 1.26).

Discussion

Day-roost removal treatments did not result in abandonment of roosting areas by northern long-eared bats – a finding conveying tremendous conservation implications for this species and perhaps other bats in temperate deciduous forested environments. Colony persistence after exclusion from a day-roost also has been observed in big brown bats (*Eptesicus fuscus*) in northern forest-prairie transitions zones in Canada (Brigham and Fenton 1986) and disc-winged bats (*Thyroptera tricolor*) in Costa Rican tropical forests (Chaverri and Kunz 2011) that both

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exhibit day-roost switching behavior roughly similar to that of the northern long-eared bat. In contrast, little brown bats (*Myotis lucifugus*), which form larger colonies and day-roost-switch less than northern long-eared bats, appear to abandon roosting areas after exclusion (Neilson and Fenton 1994). Persistence after day-roost loss may be related to the greater number of roosts used by colonies and to day-roost ephemerality. Day-roost fidelity is less in species with more ephemeral roosts (Lewis 1995), therefore, having a variety of alternate roosts or some degree of flexibility in what roosts may be selected may be an adaptation for tolerating day-roost loss for the northern long-eared bat.

Although exclusion resulted in larger individual roosting home ranges in disc-winged bats (Chaverri and Kunz 2011) and day-roost loss resulted in smaller home ranges in New Zealand long-tailed bats (*Chalinolobus tuberculatus*) (Borkin et al. 2011), colony roosting areas did not appear to change as a result of day-roost removal treatments. Increased home range size in disc-winged bats presumably was related to the need to locate a limiting resource – suitable roosts (Chaverri and Kunz 2011). In contrast to disc-winged bats, northern long-eared bats are not extreme day-roost specialists (Foster and Kurta 1999, Carter and Feldhamer 2005, Timpone et al. 2009) and potential roosts are not limited on my sites (Silvis et al. 2012). On the other hand, decreased home range size in New Zealand long-tailed bats as a result of day-roost loss following clear-cutting, probably reflects the lack of available roosts and alternative roosting areas in the harvested areas (Borkin et al. 2011). Locally, large numbers of available roosts may explain why so few roosts were used in both years of my study and why colony locations did not change.

It was surprising that so few roosts were used both pre- and post-treatment, but could be the result of tracking different bats in each year. I captured a substantial proportion of the bats within individual colonies. As such, it is unlikely that my low recapture rate was due to sampling effort. Regardless, day-roost removal treatments did not impact the number of roosts used by individual bats within treatment areas when controlling for the number of total locations and reproductive condition. The lack of difference in the number of roosts used is in contrast to Borkin *et al.* (2011), who found that bats used fewer roosts post-day-roost loss. The number of roosts used per bat was fewer in 2011 than in 2012 in my control colony, but this is likely due to the fact that the colony was tracked during parturition in 2011 (Olson and Barclay 2013); the number of roosts used per bat in the control colony in 2012 was consistent with that of all other

groups. Given the positive relationship between the number of roosts located and the number of days a bat was tracked, differences in the total number of roosts located per colony were not unexpected.

Northern long-eared bats are known to exhibit inter-annual site fidelity of at least 5 years in a mixed pine-deciduous system in Arkansas (Perry 2011), but my low recapture rates relative to my sampling effort suggest that bats marked during the first year of my study were not present in the second. Whether this is due to high annual adult mortality or some other socio-spatial assortment dynamic is unknown, but Perry (2011) also recaptured few banded individuals. Consistent patterns of space use between years suggest that, although colony composition changed, colony identity did not. Northern long-eared bat maternity colonies (Patriquin et al. 2013) as well as some other species (Metheny et al. 2008) contain maternally-related individuals, and it is possible that primarily juveniles from the first year returned in the second. In the context of having tracked different bats within colonies, my data may be interpreted best not as changes in behavior of individual bats resulting from removal treatments, but as differences in patterns of behavior at my treatment sites.

Day-roost decay stage and canopy position in the primary removal colony were the only day-roost characteristics to differ between pre- and post-treatment. Selection for more advanced stages of decay in 2011 appears to be correlated with canopy position, as trees in advanced stages of decay at my sites are primarily in suppressed canopy positions. Although the difference in decay stage and canopy position pre- and post-treatment is statistically significant only for the primary removal colony, a similar trend in reduced selection for suppressed roosts in later stages of decay is visible across all colonies in 2012. Although it is possible that by random chance day-roost removal caused the difference in day-roost decay stage and canopy position in my findings, given the lack of difference between day-roost dbh, height, and canopy openness in the primary removal colony, this seems unlikely. Higher summer temperatures in 2011 than in 2012 on my study site may have caused bats to select trees in more suppressed canopy positions, thereby reducing solar heating of roosts. Mean minimum temperature during June–July was 1.78 C° greater in 2011 than in 2012 (National Oceanic and Atmospheric Administration station GHCND: USC00154955); similarly small differences in temperature differences have been found to affect day-roost selection by Bechstein's bats (*Myotis bechsteinii*) (Kerth et al. 2001) and development of juvenile greater mouse-eared bats (*Myotis myotis*) (Zahn 1999). In contrast

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to Chaverri and Kunz (2011), I observed no change in day-roost species selection post-day-roost removal. This is consistent with the high day-roost availability at my sites (Silvis et al. 2014*a*), and suggests that day-roost removal did not impact negatively the ability of bats to find suitable roosts.

Patterns of northern long-eared bat day-roost use and association, as assessed through day-roost and social networks, displayed a mix of random and non-random characteristics. The overall character of day-roost networks relative to random networks was similar within and among treatments. Although there were minor differences in day-roost and social networks pre- and post-treatment, northern long-eared bat social network structure changes with reproductive condition (Garroway and Broders 2008, Patriquin et al. 2010). When accounting for reproductive condition, the character of the day-roost networks post-treatment differed only for day-roost network clustering. The change in day-roost network clustering from not significantly different from random networks to significantly greater than random networks also was reflected through increased social network density. An increase in day-roost network clustering and social network density may be an adaptive response to maintain colony stability after day-roost loss. Such an adaptive response to day-roost loss could suggest co-evolution between northern long-eared bats and the mixed mesophytic forest systems, but replication of my study across more regions and forest types is required to document this.

For the secondary day-roost removal colony, I observed a segmented day-roost network and the only statistically significant difference in the distance moved between sequentially used roosts. Division of this network into 2 halves as a result of the removal of ~20% of roosts is consistent with previous simulation based outcomes showing that loss of approximately 20% of roosts would generate a 50% chance of colony fragmentation (Silvis et al. 2014*a*). Connection of the 2 halves of this network by a single day-roost could suggest that an incomplete division of the colony or detection of a false connection between 2 separate colonies. An incomplete division may indicate that colony fragmentation occurs incrementally as roosts are lost, an outcome that theoretically should be most likely to occur if individual roosts are important locations for social interaction. Incomplete colony fragmentation is consistent with my finding that the 2 sections of this colony shared a single roosting area – an observation that was contrary to my *a priori* prediction that colony fragmentation would result in random use of the roosting area, but which may be related to the difference in distances moved between roosts by bats in

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this colony. Conversely, apparent division also could be the result of unwarranted joining of two separate neighboring colonies as a result of chance use of single day-roost. Silvis et al. (2014*a*) speculated that day-roost sharing may be infrequent and inconsequential at the periphery of the roosting area for northern long-eared bats. In this case, the shared day-roost was not at the periphery of the colony roosting area and the roosting areas of the 2 sections of the colony overlapped extensively in terms of both extent and concentration of use. Research from other bat species in both temperate and tropical regions suggests that roosting areas relatively are exclusive to individual colonies (Fortuna et al. 2009, Borkin et al. 2011, J. S. Johnson et al. 2012). Whether this apparent fragmentation is a result of day-roost removal treatments or some other process remains speculative.

Conclusions

In their review of conservation concerns for bats in the United States, Weller et al. (2009) identified a need to transition conservation priorities from focal threats to diffuse threats. In the context of the White-nose Syndrome enzootic that is threatening many species, including the northern long-eared bat, with widespread extirpation, it is necessary to link focal and diffuse threats through understanding of the impacts of specific changes to roosting habitats. Although my study contains limited replicates of my individual treatments, it is, to my knowledge the only study to perform targeted day-roost removal treatments for colonial bats in a temperate forest ecosystem. Clearly, caution should be taken in interpreting the results of individual treatments, particularly with regard to changes in day-roost and social network structure. However, my results are consistent with previous predictions and anecdotal observations that northern long-eared bats are robust to low levels of day-roost loss (Johnson et al. 2009, Lacki et al. 2009). My results also are consistent with predictions that temperate bats that use ephemeral day-roost resources should be tolerant of day-roost loss at or below rates of tree mortality in temperate forests (Moorman et al. 1999, Runkle 2012). However, the maximum levels of day-roost loss that northern long-eared bats can tolerate remains to be determined. It is important to consider that roosts were not limiting at my study sites as is the case in much of the temperate forested environments where northern long-eared bats occur (Menzel et al. 2002*a*, Ford et al. 2006*b*). In more day-roost limited areas, e.g., in agricultural landscapes with greater forest fragmentation or in industrial forest settings skewed towards younger forest age classes that function as

fragmented landscapes in the context of their roosting requirements, day-roost loss may have different consequences for bats.

Monitoring of sufficient numbers of colonies for robust inference is largely infeasible within a single study, therefore, replication across studies is needed to better confirm or refute the patterns I have observed. With the ongoing spread of white-nose syndrome in North America, and continued rapid declines in northern long-eared bat populations, replication of this study in areas not yet impacted by white-nose syndrome is urgently needed. Additionally, understanding the impacts of day-roost loss on survival and recruitment remains a critical need. My results lend support to the simulation-based predictions of Silvis et al. (2014*a*), suggesting that simulations using observed colony dynamics may be of utility in generating testable hypotheses regarding day-roost loss. I encourage development of more detailed models of the effects of day-roost loss with the incorporation of data from further studies.

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Table 3.1. Roosting movement and space use summary metrics for 3 northern long-eared bat (*Myotis septentrionalis*) maternity colonies subjected to different levels of day-roost removal on the Fort Knox military reservation, Kentucky, USA, pre- and post-day-roost removal (2011 and 2012) treatment. Where applicable, values are presented with standard deviation ($\pm$ SD) and significant differences ($P < 0.05$) between groups are indicated by superscripts a–e. Network metrics were calculated directly from the two-mode network consisting of bats and roosts; arrows indicate the direction of difference when metrics differ from random networks.

	Control		Primary Day-roost Removal		Secondary Day-roost Removal	
	Pre	Post	Pre	Post	Pre	Post
Total roosts used	4	23	33	42	21	35
Total relocations	88	86	75	130	41	108
Mean roosts used per bat	1.2 ($\pm$ 0.6) [a,b,c,d,e]	4.4 ($\pm$ 1.9) [a]	4.8 ($\pm$ 1.9) [b]	3.6 ($\pm$ 2.0) [c]	4.1 ($\pm$ 1.6) [d]	3.2 ($\pm$ 1.8) [e]
Median non-zero day-roost switching distance	111.1 ($\pm$ 157.6)	147.6 ($\pm$ 180.1)	156.2 ($\pm$ 103.2)	161.9 ($\pm$ 114.4)	100.4 ($\pm$ 146.7) [a]	219.4 ($\pm$ 173.8) [a]
Roosting area (ha)	1.3	58.3	50.0	32.3	45.3	41.1
Bhattacharya's affinity	NA	0.12	NA	0.75	NA	0.77
Difference in roosting area centroid (m)	NA	258.7	NA	71.2	NA	128.7
Network degree centralization	0.99 (>)	0.43 (>)	0.44 (>)	0.72 (>)	0.3	0.28 (>)
Network clustering coefficient	0.00	0.69	0.57	0.80 (>)	0.57	0.70 (>)
Network density	0.30	0.19	0.14	0.08	0.19	0.09

Table 3.2. Parameter summary of the Poisson model describing the number of roosts used by female *Myotis septentrionalis* from 3 maternity colonies subjected to different levels of day-roost removal (2011 and 2012) on the Fort Knox military reservation, Kentucky, USA, pre- and post-day-roost removal treatment.

Predictor	Parameter Estimate	SE	z value	*P*-value
Intercept	-0.65	0.28	-2.348	0.02
Number locations	0.15	0.02	6.442	< 0.001
Post-removal	1.13	0.28	4.018	< 0.001
Treatment: Primary	1.33	0.32	4.486	< 0.001
Treatment: Secondary	1.44	0.28	4.816	< 0.001
Repro: Non-reproductive	-0.26	0.31	-0.843	0.40
Repro: Post-lactation	0.05	0.19	0.255	0.80
Repro: Gestating	-0.14	0.20	-0.711	0.18
Post-removal x Primary	-1.54	0.36	-4.241	< 0.001
Post-removal x Secondary	-1.38	0.33	-4.223	< 0.001

* Locations = number of days bat was located; repro = bat reproductive condition.

Table 3.3. Summary of day-roost characteristics (mean ± SD) for 3 northern long-eared bat (*Myotis septentrionalis*) maternity colonies subjected to different levels of day-roost removal on the Fort Knox military reservation, Kentucky, USA, pre- and post- day-roost removal (2011 and 2012) treatment. Significant differences ($P < 0.05$) between groups are indicated by superscripts a-e.

	Control		Primary Day-roost Removal		Secondary Day-roost Removal	
	Pre	Post	Pre	Post	Pre	Post
dbh (cm)	31.6 (± 4.6)	32.2 (± 15.0)	34.6 (± 22.2)	34.5 (± 14.5)	30.5 (± 24.5)	30.8 (± 16.4)
Height (m)	13.4 (± 9.5)	18.0 (± 8.3)	15.4 (± 8.3)	17.7 (± 9.1)	14.7 (± 7.1)	15.4 (± 8.0)
Canopy openness (%)	5.7 (± 4.1)	4.1 (± 2.9) [a]	4.7 (± 4.6) [b]	5.4 (± 3.4) [c,d]	4.1 (± 8.2) [a,c]	2.0 (± 3.2) [b,d]
Decay stage (% in stage)	[a]	[b,c]	[b,d]	[a,d,e]	[a,e]	
Stage 1	0.0	17.4	15.2	35.7	9.5	17.1
Stage 2	50.0	21.7	12.1	23.8	28.6	14.3
Stage 3	0.0	21.7	12.1	14.3	19.0	17.1
Stage 4	0.0	13.0	18.2	19.0	9.5	37.1
Stage 5	25.0	17.4	18.2	4.8	28.6	11.4
Stage 6	25.0	8.7	24.2	2.4	4.8	2.9
Canopy position (% in class)	[a]	[b]	[b,c]	[a,c,d]	[d]	-
Suppressed	75.0	17.4	69.7	7.1	66.7	34.3
Intermediate	25.0	47.8	15.2	57.1	9.5	40.0
Co-dominant	0.0	21.7	6.1	26.2	9.5	14.3
Dominant	0.0	13.0	9.1	9.5	14.3	11.4

Table 3.4. Parameter summary of the linear mixed model describing the log transformed non-zero distances moved between sequentially used roosts by female *Myotis septentrionalis* in 3 maternity colonies subjected to different levels of day-roost removal on the Fort Knox military reservation, Kentucky, USA, pre- and post- day-roost removal (2011 and 2012) treatment.

