

Research Article

Forest Succession and Maternity Day Roost Selection by *Myotis septentrionalis* in a Mesophytic Hardwood Forest

Alexander Silvis,¹ W. Mark Ford,^{1,2} Eric R. Britzke,³ Nathan R. Beane,³
and Joshua B. Johnson⁴

¹ Department of Fish and Wildlife Conservation, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA

² US Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit, Blacksburg, VA 24061, USA

³ Environmental Laboratory, US Army Engineer Research and Development Center, 3909 Halls Ferry Road, Vicksburg, MS 39180, USA

⁴ Pennsylvania Game Commission, 2001 Elmerton Avenue, Harrisburg, PA 17110, USA

Correspondence should be addressed to Alexander Silvis, silvis@vt.edu

Received 17 May 2012; Revised 24 July 2012; Accepted 26 July 2012

Academic Editor: Brian C. McCarthy

Copyright © 2012 Alexander Silvis et al. This is an open access article distributed under the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

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. We tracked 58 female northern 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, we were 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 bats, we 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.

1. Introduction

Prior to the onset of white-nose syndrome (WNS) in North America [1], northern bats (*Myotis septentrionalis*) were common in most forest types in the eastern United States and southern Canada [2–9]. Northern bat foraging activity consistently has been greatest in closed-canopy forests [5, 10–13] and maternity roosts and roost areas of live trees and/or snags are typically located in upland forests [4, 7, 11, 14, 15].

Management for Myotid bats in North America often is based on the conservation of summer maternity roosts and winter hibernacula [16, 17]. 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 [16, 18]. Although northern

bats have been the focus of several recent studies [9, 19, 20], patterns of maternity roost selection at the forest stand and landscape scale are not well understood. There is considerable variation in forest conditions and roost tree species preference and differences (or lack thereof) between roosts and other available trees across the northern bat's distribution [4, 5, 21]. Nonetheless, consensus is that northern 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 [4, 7, 11].

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 nonrandom assorting social groups should be the focal point of roost conservation and that there is a need to better quantify the multiscale habitat features necessary to preserve and maintain maternity colonies [22]. In the central Appalachians, Johnson et al. [9] identified such nonrandom assorting social groups in female northern bats and further illustrated how these groups form scale-free networks of dayroosts 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 [9, 22]. 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. We collected day roost data as part of a larger long-term study on northern bat social ecology on the Fort Knox military reservation in north-central Kentucky, USA; our overall objective was to document patterns in northern bat summer maternity roost selection at Fort Knox. Because we documented strong selection of a single species as a day roost that was not historically prevalent in presettlement closed canopy forests, we attempt to describe this pattern in the larger context of forest establishment and disturbance processes related to land-use history using our data and examples from previous northern bat research.

2. Methods

2.1. Study Site Description. We conducted our northern 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 [23]. 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 [23]. Forest cover is predominantly a western mixed-mesophytic association [24], with second- and third-growth forests dominated by white oak (*Quercus alba*), black oak (*Q. velutina*), chinkapin oak (*Q. muehlenbergii*), shag-bark 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 [25]. 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.

2.2. Data Collection. We captured northern 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 bats netted, we determined age (by degree of epiphyseal-diaphyseal fusion [26]), mass, forearm length, sex, and reproductive condition [27] and placed uniquely numbered lipped aluminum bands on the forearms. We also attached LB-2 radio transmitters (0.46–0.54 g; Holohil Systems Ltd. Woodlawn, ON, Canada) between the scapulae of female northern bats using Perma-Type Surgical Cement (Perma-Type Company Inc., Plainville, CT, USA). We released tagged bats near net sites within a few minutes of capture. We 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), we located northern bat day roosts every day for the life of the transmitter or until the unit dropped from the bat. We georeferenced all day roosts located using a Garmin GPSmap 60CSx global positioning system (Olathe, KS, USA). At each female northern bat day roost, we recorded roost species, diameter at breast height (dbh), height, crown class ([28]; i.e., 1 = suppressed, 2 = intermediate, 3 = codominant, 4 = dominant), and decay class ([29]; 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, we measured the nearest four trees using the point-quarter system [30]; for each of these trees we determined species and measured distance to roost, dbh, decay class, and crown class. To assess canopy cover and canopy gap characteristics of day roosts we measured gap fraction, leaf area index (LAI), and total below canopy photosynthetically active photon flux density (PPFD) using WinSCANOPY and XLScanopy softwares (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, we 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, we recorded potential roosts (i.e., boles with loose/exfoliating bark, visible cavities, or other defects) by species along randomly directed 20 × 100 m belt transects from the periphery of each point-quarter plot [15].

2.3. Data Analysis. We 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. We used chi-square goodness-of-fit tests to determine if day roosts were equitably distributed 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 relocations of individuals [31, 32]. By pooling use data across individuals and counting each tree as a single location rather than each use, we assumed independence of individual

TABLE 1: Candidate model sets used to compare female *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 + PPF
2	dbh + height + Decay + percent bark
3	dbh + height
4	Decay + percent bark
5	Decay + percent bark + gap fraction + LAI + PPF
6	Gap fraction + LAI + PPF
7	Percent + sin (aspect) + cos (aspect) + elevation + gap fraction + LAI + PPF
8	Percent slope + sin (aspect) + cos (aspect) + elevation
9	Null model

trees. We used an information theoretic approach (IT) to compare day roosts used by bats during pregnancy to those used by bats during lactation and nonlactation 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 we measured canopy position, we removed it from all models due to unacceptably high-standard errors. We followed Garroway and Broders [33] in separating day roost maternity use status (lactation or nonlactation) by date of capture of the first lactating female and volant juvenile. We used the same IT approach and candidate model set to compare the most selected day roost species to the collective of all other species. We ranked models using Akaike's criteria (AIC), the difference between the model with the lowest AIC and the AIC of the i th model (Δ_i) and Akaike's weights (w_i) [34]. We 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 receiver operating characteristic (AUC), and percent correct classification. To avoid problems of circularity when analyzing aspect, we used sine and cosine transformations of aspect for logistic analysis. All tests were performed using the R statistical program (version 2.14) [35] with significance for all tests accepted at $\alpha \leq 0.05$.

3. Results

We mist-netted on 33 nights between 24 May and 17 July 2011 and captured fifty-eight adult females, two juvenile females and 16 adult male northern bats. Eighteen of the adult females were pregnant, 29 were lactating, 3 had ceased lactation, and 8 were nonreproductive. Transmitters were attached to all 58 adult female northern bats