Predictor	Parameter Estimate	SE	t value	*P*-value
Intercept	4.50	0.5	0.503	< 0.001
Post-removal	0.47	0.52	0.520	0.37
Treatment: Primary	0.41	0.52	0.519	0.43
Treatment: Secondary	-0.23	0.55	0.547	0.68
Repro: Non-reproductive	0.79	0.43	0.433	0.07
Repro: Post-lactation	-0.17	0.22	0.217	0.44
Repro: Gestating	0.53	0.23	0.227	0.02
Post-removal x Primary	-0.36	0.55	0.549	0.52
Post-removal x Secondary	0.46	0.58	0.580	0.43

* Repro = bat reproductive condition.

Table 3.5. Pre- and post- day-roost removal (2011 and 2012) treatment social network metrics for 3 northern long-eared bat (*Myotis septentrionalis*) maternity colonies subjected to different levels of day-roost removal on the Fort Knox military reservation, Kentucky, USA. Where appropriate, when network metrics differed from random networks, the arrow indicates the direction of difference.

	Control		Primary Day-roost Removal		Secondary Day-roost Removal	
	Pre	**Post**	**Pre**	**Post**	**Pre**	**Post**
Minimum colony size	18	20	14	25	13	24
Number of bats tracked	15	14	13	25	8	23
Mean bat degree	14.0 (± 0.0)	6.7 (± 2.7)	4.6 (± 2.6)	15.9 (± 5.3)	3.5 (± 1.9)	6.1 (± 2.1)
Network degree centralization	0 (<)	0.38	0.33	0.37 (>)	0.48	0.14
Network clustering coefficient	1 (>)	0.76 (>)	0.74 (>)	0.93 (>)	0.64	0.77 (>)
Network density	1	0.51	0.38	0.66	0.5	0.28
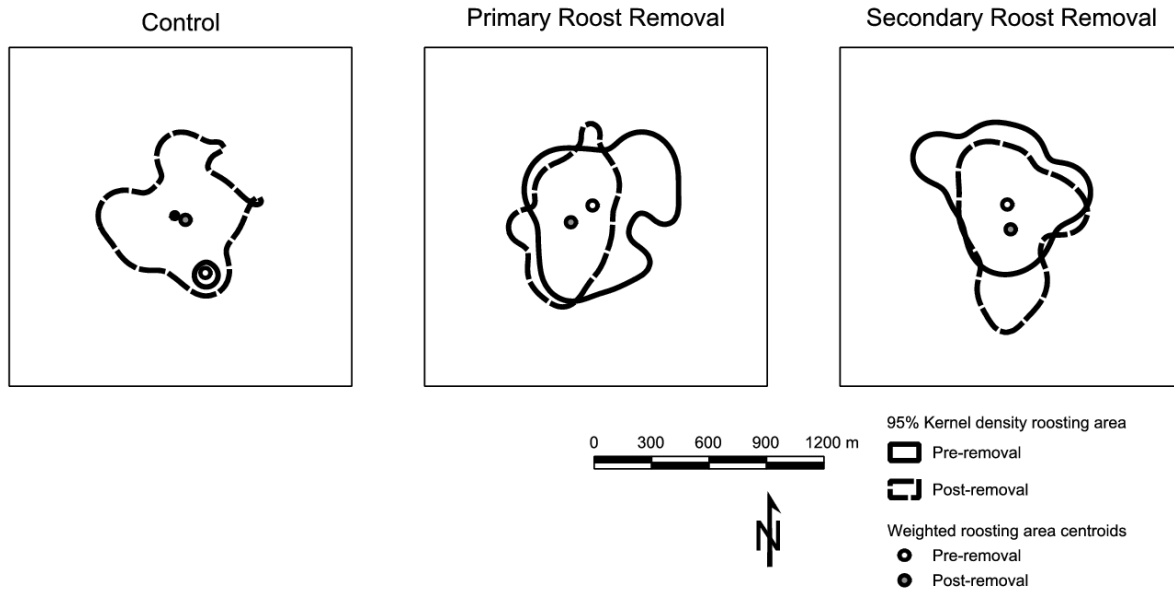
Figure 3.1. Roosting areas (95% utilization distribution) of 3 northern long-eared bat (*Myotis septentrionalis*) maternity colonies subjected to different levels of day-roost removal on the Fort Knox military reservation, Kentucky, USA, pre- and post- day-roost removal (2011 and 2012).
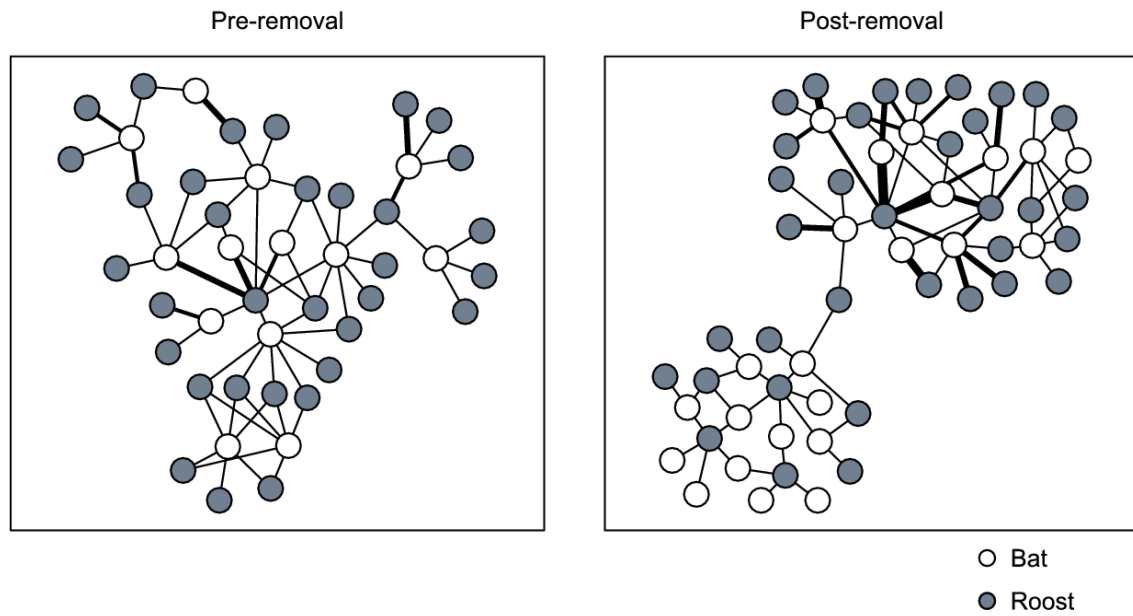
Figure 3.2. Pre- and post- day-roost removal treatment (2011 and 2012) 2-mode day-roost network map of a northern long-eared bat (*Myotis septentrionalis*) maternity colony subjected to removal of 5 secondary roosts on the Fort Knox military reservation, Kentucky, USA. Edge width is scaled by the number of connections between a bat and an individual day-roost.

Chapter 4: Inter-annual Variation in Day-roost Tree Selection by *Myotis septentrionalis*– What Does One Year of Data Really Tell Us?

Alexander Silvis

Abstract

Bat day-roost selection often is described by outcomes derived from comparisons of day-roosts to randomly selected, supposedly unused, trees. Relatively few studies, however, look at patterns of multi-year selection or compare day-roosts used across years, despite the fact that roost selection is influenced by weather factors that vary from year to year. I explored the process determining day-roost selection using 2 years of roost selection data for northern long-eared bat (*Myotis septentrionalis)* maternity colonies on the Fort Knox Military Reservation, Kentucky, USA. I compared characteristics of random trees and day-roosts used in 2 different years using a multinomial logistic model and day-roost species selection using chi-squared tests. I found that the factors differentiating day-roosts from non-roosts and day-roosts between years varied substantially. Day-roosts differed from random trees in the first year of data in all measured factors, but only in diameter at breast height and decay stage in the second year. Between years, day-roosts differed in roost size and canopy position, but not decay stage. Day-roost species selection was non-random and did not differ significantly between years. Although bats use multiple trees within a colony, my results suggest that there were unused trees that were suitable for roosts at any time. I believe day-roost selection pattern descriptions will be inadequate if based only on a single year of data, and that comparisons with random trees may be more impactful if paired with intra-roost comparisons.

Introduction

Day-roost selection is a common topic of study in bat ecology. Selection typically is assessed through comparisons of day-roosts to other trees (hereafter "non-roosts") on the landscape, either by random selection or examination of potentially available day-roosts assumed to be unoccupied. Non-roosts used for comparison historically have been those measured in radius plots (Lacki and Schwierjohann 2001) or belt transects (Ford et al. 2006, Silvis et al. 2012) or arise as paired random trees (Miles et al. 2006, Perry and Thill 2007, Johnson et al. 2009). Statistical analysis of selection generally is conducted using a set of candidate models that

represent various combinations of measured tree and/or landscape characteristics that may distinguish day-roosts from non-roosts. In information theoretic approaches (Burnham and Anderson 2002), either the best supported model or a model containing model-averaged parameters are reported. Less commonly in recent studies, individual characteristics of day-roosts and non-roosts are compared using univariate null hypothesis tests. Inference from comparisons of day-roosts with non-roosts is context dependent, depending on whether non-roosts are considered random trees or potentially available trees, the number of non-roosts measured (e.g., case-control or use-availability design), and the scale of data collection (e.g., stand or landscape level).

Comparison of day-roosts to non-roosts provides a basis for assessing roost preferences that are useful in guiding bat habitat management activities at both the forest stand and landscape level. Such research suggests that bats select roosts based on a number of possible criteria acting either independently or in concert. Examples of criteria for day-roost selection include distance to foraging habitat (O'Keefe et al. 2009), solar exposure and microclimate (Kerth et al. 2001, Lourenço and Palmeirim 2004, Boyles 2007), cavity volume (Parsons et al. 2003, Willis et al. 2006), surrounding landscape condition and quality (Ruczyński et al. 2010) and weather (Lewis 1996, Kerth et al. 2001). Despite the fact that some of these criteria are subject to inherent year to year variability (e.g., weather, prey distribution and availability), relatively few studies assess patterns of bat day-roost selection using multi-year datasets. As broadly discussed by Miller et al. (2003), the use of short term datasets to assess patterns of bat habitat use clearly is problematic, as variability in day-roost selection criteria likely will be underestimated. For land managers, bias in estimates of local day-roost selectivity has practical implications for forest management. The potential of underestimating bias in day-roost selection by female northern long-eared bats (*Myotis septentrionalis*) is a current concern as the species has been proposed for endangered species listing by the US Fish and Wildlife Service (Federal Register § 78:61045-61080).

Currently, understanding of northern long-eared bat day-roost selection criteria is minimal at best, especially as related to providing guidance on coarse scale habitat management. Within local landscapes and regions, few studies have examined potential variation in day-roost selection by northern long-eared bats, and important questions remain about fine-scale differences in the types of roosts used. Performing comparisons among day-roosts in conjunction with comparisons of day-roosts to random trees has the potential to provide more nuanced

understanding of day-roost selection processes. For example, both Garroway and Broders (2008) and Silvis et al. (2012), when examining day-roosts used by female northern long-eared bats in different reproductive conditions, discovered that lactating females selected for larger, more exposed roosts than did non-lactating bats. Further, Johnson et al. (2012), in their examination of primary roosts used by groups of female northern long-eared bats, discovered that primary roosts were smaller than secondary roosts. Manipulative field experiments of other bat species also have found that bats differentiate among roosts within a season (Kerth et al. 2001, Lourenço and Palmeirim 2004). As populations of northern long-eared and other tree-roosting bat species continue to decline in the face of White-nose Syndrome (WNS), deeper understanding of the ecology of WNS-impacted bats will better inform assessment of recovery strategies and management options, and provide managers useful guidance on avoiding "take" of individuals or inflicting damage to important habitat components under the aegis of the Endangered Species Act.

My objective was to describe day-roost selection by female northern long-eared bats via comparisons of day-roosts use between years and with randomly selected trees. I hypothesized *a priori* that day-roost selection would differ between years due to differences in overall summer temperatures, with selection for day-roosts with either smaller and less exposed canopy conditions or wider variation in these characteristics under warmer overall summer conditions. I also hypothesized that day-roosts would be larger and in more exposed canopy conditions, as well as more advanced stages of decay, than randomly identified trees.

Methods

I conducted my study on the Fort Knox military reservation in Meade, Bullitt, and Hardin Counties, Kentucky, USA, from May through July of 2011 and 2012. My sites fall predominantly within the western mixed-mesophytic deciduous forest association and lie in the Western Pennyroyal subregion of the Mississippian portion of the Interior Low Plateau physiographic province (Arms et al. 1979). I captured northern long-eared bats over small woodland pools or at known roosts and attached a radiotransmitter (LB-2, 0.31 g: Holohil Systems Ltd., Woodlawn, ON, Canada) between the scapulae of each captured female bat using Perma-Type surgical cement (Perma-Type Company Inc., Plainville, CT, USA). A uniquely

numbered lipped band was attached to the forearm of all captured bats. Captured bats were released within 30 minutes of capture at the net site. This study was carried out in accordance with state requirements for capture and handling of wildlife (Kentucky Department of Fish and Wildlife Resources permit numbers SC1111108 and SC1311170). My capture and handling protocol followed the guidelines of the American Society of Mammalogists (Sikes et al. 2011) and was approved by the Virginia Polytechnic Institute and State University Institutional Animal Care and Use Committee (protocol number 11-040-FIW).

I attempted to locate each radio-tagged bat daily for the life of the transmitter or until the unit dropped from the bat. For each located day-roost, I recorded tree species, diameter at breast height (dbh), height, crown class (Nyland 2002; i.e., suppressed, intermediate, co-dominant, dominant), decay class (Cline et al. 1980; live, declining, recent dead, loose bark, no bark, broken top, broken bole). I recorded these same measurements for one randomly located tree for each day-roost located during the first year of my study. Random tree locations were identified using randomly generated points within roosting areas used by bats as identified in Silvis et al. (2014) with the nearest tree to the point location selected as the measurement tree.

I performed a chi-squared test of independence to assess differences in tree species composition among my groups and examined standardized Pearson residuals from that analysis to determine which species were used more or less than expected. I compared characteristics of day-roosts (dbh, height, canopy position, decay stage, canopy openness) used in different years and random trees using multinomial logistic regression. The use of multinomial logistic regression, rather than 3 separate logistic models (i.e., 2011 day-roosts vs. non-roosts, 2012 day-roosts vs. non-roosts, 2011 roosts vs. 2012 roosts) provided several benefits, including reduced error propagation and more precise estimates of regression parameters. To use the multinomial modeling method, I assumed that the odds of a tree being in any class (random or day-roost in either year) were independent of the presence or absence of the other classes as alternatives. Prior to modeling, I tested for correlations among continuous variables and, where strong correlations existed, conducted a principal components analysis (PCA) to create orthogonal synthetic variables. I used eigenvectors accounting for >75% of the observed variation as predictors in my multinomial model. I centered and scaled my independent continuous variables so that I could assess directly effect sizes (Schielzeth 2010), and treated crown and decay class as ordinal variables. When a day-roost was used in multiple years, I included it in the analysis only

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in the year that it was first used; thus a day-roost used in both 2011 and 2012 was represented only as a 2011 day-roost. Similarly, I included each day-roost only once in my dataset regardless of the number of times that tree was used. Because I was conducting an exploratory analysis, I used an all subsets regression approach rather than a comparison of *a priori* hypotheses. I ranked models using Akaike's information criterion corrected for small sample size (AIC_c), the difference between the model with the lowest AIC and the AIC_c of the ith model (Δ_i) and Akaike's weights (w_i) (Burnham and Anderson 2002). I considered models with $\Delta_I \leq 2$ to have strong empirical support among all models. I assessed the overall fit of the model using McFadden's pseudo R^2, through assessment of a model confusion matrix and the multiclass area under the curve of the receiver operating characteristic (AUC) (Hand and Till 2001) and the % correct classification by sample group. McFadden's pseudo R^2 is interpreted similarly to traditional R^2 values, but values > 0.2 are considered to explain a substantial proportion of variation (Hensher and Johnson 1981, Hosmer, Jr. and Lemeshow 2004). All analyses were performed in the R statistical program (R. Development Core Team 2014). I fit multinomial models using neural networks with the package *nnet* (Venables and Ripley 2002).

Results

I captured 58 female northern long-eared bats in 2011 and 71 in 2012 belonging to 4 separate colonies (Silvis et al. 2014). I obtained relocation data for 54 individuals (16 gestating, 29 lactating, 3 post-lactation) in 2011 and 67 (5 gestating, 48 lactating, 10 post-lactation, 4 non-reproductive) in 2012. I located 108 day-roosts over 271 relocations in 2011 and 112 day-roosts (6 of which were used in 2011) over 334 relocations in 2012. I recorded a mean ($\pm$ SD) of 5.0 ($\pm$ 1.9) locations per bat in 2011 and 5.1 ($\pm$ 2.9) in 2012. I recorded measurements for 108 random trees (Table 1).

Random trees comprised 27 species, whereas day-roosts represented 21 and 17 species in the first and second years of my study, respectively. In total, I recorded the presence of 30 tree species within the day-roost and immediate adjacent forest stands. Tree species were not distributed equitably among random trees or day-roosts ($\chi2 = 103.04$, $d.f. = 58$, $P = 0.003$). Sugar maple (*Acer saccharum*) and sassafras (*Sassafras albidum*) were the most common random tree species, accounting for 25% and 15% of all random trees, respectively. Sugar maple and sassafras also were the most commonly used day-roost species (9% and 47% in 2011, and 15%

and 49% in 2012, respectively). Sassafras was used more than expected in both 2011 and 2012, whereas sugar maple was used less than expected (Table 2). All other tree species were used by northern long-eared bats as expected relative to their abundance in the random tree pool.

I detected strong, positive correlation (r = 0.69, $P < 0.001$) between tree dbh and height. The first eigenvector from the PCA of these variables explained 84.7% of the variation in tree size and was correlated positively with both dbh and height. My global model presented the best supported model to differentiate day-roosts trees from random trees (receiving 99% of the overall model support) (Table 3). Because no other models had $\Delta_i < 2$, I did not model average parameters, but instead used estimates directly from my best supported model. My model fit the data better than a null model (*chi-squared* = 235.98, *d.f.* = 20, $P < 0.001$), and explained a substantial amount of the variation in the data (McFadden pseudo $R^2 = 0.33$). However, predictive performance was relatively low (multi-class AUC = 0.73, overall correct classification rate = 68.1%; Table 4), with within-class accuracy rates of 71.3, 71.3, and 61.7% for random trees, 2011 roosts, and 2012 roosts, respectively. Model results indicate that 2011 day-roost trees were larger, had greater canopy openness, were in later decay stages, and more likely to be in suppressed canopy positions than random trees,, whereas day-roost trees in 2012 were larger and in later stages of decay than random trees, but did not differ in canopy openness or position (Table 5). Between years, day-roost trees differed in size, canopy openness, and decay stage, where 2011 day-roost trees were physically larger, but in earlier decay stages, exhibited more suppressed canopy positions, and displayed less canopy openness (Table 6).

Discussion

The global model ended up being the most parsimonious model to differentiate day-roosts and non-roosts, confirming that the variables incorporated into the model are important predictors of roost status for many bat species, as has been found in many studies (Kalcounis-Rüppell et al. 2005). Under the best supported model, as I predicted, and consistent with previous studies (Lacki and Schwierjohann 2001, Perry and Thill 2007, Garroway and Broders 2008, Johnson et al. 2009), day-roosts used by female northern long-eared bats in both years were larger, in later stages of decay, and located under more open canopies than randomly selected non-roosts. The effect sizes for overall difference in tree size between day-roosts and non-roosts was greater than the individual effect sizes of dbh and height reported by Kalcounis-

Rüppell et al.'s (2005) review for cavity roosting bats in North America. The effect size for canopy openness also was greater than that reported for North American bats (Kalcounis-Rüppell et al. 2005). The larger effect sizes may indicate greater selection preferences for day-roost size and canopy closure by northern long-eared bats than most other North American cavity roosting species, but overall levels of model predictive accuracy suggest that roosts may not differ substantially from random trees in some cases.

Day-roost species selection patterns that I observed differed from those reported in Arkansas, Illinois, West Virginia, central Ontario, Prince Edward Island, and eastern Kentucky (Lacki and Schwierjohann 2001, Menzel et al. 2002, Jung et al. 2004, Carter and Feldhamer 2005, Perry and Thill 2007, Henderson and Broders 2008, Johnson et al. 2009), as I observed a wider use of tree species. Differences in individual species selection undoubtedly are related to local species candidate pools and past land use history (Silvis et al. 2012). In terms of the characteristics of my most common roost species, my patterns of roost selection are similar to those observed by Ford et al. (2006) and Menzel (2002) in West Virginia in that bats selected primarily for an early successional species that has been overtopped by faster growing and larger tree species.

Because bat day-roosts selection criteria are related to climate and roost temperature (Lewis 1996, Kerth et al. 2001), I predicted *a priori* that, relative to non-roosts, day-roosts would be smaller and less exposed in 2011 or that variation in characteristics would be greater in response to decreased constraints on selection. During the first year of this study (2011), mean minimum temperature June–July was 1.78 C° greater in 2011 than in 2012 (National Oceanic and Atmospheric Administration station GHCND: USC00154955) and I therefore expected selection for smaller day-roosts in 2011. Contrary to my predictions, my model indicated that, relative to non-roosts, day-roosts used in 2012 actually were smaller and in less exposed canopy positions than those used in 2011. Standard errors for model parameters differentiating day-roosts from non-roosts almost universally were larger in 2011. Interestingly, despite apparently overall greater size and canopy openness, day-roosts used in 2011 were more likely to be in suppressed canopy conditions than those used in 2012. Because I used a composite variable representing the combination of dbh and height, it is difficult to decouple the specific effects of each variable in differentiating day-roosts used in different years. Assessment of raw mean and standard deviation values for height and dbh values for roosts provides some insight, indicating

that day-roosts used in 2011 were shorter and of less dbh than those used in 2012, but, were more variable in dbh. As such, I posit that stronger selection for larger trees in suppressed canopy classes in 2011 may be related to thermal buffering capacity of physically larger trees.

The extent to which day-roosts differed between years was surprising, as some tree characteristics differed more strongly between roosts than between day-roosts and non-roosts. To my knowledge, no other studies have compared the characteristics of day-roosts used by female northern long-eared bats in different years in this manner, and it therefore is unclear whether such large variability in the characteristics of day-roosts used in different years is common. Similarly, no meta-analyses have analyzed day-roost selection of the species, and it is unclear whether the effect sizes that I observed are similar to those from other studies. My results suggest that, while overall patterns of differences between day-roosts and non-roosts may be suitably described using a single year of data, actual estimates of the extent of difference between day-roosts and non-roosts likely will be biased. Furthermore, my results suggest that day-roost selection by northern long-eared bats is more variable than currently thought, with variation potentially related to differences in environmental conditions.

Conclusions

Failure to assess multi-year patterns in day-roost selection may yield inaccurate estimates of the variability of day-roost selection by female northern long-eared bats. Future studies on day-roost selection by female northern long-eared bats, as well as other species, should attempt to collect data over more than a single season, and estimates of roost selectivity based on a single year of data should be questioned. Multi-year studies also provide important insight into the relative availability of roost trees in an area. As my study shows, the full complement of available day-roosts may not be used in a single year, even as large numbers of radio-tracked individuals yield a probability of locating numerous roosts. Although the comparison of day-roosts with non-roosts clearly has utility for identifying and describing bat habitat, comparisons of different classes of day-roosts should provide greater insight of the ecology of bat species for whom basic day-roost selection criteria are reasonably well known than additional comparisons with random trees. This study provides one such insight- differences in day-roost characteristics used in different years may be stronger than differentiation between day-roosts and random trees.

More detailed information on roost selection preferences may be useful in management

of WNS-impacted species. In WNS-impacted areas, collection of additional data on the day-roost preferences of cave hibernating bats no longer may be practical, so I encourage the re-analysis of multi-year datasets, and datasets that include information on different classes of day-roosts. In particular, I believe there would be great utility in making comparisons of roosts used by female bats in different reproductive conditions, as well as comparisons of roosts used by male and female bats, as these comparisons have direct conservation implications. As I have demonstrated, use of the multinomial logistic model is a parsimonious method for comparing >2 classes of trees, and I encourage researchers to use this model for future multi-class comparisons. The use of centered and scaled variables also is recommended, as such standardization permits direct comparisons of effect sizes (Schielzeth 2010) of day-roost selection criteria across studies. Finally, comparisons of day-roosts with non-roosts also can be used to assess evidence for hypotheses regarding roost selection criteria (Clement and Castleberry 2013), and I encourage such hypothesis testing.

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Table 4.1. Summary of characteristics of random trees and day-roosts used by female northern long-eared bats (*Myotis septentrionalis*) on the Fort Knox Military Reservation in 2011 and 2012. Continuous variables are presented as mean ± SD, while categorical variables are presented as percent in class.

	Random	2011 Roost	2012 Roost	Pooled Roost
Height	15.0 ± 7.1	14.8 ± 7.1	17.0 ± 8.7	15.9 ± 8.0
DBH	24.9 ± 13.9	30.7 ± 18.8	32.8 ± 15.7	31.8 ± 17.3
Canopy openness	2.2 ± 2.8	5.0 ± 6.0	4.0 ± 4.2	4.5 ± 5.2
Suppressed (% in class)	35.2	69.4	16.8	43.3
Intermediate (% in class)	50.0	18.5	51.4	34.9
Codominant (% in class)	12.0	5.6	20.6	13.0
Dominant (% in class)	2.8	6.5	11.2	8.8
Decay stage 1 (% in stage in class)	59.3	11.1	25.2	18.1
Decay stage 2 (% in stage)	24.1	24.1	20.6	22.3
Decay stage 3 (% in stage)	3.7	16.7	17.8	17.2
Decay stage 4 (% in stage)	9.3	16.7	24.3	20.5
Decay stage 5 (% in stage)	1.9	17.6	9.3	13.5
Decay stage ≥ 6 (% in stage)	1.9	13.9	2.8	8.4

Table 4.2. Standardized Pearson's residuals for chi-squared analysis comparing abundance of random tree species, and species used as day-roosts by female northern long-eared bats (*Myotis septentrionalis*) on the Fort Knox Military Reservation in 2011 and 2012. Values close to 2 are considered influential (values > |1.75| bolded). Negative and positive values indicate less than and greater than abundance than expected. Overall $\chi 2$= 103. 04 (d.f. = 58, P = 0.003).

Species	Random	2011	2012
Box elder (*Acer negundo*)	-0.58	1.15	-0.58
Sugar maple (*Acer saccharum*)	**2.34**	**-1.90**	-0.45
Tree of heaven (*Ailanthus altissima*)	1.15	-0.58	-0.58
Pignut hickory (*Carya glabra*)	**2.03**	-1.02	-1.01
Shagbark hickory (*Carya ovata*)	0.91	0.36	-1.27
Eastern redbud (*Cercis canadensis*)	0.57	0.57	-1.15
Hackberry (*Celtis occidentalis*)	0.41	0.41	-0.81
Flowering dogwood (*Cornus florida*)	**1.99**	-1.00	-1.00
Common persimmon (*Diospyros virginiana*)	**1.99**	-1.00	-1.00
American beech (*Fagus grandifolia*)	-0.52	1.03	-0.51
White ash (*Fraxinus americana*)	-0.25	-0.61	0.86
Blue Ash (*Fraxinus quadrangulata*)	-0.58	1.15	-0.58
Black walnut (*Juglans nigra*)	-0.29	0.57	-0.28
Eastern redcedar (*Juniperus virginiana*)	0.25	-0.52	0.27
Sweet gum (*Liquidambar styraciflua*)	1.15	-0.58	-0.58
Yellow poplar (*Liriodendron tulipifera*)	1.42	-1.64	0.21
Blackgum (*Nyssa sylvatica*)	0.41	0.41	-0.81
Loblolly pine (*Pinus taeda*)	1.15	-0.58	-0.58
American sycamore (*Planatus occidentalis*)	-0.82	0.41	0.41
Black Cherry (*Prunus serotina*)	0.00	-1.00	1.01
White oak (*Quercus alba*)	-1.55	1.39	0.16
Chinkapin oak (*Quercus muhlenbergii*)	1.73	-0.87	-0.86
Northern red oak (*Quercus rubra*)	-1.16	-0.29	1.46
Black oak (*Quercus velutina*)	0.00	-0.71	0.72
Black locust (*Robinia pseudoacacia*)	0.81	-0.41	-0.40
Sassafras (*Sassafras albidum*)	**-3.77**	**1.78**	**2.00**
Basswood (*Tilia americana*)	1.63	-0.82	-0.81
Winged elm (*Ulmus alata*)	0.00	1.41	-1.41
American elm (*Ulmus americana*)	1.15	-0.58	-0.58
Slippery elm (*Ulmus rubra*)	0.00	1.00	-1.00

Table 4.3. Model selection table for the top 3 best supported multinomial models comparing random trees and female northern long-eared bat (*Myotis septentrionalis*) day-roosts on the Fort Knox Military Reservation in 2011 and 2012. Model parameters are given as well as the effective degrees of freedom (df), log likelihoods (logLik), Akaike's information criterion corrected for small sample size (AIC$_c$), difference in AIC$_c$ value between top model and i[th] model (Δ_i), and model support (w_i). PCA1 represents the first eigenvector of a principal components analysis on tree dbh and height, openness represents percent canopy openness, decay represents tree decay stage, and position represents tree position in the forest canopy.

Model	df	logLik	AICc	Δ_i	w_i
Intercept + PCA1 + Openness + Decay + Position	22	-236.86	521.1	0	0.996
Intercept + PCA1 + Decay + Position	20	-244.75	532.3	11.19	0.004
Intercept + Openness + Decay + Position	20	-264.94	572.7	51.57	0

Table 4.4. Classification table of predicted vs observed tree status for the multinomial model comparing random trees and female northern long-eared bat (*Myotis septentrionalis*) day-roosts on the Fort Knox Military Reservation in 2011 and 2012. Numbers are raw counts.

		Actual		
		Random	**2011 Roost**	**2012 Roost**
Predicted	Random	77	14	19
	2011 Roost	12	77	22
	2012 Roost	19	17	66

Table 4.5. Parameter summary of the best supported multinomial model comparing random trees to female northern long-eared bat (*Myotis septentrionalis*) day-roosts on the Fort Knox Military Reservation using in 2011 and 2012. Coefficients, standard errors, and *P*-values are presented for both 2011 and 2012 day-roosts. PCA1 represents the first eigenvector of a principal components analysis on tree dbh and height, openness represents percent canopy openness, decay represents tree decay stage, and position represents tree position in the forest canopy.

	Estimates		SE		*P*-values	
	2011	2012	2011	2012	2011	2012
Intercept	-0.11	-1.85	0.56	0.52	0.85	< 0.001
PCA1	1.84	0.77	0.28	0.24	< 0.001	< 0.001
Decay stage 2	2.55	1.63	0.59	0.46	< 0.001	< 0.001
Decay stage 3	3.98	3.45	0.81	0.69	< 0.001	< 0.001
Decay stage 4	3.32	3.00	0.69	0.56	< 0.001	< 0.001
Decay stage 5	4.75	3.86	0.95	0.89	< 0.001	< 0.001
Decay stage 6	4.53	3.34	1.06	1.06	< 0.001	< 0.001
Position intermediate	-3.22	0.48	0.59	0.49	< 0.001	0.33
Position co-dominant	-4.99	0.44	1.01	0.80	< 0.001	0.58
Position dominant	-4.44	0.98	1.27	1.07	< 0.001	0.36
Openness	0.89	0.45	0.26	0.24	< 0.001	0.07

Table 4.6. Parameter estimates comparing day-roosts used on 2011 and 2012 from the best supported multinomial model comparing random trees to female northern long-eared bat (*Myotis septentrionalis*) day-roosts on the Fort Knox Military Reservation using in 2011 and 2012. PCA1 represents the first eigenvector of a principal components analysis on tree dbh and height, openness represents percent canopy openness, decay represents tree decay stage, and position represents tree position in the forest canopy.

	Estimate	**SE**	*P*-value
Intercept	-1.75	0.56	< 0.001
PCA1	-1.07	0.24	< 0.001
Decay stage 2	-0.92	0.57	0.11
Decay stage 3	-0.53	0.67	0.43
Decay stage 4	-0.32	0.63	0.62
Decay stage 5	-0.89	0.72	0.22
Decay stage 6	-1.19	0.93	0.20
Position intermediate	3.70	0.53	< 0.001
Position co-dominant	5.44	0.87	< 0.001
Position dominant	5.42	1.03	< 0.001
Openness	-0.44	0.17	0.01

Chapter 5: Day-roosting and Foraging Social Structure of the Endangered Indiana Bat (*Myotis sodalis*)

Alexander Silvis

Abstract

Social dynamics are an important but poorly understood aspect of bat ecology. Herein I use a combination of graph theoretic and spatial approaches to describe the day-roost and social network characteristics and foraging associations of an Indiana bat (*Myotis sodalis*) maternity colony in an agricultural landscape in Ohio, USA. Forty six 46 bats were tracked to 50 day-roosts (423 total relocations) and 2,306 foraging locations collected for 40 bats during the summers of 2009 and 2010. I found the colony day-roosting network was highly centralized in both years and that day-roost and social networks differed significantly from random networks. Day-roost and social network structure also differed substantially between years. Social network structure appeared to be unrelated to segregation of day-roosts between age classes. For bats whose individual foraging ranges were calculated, many shared foraging space with at least one other bat. Compared across all possible bat dyads, 47% and 43% of the dyads showed more than expected overlap of foraging areas in 2009 and 2010 respectively. Colony day-roosting area differed between years, but the day-roosting area centroid shifted only 332 m. In contrast, whole colony foraging area use was similar between years. Random day-roost removal simulations suggest that Indiana bat colonies may be robust to loss of a limited number of day-roosts but may respond differently from year to year. My study emphasizes the utility of graphic theoretic and spatial approaches for examining the sociality and day-roosting behavior of bats. Detailed knowledge of the relationships between social and spatial aspects of bat ecology could greatly increase conservation effectiveness by allowing more structured approaches to day-roost and habitat retention for tree-day-roosting, socially-aggregating bat species.

Introduction

Sociality is as an important contributor to day-roosting behavior in bats (Kerth 2008*a*, Chaverri et al. 2013) and day-roost fidelity is at least partly a group decision (Kerth and Reckardt 2003, Kerth et al. 2006). The social systems for only a small number of bat species have been studied (Kerth 2008*a*, Johnson et al. 2013), but individual bats within maternity colonies

typically exhibit non-random social assortment dynamics (Kerth and Konig 1999, Willis and Brigham 2004, Garroway and Broders 2007, Rhodes 2007). Non–random social assortment among bats typically is reflected through coincident day-roost use (Kerth 2008*a*) but association is not restricted solely to day-roosting behavior. Bats also are known to communicate day-roost and feeding site information (Wilkinson 1992, Jonker et al. 2010) and recognize familiar conspecifics during flight (Mann et al. 2011). Although relationships between foraging and association have rarely been examined (Chaverri et al. 2007), these may also constitute an important part of bat sociality. Asynchronous day-roost use among individuals as a result of day-roost switching can, in some instances, result in social structures where individuals are both casual acquaintances and constant companions (Garroway and Broders 2007). More generally, day-roost switching and asynchronous day-roost use results in a fission–fusion social system (Kerth 2008*a*). Fission-fusion social systems have been documented in several bat species (Kerth and Konig 1999, Willis and Brigham 2004, Rhodes 2007, J. B. Johnson et al. 2012, J. S. Johnson et al. 2012). These social systems are flexible and variable but often occur when the benefits of group membership are temporary (Aureli et al. 2008). Although it is unclear whether individuals form stronger associations with close relatives than less related individuals (Kozhurina 1993, Kerth et al. 2011, Patriquin et al. 2013), maternity colonies of some bat species do appear to be based on matrilines (Kerth 2008*b*, Metheny et al. 2008, Patriquin et al. 2013). There is also evidence indicating that reproductive condition impacts association and day-roost-mate choice at the individual level (Patriquin et al. 2010, J. S. Johnson et al. 2012). At the colony level, social structure may be related to local day-roost availability and therefore dependent upon the spatio-temporal aspects of habitat quality and configuration (Chaverri and Kunz 2010, J. S. Johnson et al. 2012).

In North America, research on bat association largely has been limited to forested habitats and to relatively few species (Willis and Brigham 2004, Garroway and Broders 2007, Metheny et al. 2008, Patriquin et al. 2010, 2013, J. B. Johnson et al. 2012, J. S. Johnson et al. 2012). Notably, the social structure of the endangered Indiana bat (*Myotis sodalis*), whose Latin epithet *sodalis* (meaning "companion") was selected due to an early perception of sociality (Miller and Allen 1928), has not been described beyond classification as fission-fusion (Gumbert et al. 2002, Carter and Feldhamer 2005). Indiana bats are widely distributed across the eastern and midwestern United States (Gardner and Cook 2002) and form maternity colonies in summer

wherein groups of bats generally day-roost beneath exfoliating bark of live trees or snags (Callahan et al. 1997, Foster and Kurta 1999, Britzke et al. 2003, Carter and Feldhamer 2005). Estimates vary but most maternity colonies appear to consist of fewer than 100 individuals (Harvey 2002) although >300 bats have been observed emerging from maternity day-roosts (Whitaker and Brack 2002). Over the summer maternity season female Indiana bats use multiple day-roost trees; however, usually 1 to 3 day-roosts receive consistent and/or repeated use by the majority of bats in the colony and are referred to as "primary day-roosts" but . The day-roosts used by individual or small numbers of bats intermittently or only for one to a few days are considered "secondary" or "alternate day-roosts." Due to its perceived sociality, the Indiana bat potentially provides a model species to investigate the social dynamics of bats. Additionally, because of its endangered status and wide distribution across highly anthropogenically altered landscapes (Gardner and Cook 2002, Kniowski and Gehrt 2014), an improved understanding of Indiana bat social structure and day-roosting behavior could greatly benefit efforts to minimize impacts of human land use on the species and provide insight into habitat management efforts.

Observing associations and interactions between individual bats in species that day-roost under bark or in cavities and that switch day-roosts frequently, such as the Indiana bat, is extremely difficult. In previous studies of bat sociality (Willis and Brigham 2004, Garroway and Broders 2007, Popa-Lisseanu et al. 2008, Kerth et al. 2011), association has been assessed using indices that document the amount of time that bats share day-roosts. An alternative approach however, is to infer association from use of a common resource (Fortuna et al. 2009, J. S. Johnson et al. 2012). Network (graph theoretic) analysis offers a useful analytical framework, specifically two-mode networks, to assess such common resource use (Borgatti and Everett 1997, Williams 2011). As a special case of complex networks, two-mode networks contain two sets of nodes with connections only between nodes of the opposite set; in the study of bat sociality, bats and day-roosts can be considered separate sets of nodes (Fortuna et al. 2009, J. S. Johnson et al. 2012). Analysis of the two-mode networks directly, or of one set of nodes individually through projection to a single-mode network, can be used to address questions regarding one or both sets of nodes (Borgatti and Everett 1997). Two-mode and other graph theoretic network analyses have been successfully used in animal studies to quantify social structure (Lusseau and Newman 2004, Wey et al. 2008, Sih et al. 2009) and provide a broad

framework for modeling and testing social, spatial and temporal hypotheses (Wey et al. 2008, Jacoby et al. 2012).

In this study, I combined graph theoretic and spatial methods to: 1) describe the day-roosting social structure of the Indiana bat and 2) determine colony robustness to fragmentation as a result of day-roost loss through simulations. Secondarily, I assessed whether Indiana bats exhibit social foraging behavior and evaluated the overall size and stability of maternity colony day-roosting and foraging areas. Based on observed patterns of differential day-roost use by Indiana bats (Kurta et al. 1993, 2002, Callahan et al. 1997, Miller et al. 2002, Britzke et al. 2003), I predicted that day-roost networks would be centralized whereas social networks would be decentralized. Because individuals of other tree-day-roosting bats form preferential associations (Willis and Brigham 2004, Garroway and Broders 2007, Kerth et al. 2011), I further predicted that both day-roost and social networks would exhibit high clustering and modularity values indicative of the presence of preferentially associating cliques with preferred day-roosts (Watts and Strogatz 1998, J. S. Johnson et al. 2012).

Methods

Data for this study was collected along Big Darby Creek in Pickaway County, Ohio, USA (Figure 1) by A.B. Kniowski (Kniowski 2011). Pickaway County is characterized by flat to gently rolling terrain with elevations ranging from 190 to 330 m above sea level. The Scioto River bisects the county and numerous smaller streams are present throughout. Cultivated cropland was the dominant land use within the county comprising 74% of the land area (Homer et al. 2004). Woodlands composed 9% of the land area and were generally limited to field edges, creek banks, and small, widely scattered woodlots. Extant woodlots and/or riparian forests were commonly composed of box elder (*Acer negundo*), silver maple (*Acer saccharinum*), sugar maple (*Acer saccharum*), shagbark hickory (*Carya ovata*), common hackberry (*Celtis occidentalis*), white ash (*Fraxinus americana*) and American elm (*Ulmus americana*). I chose my general study location based on previously known Indiana bat day-roost locations with specific site locations determined by outreach to private landowners.

Indiana bats were captured using mist nets, 6–12 m in length and up to 8 m in height, at 21 sites along a 14–km section of Big Darby Creek. Mist nets were placed across access roads,

trails, along field edges, or across creek channels as conditions permitted. I attached radio transmitters (0.36 g, LB–2N, Holohil Systems Ltd., Carp, Ontario, Canada) between the scapulae of captured Indiana bats with surgical cement (Perma-Type, The Permatype Company Inc., Plainville, CT, USA) or eyelash adhesive (LashGrip, A.I.I., Los Angeles, CA, USA). All captured bats received lipped metal forearm bands (2.4 mm, Porzana Ltd., East Sussex, United Kingdom) and the age, sex, and reproductive condition were recorded for each. Bats were released at their capture site within 45 minutes of capture.

The diurnal day-roost location of each bat was recorded daily until the transmitter detached from the bat or the battery expired. I evaluated observation bias in the number of day-roosts used by individual bats by regressing the number of day-roosts used against the number of relocations. Because the number of day-roosts used is an integer count, I used a Poisson generalized linear model for my regression and evaluated the amount of deviance explained using maximum adjusted D^2 (Guisan and Zimmermann 2000). As permitted by logistical considerations (i.e., private property access and radio-tracking), emergence counts were conducted throughout the field season. Counts began at dusk and ran until five minutes after the last bat emerged or until insufficient light remained to see emerging bats. Due to logistical constraints, exit counts were not always on days when radiotagged bats were present. I assessed whether patterns of day-roost use by radio-tagged bats were reflective of overall colony day-roost use by conducting correlation tests among the number of days a day-roost was used by radio-tagged bats and the maximum observed day-roost emergence.

When bats were active during the night, their locations were estimated in LOCATE III (Nams 2006) using simultaneous bi- or tri-angulation bearings from mobile tracking stations. Three bearings per location were used most commonly—2 bearings/location comprised <3% of all locations. Three or 4 element handheld yagi antennas and telemetry receivers (R2000, R4000, Advanced Telemetry Systems, Isanti, Minnesota, USA) were used to determine the most likely bearing from a given station to a bat. All azimuth bearings were recorded synchronously and 3 or more minutes apart for a given bat. Bats were followed from the time they emerged in the evening until all bats in the tracking area day-roosted (generally 0000–0200 hours). Foraging location data collection each night was prioritized based on transmitter age and amount of data previously collected so that foraging data was collected at a comparable level for each individual.

This study was carried out in accordance with state and federal requirements for capture and handling of endangered wildlife (Ohio Division of Wildlife wild animal permit number 11-297; United States Fish and Wildlife Service native endangered species recovery permit number TE06843A-0). Capture and handling protocol followed the guidelines of the American Society of Mammalogists (Sikes et al. 2011) and was approved by the Ohio State University Institutional Animal Care and Use Committee (protocol number 2008A0102). Study sites were located on private lands which were accessed by explicit permission of the landowners. Data used in this study are archived in the Virginia Polytechnic Institute and State University VTechWorks institutional repository and are available at http://hdl.handle.net/10919/25802.

I defined an Indiana bat maternity colony as all female and juvenile bats connected by coincident day-roost use. I represented the colony graphically and analytically as a two-mode network that consisted of bats and day-roosts (hereafter day-roost network). I used this two-mode representation to assess patterns of day-roost use by the colony. I used the single-mode projection of the bat nodes (hereafter social network) to assess colony social structure as this provides a more generalized picture of how bats may associate than observations from the two-mode network. To reduce bias resulting from uneven tracking periods and observing only a portion of the colony, I did not assign edge weights. I assessed day-roost and social network structure using mean degree, network degree centralization, network density and clustering. I calculated degree centralization and density for day-roost and social networks using two-mode (Borgatti and Everett 1997, Opsahl 2009) and single-mode formulations (Freeman 1978, Wasserman and Faust 1994, Watts and Strogatz 1998), respectively. For the social network only, I also used leading eigenvector modularity (hereafter modularity) (Newman 2006*a*), shortest path length (West 1996), and tested for homophily (McPherson et al. 2001) by age class. Degree centralization, density, and clustering have values between 0 and 1 (0 = low, 1 = high). These measures represent the extent that the network is structured around individual nodes and the distribution of connections between nodes (Freeman 1978, Wasserman and Faust 1994, Borgatti and Everett 1997, Watts and Strogatz 1998, Dong and Horvath 2007). Leading eigenvector modularity values range from 0 to 1 and provide a measure of how distinctly a network is separated into different communities (Newman 2006*a*, *b*). Average shortest path length is the average geodesic distance between any two nodes. Average shortest path length provides the social distance among individuals and therefore a measure of how information may flow through

the network. Homophily values range from -1 to 1 with negative values indicating avoidance and positive values indicating preference for connections with individuals sharing a specific characteristic (McPherson et al. 2001).

To determine whether my observed network values differed from those of random networks, I performed 500 Monte Carlo simulations and compared observed network metrics to random network metrics using two-tailed permutation tests (Hope 1968, Davison 1997). Because network metrics are dependent upon the size of an individual network, values from networks of differing size are challenging to compare (James et al. 2009). Therefore, I generated my random networks with the same number of nodes as my observed networks and with a constant probability of link establishment using the Erdős-Réyni model (Erdős and Rényi 1960, Newman 2006c). I used the *igraph* (Csardi and Nepusz 2006) and *tnet* libraries (Opsahl 2009) in R (R. Development Core Team 2014) to visualize networks and calculate metrics. My permutation tests were performed in R using a custom script with dependencies on the *igraph* and *tnet* libraries. I calculated all network values on a year-to-year basis because few individual bats were tracked during both years.

I assessed the potential for nightly association during flight by calculating the joint use of foraging space by dyads of bats using the utilization distribution overlap index (UDOI) (Fieberg and Kochanny 2005). The UDOI uses the joint distribution of two utilization distributions to assess spatial overlap relative to the volume of use within the area of overlap. UDOI values <1 indicate relatively uniform and independent space use, whereas values >1 indicate non-uniform space use with a high degree of overlap (Fieberg and Kochanny 2005). I generated foraging area utilization distributions for individual bats with ≥ 40 locations using biased random bridges (BRB) (Benhamou 2011). Use of BRBs allowed me to use serial autocorrelation in my foraging locations to better represent the actual movement pathways of bats. I estimated the diffusion parameter for BRB foraging utilization distributions using the plug-in method (Benhamou 2011) with a maximum duration allowed between successive relocations of 60 minutes and a minimum distance between successive relocations of 50 meters. I used these same values in calculating the BRB where I set the minimum smoothing parameter to 88 meters and specified that the relocation variance have constant weight. I calculated the UDOI for all dyads of bats within years using the 95% BRB utilization distributions. I used a network map to visually represent the distribution of connections among bats given by overlapping foraging areas.

I also evaluated whole-colony space use using 95% utilization distributions calculated separately for day-roosting and foraging areas using the pooled locations of all bats. I calculated utilization distributions for the day-roosting and foraging areas using bivariate normal fixed kernel methodology. To reflect the concentration of day-roost use, I weighted day-roost locations by the number of days the day-roost was used by radio-tagged bats (Popa-Lisseanu et al. 2008). I used the reference method for smoothing parameter estimation as appropriate for weighted locations (Gitzen et al. 2006). I assessed annual changes in day-roosting and foraging area use for the whole colony using Bhattacharya's affinity (BA) (Fieberg and Kochanny 2005). Similar to the UDOI, BA uses a joint distribution of two utilization distributions, but in contrast to the UDOI, quantifies similarity between utilization distributions and is more appropriate for comparisons of utilization distributions for the same individual or group (Fieberg and Kochanny 2005). BA values range from 0 to 1 with values close to 1 indicating highly similar utilization distributions (Fieberg and Kochanny 2005). To assess overall spatial drift in day-roosting area, I calculated the day-roosting area centroids in each year and the difference between these centroids. I calculated utilization distributions, BA and the UDOI using the *adehabitatHR* package (Calenge 2006) in R.

I assessed the potential impact of day-roost loss on colony fragmentation using random and targeted node removal simulations (Silvis et al. 2014) . I conducted these simulations using the single-mode projection of the day-roosting network to best reflect the knowledge that bats have of multiple day-roosts and their possible movement pathways between those day-roosts. I performed random removal simulations by iteratively removing an increasing number of random nodes until only 30% remained. Because the number of nodes differed between years, removal by percentage allowed me to compare the relative effects of day-roost loss between networks. I repeated removal simulations 1,000 times per proportion of nodes removed and calculated the mean and standard error of the number of resultant components; a component may be either a network fragment or an individual node. For my targeted removal simulation, I removed the most degree-central day-roost in the network and calculated the number of remaining components. Removal simulations were performed in R using a custom script with dependencies on the *igraph* and *tnet* libraries.

Results

23 Indiana bats were captured between 18 June and 30 August 2009, and 26 between 21 April and 6 August 2010. Of those bats captured in 2009, 14 were adult females (7 lactating, 2 post-lactating, 5 undetermined) and 7 were juveniles (3 male, 4 female). Twenty of the bats captured in 2010 were adult females (3 pregnant, 7 lactating, 2 post-lactating, 6 undetermined, 2 non-reproductive) and 5 were juveniles (2 male, 3 female). Mean transmitter mass ($\pm$ SD) was 5.0 ($\pm$ 0.8) percent of body mass in 2009 and 5.0 ($\pm$ 0.7) percent in 2010. Day-roost locations were recorded for 21 bats 195 times in 2009 and the day-roost location for 25 bats 228 times in 2010. These relocations represented 33 day-roosts in 2009 and 17 day-roosts in 2010; 7 day-roosts located in 2009 were also used in 2010. The mean ($\pm$ SD) number of locations recorded per bat was 9.3 ($\pm$ 5.0) in 2009 and 9.1 ($\pm$ 5.4) in 2010. Day-roost switching occurred every 3.3 ($\pm$ 1.4) days in 2009 and every 4.0 ($\pm$ 3.1) days in 2010. The mean number of day-roosts used by a bat was 3.05 ($\pm$ 1.77) in 2009 and 2.56 ($\pm$ 1.33) in 2010. The number of day-roosts located per bat was weakly related to the number of locations recorded in both 2009 (β = 0.08, 95% CI: 0.0.03 – 0.13, D^2 = 0.49) and 2010 (β = 0.04, 95% CI: -0.00 – 0.09, D^2 = 0.19). The mean number of radiotagged bats that visited a day-roost was 1.94 ($\pm$ 2.11) in 2009 and 3.76 ($\pm$ 5.07) in 2010. Nine hundred forty four foraging locations were recorded for 16 bats in 2009 and 1362 foraging locations for 24 bats in 2010.

Exit counts were conducted at all 43 day-roosts; 11 and 7 day-roosts had non-zero counts in 2009 and 2010, respectively. Exit counts of zero occurred when exit counts were conducted on days when no radio-tagged bats were in the day-roost. Maximum emergence count was 97 in 2009 and 109 in 2010 (Figure 2). The maximum cumulative number of days an individual day-roost was used by radio-tagged bats was 40 in 2009 and 137 in 2010. The total number of days a day-roost was used by radio-tagged bats was positively correlated with the highest emergence count in both 2009 (r = 0.86, $P < 0.001$) and 2010 (r = 0.85, $P < 0.001$).

Indiana bat day-roost network structure differed significantly from equivalent random networks and varied year-to-year (Table 1). Day-roost network density was low in 2009 indicating day-roosts were poorly connected overall (Figure 3). However, in 2010 day-roost network density was no different than random networks. The network was highly clustered in both years. That is, associate day-roosts (two nodes with a third node in common) were more frequently connected than in random networks suggesting day-roosts occurred in small but

highly connected groups. Also, the network was more centralized than random networks in both years suggesting one or a small number of day-roosts were more connected and central within the network, although centralization was greater in 2010. Likewise, the observed mean number of uses of an individual day-roost was 5.91 (± 10.17) in 2009 and 13.41 (± 31.77) in 2010, indicative of a difference in network structure year-to-year.

Indiana bat social network density and clustering were consistently greater than computed random social networks (Table 2) suggesting bats were more highly connected to one another than expected by chance (Figure 4). Network mean shortest path length was 1.8 in 2009 and 1.2 in 2010. I observed a high degree centralization value for the social network in 2009 indicating a small number of bats were better connected within the network. However, in 2010, degree centralization was no different than that of random networks suggesting that bats were equally connected throughout the network. My modularity values indicate that the Indiana bat network contained no more modules than would be expected by chance occurrence in 2009 but fewer modules than would be expected by chance in 2010. Connections among bats were more homophilous than expected by age class in 2009, although the value was low. In contrast, homophily values were no different than those expected by chance in 2010.

Greater than 39 foraging telemetry locations for each of 10 bats in 2009 (representing 45 possible dyads) and 19 bats in 2010 (representing 171 possible dyads). An average of 70.9 (± 3.1) foraging locations was recorded per tracked individual. Overall mean BRB foraging range area was 376.0 ha (± 40.6) (individual home range and habitat selection of this colony was reported in Kniowski and Gehrt (Kniowski and Gehrt 2014)). Twenty-one dyads in 2009 (47%) and 74 dyads in 2010 (43%) exhibited greater foraging area overlap than expected with the result that most bats shared foraging space with at least one other bat (Figure 5). Of those dyads with more than expected foraging area overlap, 11 (24% of total dyads) and 74 (43% of total dyads) also were in close proximity in the social network (i.e., shortest path lengths less than the colony average) in 2009 and 2010, respectively. Day-roost area for the entire colony was 1704.0 ha in 2009 and only 174.9 ha in 2010 (Figure 6), whereas foraging area was relatively constant at 3609.0 ha in 2009 and 3555.3 ha in 2010. Colony day-roosting area use differed between years (BA = 0.53); however, colony foraging area use did not differ as substantially (BA = 0.81). Despite the difference in overall colony day-roosting area between years, the day-roosting area

centroids remained in approximately the same location (near the most central day-roost in the day-roost network) and differed only by 332 m.

In 2009, the number of network fragments was linearly related to the proportion of day-roosts removed, with removal of approximately 5% of day-roosts generating a 50% chance (number of networks = 1.5) of network fragmentation (Figure 7). Similarly, the number of components was linearly related to the proportion of day-roosts removed in 2010, but less severely so as removal of approximately 30% of day-roosts was required to generate a 50% chance of network fragmentation. Targeted removal of the most central day-roost generated 4 network components in 2009 and 2 components in 2010.

Discussion

Day-roost switching by Indiana bats resulted in formation of highly structured day-roosting and social networks. These networks differed significantly from random networks suggesting that the characteristics I observed were unlikely to have arisen by chance. As I predicted, day-roost networks were highly centralized relative to random networks whereas social networks were not. Social network modularity was low or no different than would be expected at random. Although the differences between my observed values and those of random networks were consistent across years, I found that some aspects of day-roost and social network structure and day-roosting space use differed between years. The most substantial differences include increased day-roost network centralization and connectedness among bats, a rarity of multiple-year use of day-roosts, and a concentration of day-roosting space use.

The differences in the network metrics between years for Indiana bats may be related to ecological factors such as day-roost quality, temperature (Humphrey et al. 1977, Willis and Brigham 2007), suitability (Callahan et al. 1997, Foster and Kurta 1999, Britzke et al. 2003, Carter and Feldhamer 2005), behavioral flexibility (J. S. Johnson et al. 2012), or simply the result of tracking different individuals in each year. Because I tracked only three of the same bats in both years, my results do not necessarily indicate a change in network structure as differences may simply reflect different behavior by subsets of the colony at that site. However, the day-roosting behavior and social structure of bat maternity colonies may be inherently flexible and perhaps the differences between years such as I observed are common for the Indiana bat.

Flexibility in day-roosting social behavior may be a useful adaptation given snag ephemerality (Moorman et al. 1999, Bagne et al. 2008, Wisdom and Bate 2008) and has been documented in other species. For example, Silvis et al. (2014) documented similar differences among the day-roosting and social networks of the northern long-eared bat (*Myotis septentrionalis*) and J. S. Johnson et al. (2012) documented differences among network characteristics of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in forested habitats.

In general, the high day-roost network degree centralization that I observed is consistent with the currently held idea that some Indiana bat day-roosts are "primary" and others "secondary." In my study, the most central day-roost was the same in both 2009 and 2010. This day-roost was not only the most degree-central in the day-roost network, but it was used by the most radio-tagged bats, received the largest number of revisits, and had the largest exit counts. However, my emergence counts and other day-roost network structural characteristics indicate that the central day-roost did not necessarily contain the majority of bats within the colony at any given time. Distribution of the colony through multiple day-roosts, some of which at times contained substantial numbers of bats, suggests that exit counts of the primary day-roost provided limited information on colony size. Based on the distribution of bats throughout the day-roost network, even a large number of repeated counts at the primary day-roost will fail to account for bats that are spread consistently across multiple day-roosts. The small number of day-roosts located in 2009 that were re-used in 2010 also suggests that even if multiple day-roosts are monitored, exit counts may not convey the same ecological meaning across years. As such, understanding how bats are distributed through their day-roost network and how day-roosting behavior differs between years is necessary for robust estimation of colony size and evaluation of population trends from count data.

Little is known about secondary day-roost use by Indiana bats, but they appeared to be used selectively in my study. For bats generally, the use of multiple day-roosts is related to minimizing exposure to parasites (Reckardt and Kerth 2007), predator avoidance (Kunz and Lumsden 2003), and maintenance of social contacts (Willis and Brigham 2004). For the Indiana bat, selective use of secondary day-roosts could help bats maintain preferred day-roosting companions, reflect incomplete individual knowledge of the day-roost network and greater communication within cliques, or possibly serve as a strategy for coping with day-roost loss. Because of my short tracking periods I was unable to fully document specific preferential

associations among bats, but this has been shown in the congener northern long-eared bat (Garroway and Broders 2007) and may ensure a level of thermoregulatory stability. Despite selective use of secondary day-roosts, I found no evidence that Indiana bat maternity colony social networks had a modular structure. Indeed, my analysis indicates that bats within the colony largely were all in close social proximity as a result of coincident use of the most central day-roost in the day-roost network. Similarly, I found limited evidence that bats within age classes preferentially made connections with others in the same class. This suggests that my observed network structure was likely not a result of segregation of day-roosts by age class. Juvenile bats may have other impacts on aspects of network structure, and it is possible that network configuration changes with the addition of juvenile bats.

I found that nearly half of all Indiana bat dyads within years displayed more foraging overlap than expected, suggesting that association during foraging bouts may occur at some level. Echolocation calls such as "feeding buzzes" and other public foraging information are not believed to influence behavior of bats sufficiently to explain sociality (Kerth et al. 2001, Jonker et al. 2010), but interaction during flight may function as a way to maintain social cohesion through recruitment of day-roost mates (Chaverri et al. 2013). If association during foraging is important in recruitment of day-roost mates by Indiana bats, individuals or cliques within a maternity colony may be affected disparately by habitat disturbance in foraging areas. Similarly, if overlap of foraging areas is important in day-roost mate recruitment, disturbance of foraging areas may therefore also impact day-roosting network social structure and could pose a risk to persistence of maternity colonies. More foraging area overlap relative to the distribution of use within foraging ranges does not necessarily equate to association, and further may be an artifact of the location of the highest quality foraging habitat. However, a high level of overlap should be positively related to the potential for association.

The Indiana bat is known to exhibit strong fidelity to maternity day-roost areas (Gumbert et al. 2002, Kurta and Murray 2002, Sparks et al. 2005). The short distance between day-roosting area centroids and multi-year use of the most central day-roost in the day-roost network in my study support the idea of "general" day-roost area fidelity by Indiana bats in local landscapes. However, the number of day-roosts used in multiple years was limited and I did detect a substantial difference in the pattern of colony day-roost and space use between years. Why day-roost use and day-roost area differed so dramatically is unclear, but the more concentrated and

spatially limited colony day-roosting area in 2010 is consistent with the increased day-roost network centralization in that year.

Given the ephemeral nature of day-roosts and the apparent relationship between day-roost network structure and day-roosting area, it seems likely that day-roosting areas could shift with day-roost loss (see also, Kurta et al. 2002). Although little is known about how colony day-roost network structure and day-roosting area change in relation to day-roost deterioration and abandonment of primary day-roosts (Kurta 2005), I suggest the processes may be linked. For example, the colony may be scattered across numerous day-roosts in the season following abandonment of a primary day-roost as the colony locates and "chooses" another suitable primary day-roost. In following years, so long as the chosen primary day-roost remains suitable, the colony may concentrate day-roosting activity in the proximity of the new day-roost. Such a behavioral change is likely to be reflected in both network structure and day-roosting area use similar to what I observed. In central Indiana, Sparks et al. (2003) found that Indiana bats used more day-roosts and congregated less the year following the natural loss of a single primary day-roost. My data are limited temporally to only two years; however, there is evidence that the colony was using a different primary day-roost 2 years prior to my study (J. Chenger and K. Papenbrock, Bat Conservation and Management, Inc., unpublished report) and I may have observed part of the behavior change associated with the process of selecting a new primary day-roost. As the ephemerality of day-roost trees likely cause Indiana bat maternity colonies to experience frequent day-roost loss, including that of primary day-roosts, fission-fusion dynamics may provide a mechanism for the formation of new maternity colonies by presenting opportunities for the colony to split. Finally, habitat configuration may also influence changes in colony day-roosting area. Because my study was located in a highly agricultural area, forested habitats, and therefore likely also day-roosting resources, were limited and widely scattered across the landscape. In areas with greater amounts of forest or day-roosting resources, bats may not need to disperse as far in search of new day-roosts allowing a more stable day-roosting area. However, no information is currently available regarding whether day-roosting area is related to habitat configuration or resources.

Understanding day-roost area integrity and functionality is a primary concern in Indiana bat conservation. My day-roost removal simulation results increase the understanding of how day-roost loss may impact bat colonies. Importantly, because it is possible to infer sociality from

coincident day-roost use, fragmentation of the day-roost network also provides a method to begin to understand social aspects of colony fragmentation. In 2009 when I observed a less centralized day-roost network, connections between day-roosts, and by inference, between bats, in the colony were less robust to random day-roost loss than in 2010 when the network was more centralized. Similarly, the connections were more robust to targeted removal of the most central day-roost in 2010 than in 2009. The increased level of robustness to both random and targeted day-roost loss in 2010 was a result of a greater number of bats sharing secondary day-roosts. The greater number of connections allowed bats to maintain contact if a separate, shared day-roost was lost. In 2010, the level of colony social robustness to simulated random day-roost loss was greater than that of the northern long-eared bat (Silvis et al. 2014) a species whose day-roosting ecology is frequently compared to that of the Indiana bat (Foster and Kurta 1999, Carter and Feldhamer 2005, Timpone et al. 2009). Conversely, in 2009 the Indiana bat colony was less robust to random day-roost loss than northern long-eared bat maternity colonies. Although my simulations suggest that in some instances Indiana bat colonies may fragment with the loss of a small proportion of day-roosts, this is based solely on the potential for association at the remaining day-roosts. Association by bats is not limited to day-roosts. Indeed, studies of bat communication (Jonker et al. 2010) suggest it is possible for social connections to be re-established outside of day-roosts. In my study, foraging area overlap supports the idea that social connections could be re-established during foraging bouts. However, given the susceptibility to colony fragmentation that I observed in my simulations and the possible importance of foraging areas in the maintenance of colony structure, simultaneous loss of both day-roosting and foraging habitat likely has negative impacts on its social structure.

I did not incorporate day-roost specific (e.g., day-roost size, condition, or importance) and spatial factors (e.g. distribution of day-roosts) into my removal simulations, and therefore cannot predict certain network structural or spatial responses to specific day-roost loss. In particular, if individual day-roosts provide novel or highly preferred conditions for bats that are not replicated in another day-roost or potential day-roost, loss of that day-roost may cause changes in both association and space use. There is evidence that individual day-roosts are important and cannot be easily replaced in some bat species (Brigham and Fenton 1986, Chaverri and Kunz 2011), but the severity of impact caused by day-roost loss may be related to the degree of resource specialty and availability (Chaverri and Kunz 2011). I suggest that Indiana bat

colonies could respond to loss of an irreplaceable day-roost in several ways: 1) the entire colony could relocate to a nearby area with suitable replacement day-roosts; 2) the colony may fragment and occupy multiple areas or merge with other colonies reducing requirements for local day-roosting resources; or 3) the day-roosting area used by the colony could increase in size to incorporate suitable replacement day-roosts. Indiana bat colonies in the Midwest exhibit strong site fidelity (Gumbert et al. 2002, Kurta and Murray 2002, Sparks et al. 2005) and it is not known to what extent Indiana bats are able to relocate geographically even if suitable replacement day-roosts exist in another area. Site fidelity appears to be more variable in the Appalachians however (Britzke et al. 2003), and it is possible that colonies readily are able to relocate when day-roosting and foraging habitats are abundant. How or if multiple Indiana bat maternity colonies are able to coexist or merge is unknown, but this dynamic also may vary with the level of day-roost availability in a region. In the case of the loss of an irreplaceable day-roost where no adequate replacement exists and the colony does not relocate, there is risk that the colony becomes a non-contributing sink due to the impact of inadequate resources.

Conclusions

To my knowledge, I am the first to describe the day-roosting social structure and foraging associations of the Indiana bat and my study highlights the utility of examining sociality and day-roosting behavior of bats through a combination of graph theoretic and spatial methods. My results support currently held ideas that Indiana bat maternity colonies utilize day-roosts differentially and are loyal to day-roosting areas but also highlight a level of complexity in both day-roost and day-roosting area use that has not been previously described. Further, my study raises questions about the resiliency of Indiana bats to day-roost loss at 'primary' and 'secondary' day-roosts. Identifying how Indiana bat maternity colonies incorporate structured, non-random use of ephemeral day-roosting resources with relatively stable foraging areas remains a critical component for conservation planning. In addition, understanding colony mobility within landscapes in response to day-roost availability is critical for conservation and management of this endangered species as well as other bat species. Although my study begins to address the issues of how Indiana bat maternity colonies are structured socially and spatially, my understanding of the interactions between day-roost network structure, habitat, and

geographical space use remains greatly limited. Additionally, because I did not track adult males, my work addresses only part of the Indiana bat population. The social structure of adult males remains an enigma, but it seems unlikely that my results will apply. Replication of this study with longer duration and greater sample size across different habitat types is needed to fully describe these processes. Identifying the similarities and differences in colony structure across an array of geographic locations and habitat configurations would provide insight into the biological and ecological factors influencing colony behavior. For example, in contrast to my study, Indiana bat maternity colonies located in day-roost abundant areas may be less closely associated and more mobile on the landscape as suitable day-roosts are widely distributed spatially. Finally, manipulative experiments involving day-roost removal in conjunction with day-roost removal simulations could add greatly to the utility of the simulations and my understanding of colony structure and ecology. Although such experiments may have been possible in conjunction with habitat alteration work in previous years, reductions in population size due to white-nose syndrome (Blehert et al. 2009, Minnis and Lindner 2013) probably preclude such opportunities for the foreseeable future. Experimental manipulations on common species with similar day-roosting requirements and social behavior may provide useful information for conservation of the Indiana bat and other rare bat species.

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Table 5.1. Network metrics of an Indiana bat (*Myotis sodalis*) maternity colony day-roost network in Pickaway County, Ohio, USA, 2009-2010. Network metrics were calculated from a two-mode network consisting of bats and day-roosts. The direction of difference and *P*-values from Monte Carlo simulations are given in parenthesis.

Year	Number of day-roosts	Mean degree	Density	Clustering	Degree centralization
2009	33	1.94	0.09 (<, 0.05)	0.61 (>, 0.002)	0.47 (>, 0.002)
2010	17	3.76	0.15 (0.42)	0.81(>, 0.002)	0.81 (>, 0.002)

Table 5.2. Network metrics of an Indiana bat (*Myotis sodalis*) maternity colony social network in Pickaway County, Ohio, USA, 2009-2010. Network metrics were calculated from single-mode projections of a two-mode network consisting of bats and day-roosts. The direction of difference and *P*-values from Monte Carlo simulations are given in parenthesis.

Year	Number of bats	Mean degree	Density	Clustering	Degree centralization	Leading eigenvector modularity	Homophily
2009	21	8.00	0.40 (>, 0.002)	0.78 (>, 0.002)	0.44 (>, 0.006)	0.21 (0.54)	0.20 (>, 0.003)
2010	25	19.60	0.82 (>, 0.002)	0.96 (>, 0.002)	0.15 (0.14)	0.01 (<, 0.002)	-0.02 (0.10)
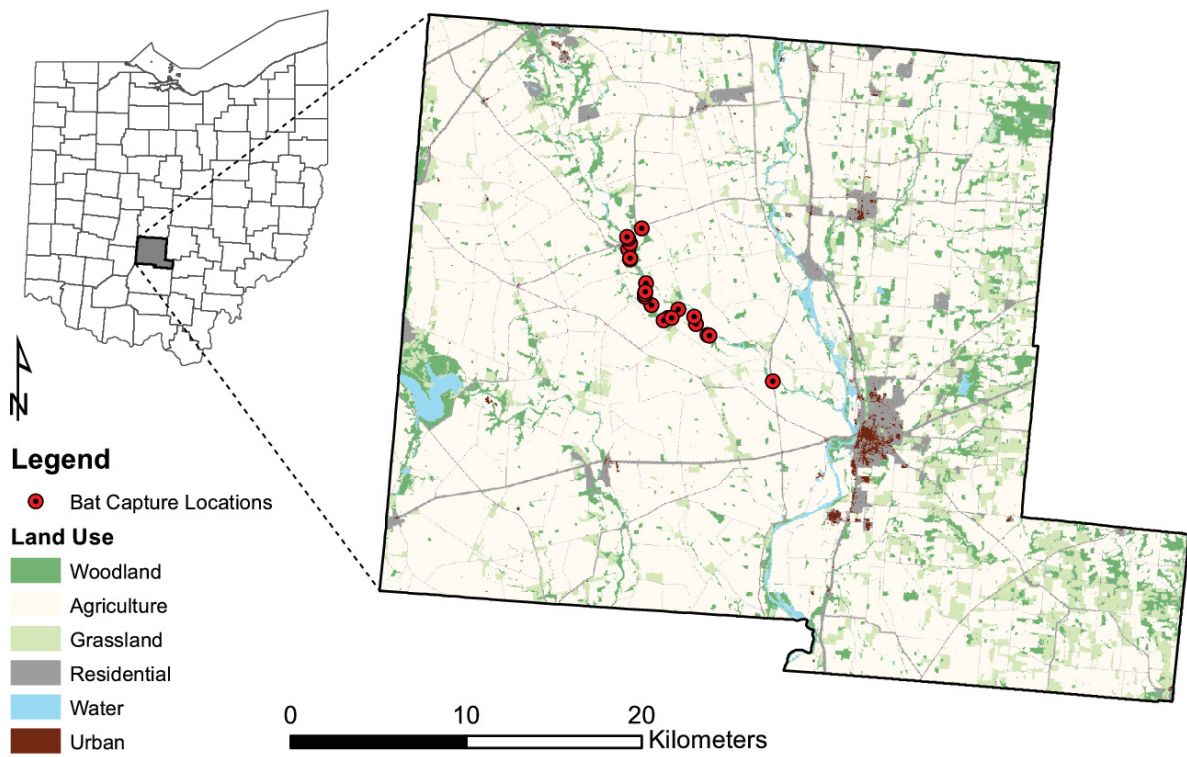
Figure 5.1. Indiana bat (*Myotis sodalis*) capture locations and landscape configuration in Pickaway County, Ohio, USA.
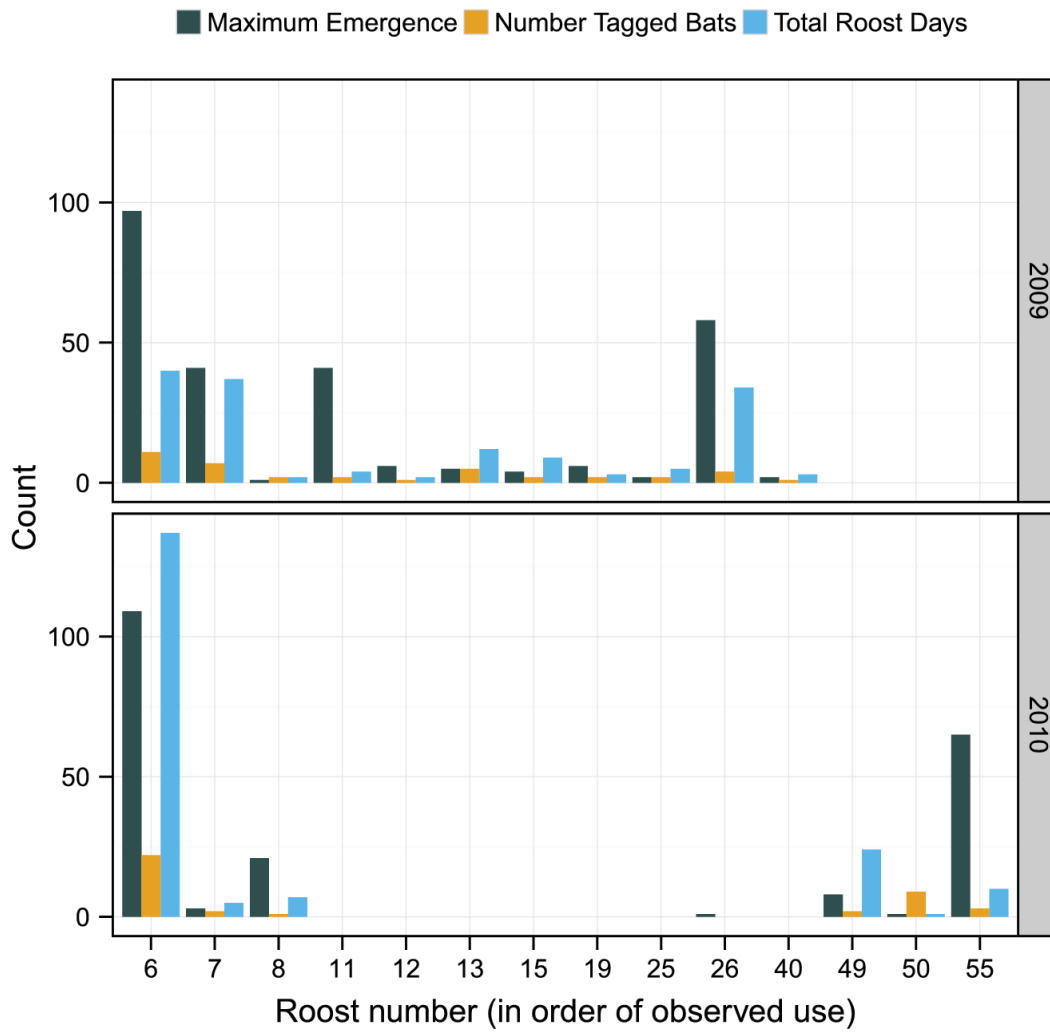
Figure 5.2. Indiana bat (*Myotis sodalis*) maternity day-roost uses. Maximum day-roost emergence, number of radio-tagged bats, and total day-roost days for day-roosts used by an Indiana bat maternity colony in Pickaway County, Ohio, USA, 2009-2010. Data are presented only for day-roosts with emergence counts.

Figure 5.3. Indiana bat (*Myotis sodalis*) day-roost network maps. Two-mode network maps of an Indiana bat maternity colony in Pickaway County, Ohio, USA, 2009 (A) and 2010 (B). Node type indicated by color, edge width scaled by the number of connections.

Figure 5.4. Indiana bat (*Myotis sodalis*) social network maps. Single-mode social network map of an Indiana bat maternity colony in Pickaway County, Ohio, USA, 2009 (A) and 2010 (B). Map projected from the two-mode network of bats and day-roosts. Nodes are colored by age class.
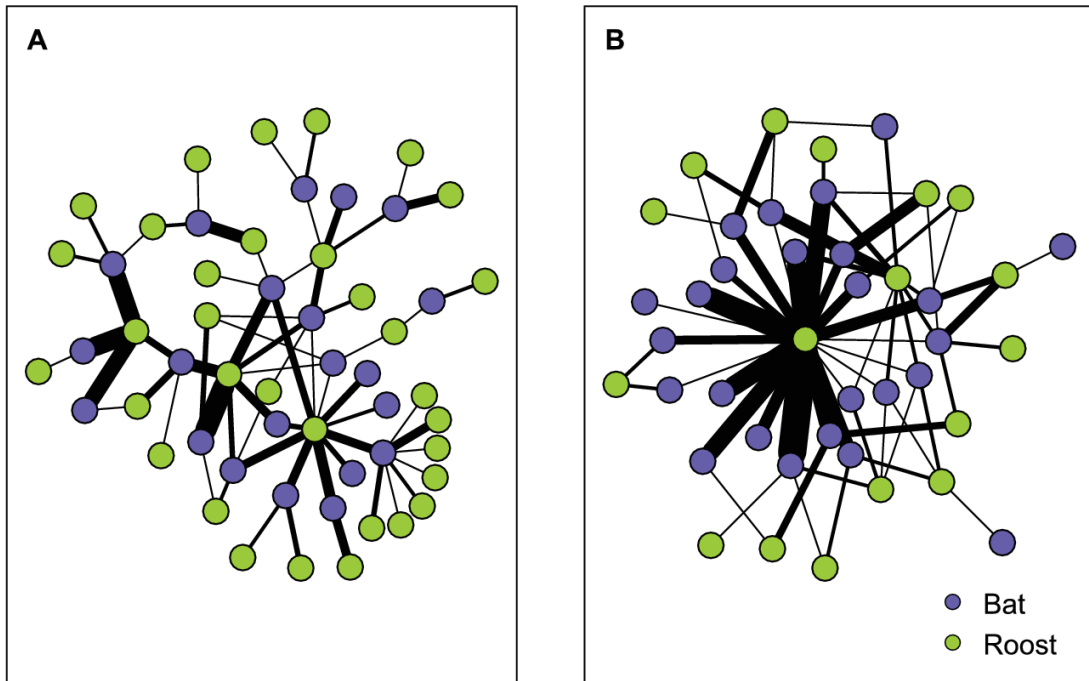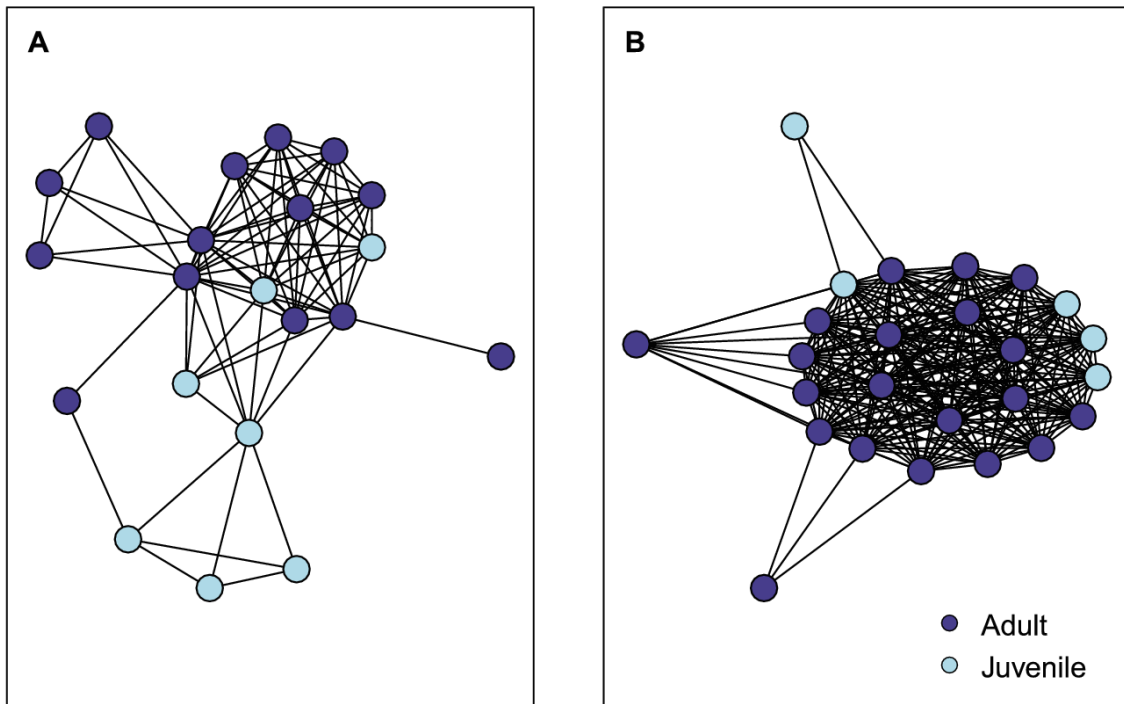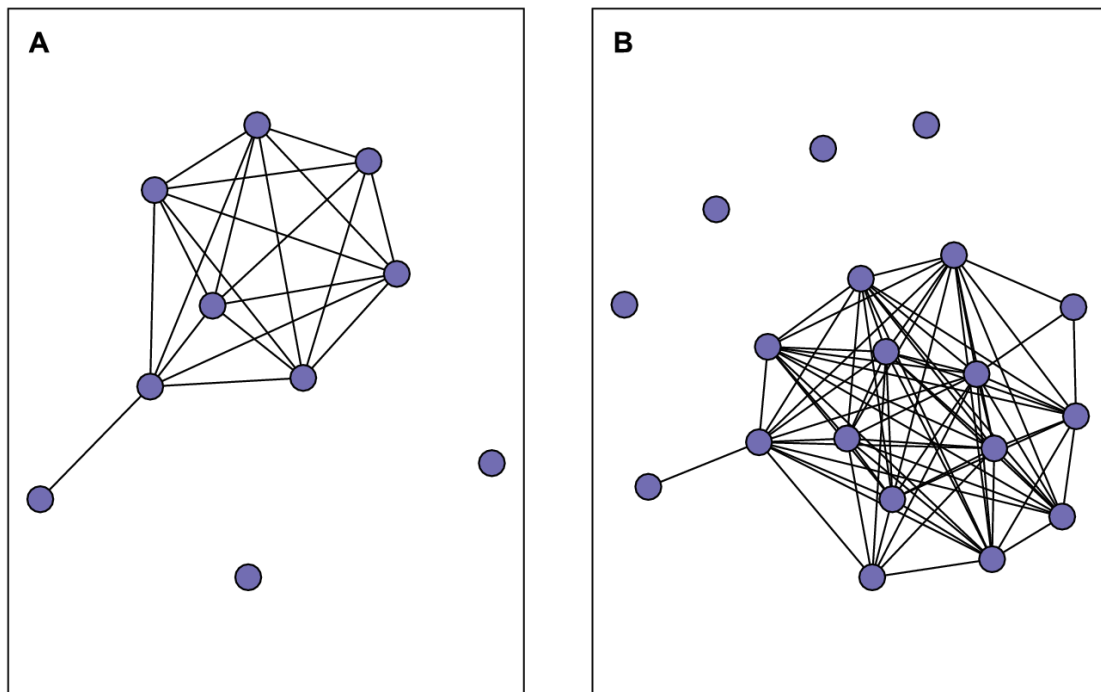
Figure 5.5. Indiana bat (*Myotis sodalis*) foraging network maps. Foraging network maps for of an Indiana bat maternity colony in Pickaway County, Ohio, USA in 2009 (A) and 2010 (B). Connections between nodes (bats) were created when the utilization distribution overlap index for a dyad was > 1.
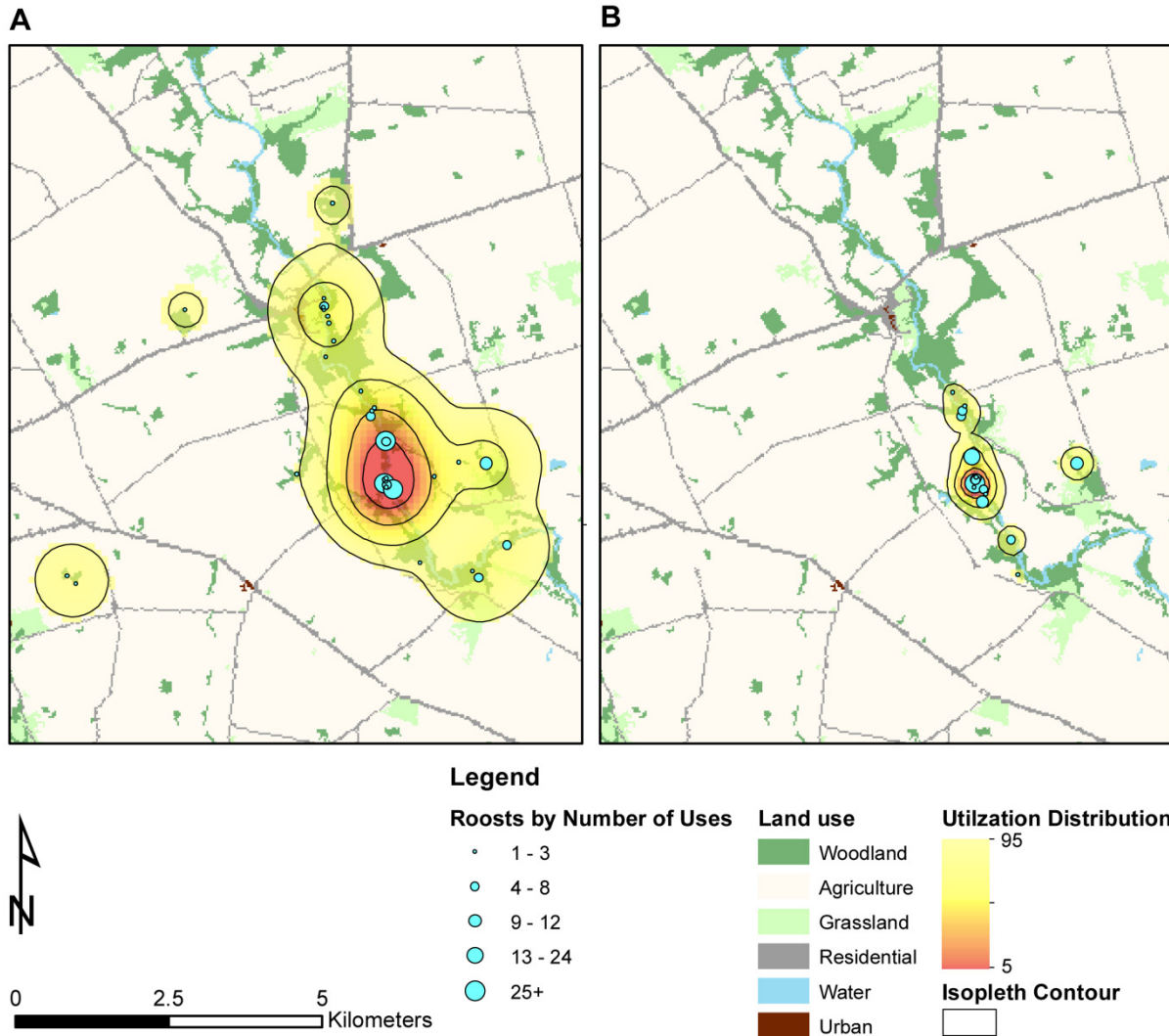
Figure 5.6. Indiana bat (*Myotis sodalis*) day-roosting areas. Bivariate fixed kernel density day-roosting area utilization distributions and day-roost locations of an Indiana bat (*Myotis sodalis*) maternity colony in Pickaway County, Ohio, USA in 2009 (A) and 2010 (B). Estimation of the utilization distributions was conducted using the pooled locations from all radio-tagged bats and weighted by the number of uses of individual day-roosts. Day-roost size is log scaled by the number of uses to show the relative contribution to the utilization distribution. The 25, 50, 75, and 95% home range contour intervals are shown.

Figure 5.7. Day-roost removal impacts on Indiana bat (*Myotis sodalis*) network fragmentation. Simulated effect of day-roost removal on the fragmentation of an Indiana bat maternity colony day-roost network in Pickaway County, Ohio, USA, 2009-2010. Random day-roost removal was performed 1,000 times per proportion of day-roosts removed; lines represent mean ± standard error number of networks after node removal.

Chapter 6: Conclusion

Alexander Silvis

Understanding of day-roost selection behavior by reproductive female bats is critical to successful management and conservation 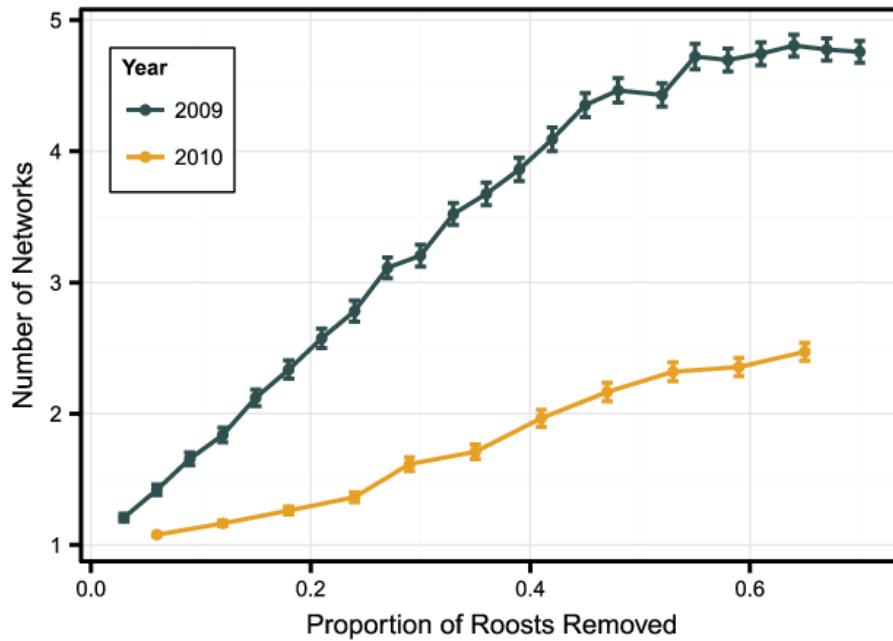efforts. Day-roosts provide bats with protection from predators and weather, sites for social interaction, nurseries, and promote energy conservation (Kunz and Lumsden 2003). Cave hibernacula and tree day-roosts of cavity day-roosting species represent the most approachable management units and habitat management for bats historically has focused on conservation of these resources (Fenton 1997). In the context of summer maternity colonies, day-roost management alone is insufficient. Since the pioneering work of Wilkinson (1984, 1986) unveiled the existence of complex social behaviors in bats and their importance in bat ecology, scientific understanding of bat social ecology has expanded greatly, but only for a select few species (Kerth 2008*a*, Johnson et al. 2013). It is clear that social group membership has important consequences for bats and may be a driver of some aspects of behavior (Chaverri et al. 2007, 2013, Kerth 2008*a*, *b*, J. S. Johnson et al. 2012), but surprisingly few studies have discussed or accounted for the social aspects of bat ecology in bat management. Understanding bat social ecology has utility in a range of management applications, including understanding potential pathways of disease transmission (Fortuna et al. 2009) and habitat disturbance (Rhodes et al. 2006, Chaverri 2010), and potentially may provide the basis for targeted management approaches directed at individual maternity colonies or other social groups.

My research began with the goal of using the relatively common and locally-abundant northern long-eared bat (*Myotis septentrionalis*) as a surrogate for the study of day-roost loss on the sympatric, and endangered, Indiana bat (*Myotis sodalis*). Prior to my study, much of the published literature on northern long-eared bats had focused on day-roost selection and comparisons with day-roosts used by the sympatric Indiana bat, but some information on the social ecology of the northern long-eared bat was available, making the species a useful and suitable study surrogate. In the intervening time since this project began, White-nose Syndrome, an invasive and lethal fungal pathogen affecting cave-hibernating bats (Fenton 2012, Francl et al. 2012, Reeder et al. 2012, Thogmartin et al. 2012, 2013), spread rapidly from the northeast across the midwestern and southeastern United States (Maher et al. 2012), greatly reducing or extirpating populations of northern long-eared bats. Now, for the northern long-eared bat, a

better understanding of social ecology is critical as the United States Fish and Wildlife Service moves to list this once common species as endangered (*Federal Register* § 78:61045-61080).

My research provides insight into the day-roosting social ecology of the northern long-eared and Indiana bats. My findings indicate that both northern long-eared bats and Indiana bats form non-random socially assorting colonies through the structured use of day-roosts. The presence of "primary" and "secondary" day-roosts, which receive differing levels of use by bats, was discussed in Callahan et al.'s (1997) study of Indiana bat ecology, and recently identified for the northern long-eared bat (J. B. Johnson et al. 2012). Despite this, little context was available relative to the possibility of such patterns of use being the result of chance observational differences for individual day-roosts. Through the use of Monte Carlo simulations, I determined that day-roost use and association within day-roost networks is non-random. Whether the level of day-roost importance within a day-roost network is dependent upon physical characteristics or social factors is unclear; this would be a productive area of future research.

Within the overall patterns of day-roost network structure, I found that colonies differed slightly in specific characteristics. Both tropical and temperate bat species social structure and day-roost use patterns are driven by the availability of day-roosts (Chaverri 2010, Chaverri and Kunz 2010, J. S. Johnson et al. 2012). I found that day-roost availability was not limiting for any of my colonies and, moreover, the number of available potential day-roosts per used day-roost was similar among my colonies. Differences in social structure and day-roost use patterns that I observed appear to be related to the reproductive condition of maternity colonies. During parturition and early lactation, I observed greater social connectedness and a greater degree of day-roost network centralization. Such increased association likely provides bats with benefits related to thermal regulation (Willis and Brigham 2007) and, potentially, communal nursing (Wilkinson 1992). Although my observations of differences in social structure and day-roost use patterns relative to reproductive condition are not definite, a similar pattern has been identified elsewhere (Patriquin et al. 2010). Moreover, day-roosts used during the physiologically demanding lactation period differed slightly from those used by non-lactating bats. Interestingly, at the individual level, reproductive condition did not appear to be an important predictor of the number of day-roosts used, but the distances moved between sequentially used day-roosts by bats in different reproductive conditions did differ, with lactating and post-lactating bats moving the shortest distances. I posit that in situations where potential day-roosts are abundant, fine-

scale aspects of social structure of the northern long-eared bat is driven by reproductive condition.

My results suggest that the areas occupied by northern long-eared bat maternity colonies are exclusive. Exclusive use of day-roosting areas probably provides numerous benefits to bats related to ease of day-roost-mate recruitment and information sharing, but, from a bat management perspective, exclusivity of day-roosting areas suggests that northern long-eared bat maternity colonies may be amenable to targeted management approaches. Potential targeted management approaches include the limited removal of day-roosts coupled with creation of supplemental day-roosting opportunities as a means to "shift" colonies on the landscape in support of other forest management objectives, and planning of forest harvesting to minimize the number of colonies impacted. In developing targeted management approaches, it is important to consider the nature of colony space use, habitat configuration, and resource selection. My results show that northern long-eared bat core day-roosting areas coincided with the location of highly central day-roosts. Anecdotally, core day-roosting areas also corresponded with the availability of a preferred day-roosting resource, sassafras (*Sassafras albidum*) trees in middle and advanced decay stages. Although future research is needed to confirm that core day-roosting areas coincide with the spatial distribution of day-roosting habitat, if this is the case, it may be possible to manage habitat within colony day-roosting areas with the use of heterogeneous management techniques like group tree selection. Nonetheless, day-roost selection preferences of northern long-eared bats differ across the species range, likely in relation to differences in overall forest conditions (Lacki and Schwierjohann 2001, Menzel et al. 2002, Perry and Thill 2007, Lausen et al. 2008). Because habitat availability and quality of specific resources are important drivers of many animal behaviors, it is important to understand day-roost selection preferences when discussing both social structure and the potential for targeted management approaches.

Wildlife and land managers tasked with bat conservation often view day-roosts and day-roosting areas as fixed landscape elements decoupled from stochastic environmental process (Dixon et al. 2013, Stone et al. 2013); frequently, managers are required to take this approach by legal and regulatory institutions. Moreover, day-roosts often are considered critically limiting resources for bats, but there is little empirical evidence of this for many species in forested habitats in North America (Kalcounis-Rüppell et al. 2005). Conservative approaches to management have little empirical justification, as the nature of day-roost and day-roosting area

disturbance has not been well studied in temperate bats. The ephemeral nature of day-roosts and the dynamic nature of forest ecosystem structure alone (Moorman et al. 1999, Runkle 2012) illustrate that management of day-roosts as fixed landscape elements is an unrealistic approach to habitat management for tree-day-roosting bats. My work is the first effort to directly examine the impacts of day-roost removal on colonial bats in temperate forest habitats, and provides the first step to linking focal and diffuse disturbance impacts on bats. My day-roost removal simulations provide the first model of the potential impacts of day-roost loss on fragmentation of northern long-eared bat maternity colonies, and suggest a level of robustness to day-roost loss that is surprisingly similar to observed turnover rates of snags following fire (Bagne et al. 2008). Results from my hierarchical day-roost removal experiment supported my simulation-based predictions regarding colony fragmentation. The apparent accuracy of my day-roost removal simulation methods in predicting colony fragmentation suggests that day-roost loss impacts for individual colonies can be predicted in advance of forest management actions. Although relatively difficult, additional parameterization of my simulation-based model to include information on day-roost availability and relative importance, colony reproductive condition, and spatial arrangement of day-roosts is tractable, and probably would provide greatly enhanced, generalized predictions for the species.

Persistence of northern long-eared bat maternity colonies after day-roost removal, and consistent patterns of day-roost use and behavior of individual bats suggest that northern long-eared bats are robust to low-moderate levels of day-roost loss. These results are consistent both with theoretical predictions and the observed positive responses of the species to prescribed fire (Johnson et al. 2009, Lacki et al. 2009a). For forest and wildlife managers, the robustness of northern long-eared bat maternity colonies to disturbance has important implications as the United States Fish and Wildlife Service moves to list the species as endangered; specifically, determination of the type and scale of forest management activities that can occur in known or suspected day-roosting habitat. My work suggests that forest management techniques that remove limited numbers of northern long-eared bat maternity roosts, outside of the maternity season, will not have significant adverse impacts on maternity colonies. Relative to specific management techniques, my results probably are best applied to the use of prescribed fire and single-tree or group select harvesting. However, while my results suggest colony robustness to limited maternity roost loss, determination of the maximum threshold of robustness remains an

unknown, but vitally important, aspect of northern long-eared bat ecology. Finally, caution should be taken in interpretation of my results. In particular, because day-roosts were not a limiting resource on my study area, the impacts of day-roost loss on northern long-eared bats may vary in other regions or forest systems that display different levels of day-roost availability.

Northern long-eared bats have been proposed as a study surrogate for the Indiana bat on the basis that day-roost selection criteria by these species overlap (Foster and Kurta 1999, Carter and Feldhamer 2005, Lacki et al. 2009b, Timpone et al. 2009). Although my results show overlap in social structure and patterns of day-roost use between Indiana bats and northern long-eared bats, they also highlight important differences in the social ecology of these two species. Differences in the social structure and patterns of day-roost use between these two species suggest that use of the northern long-eared bat as a study or possible conservation guide for the Indiana bat may be untenable, or one with substantial caveats. Relative to colony size, Indiana bat day-roost networks substantially are smaller than those used by northern long-eared bats, suggesting that Indiana bats may respond more negatively to day-roost loss. Nonetheless, the non-random nature of Indiana bat social ecology suggests that this species also may be amenable to targeted management approaches, such as roost enhancement or prescribed fire; in fact, the relatively small size of Indiana bat day-roost networks and the closeness of association among bats provides some indication that this species may be more amenable to targeted management approaches than the northern long-eared bat.

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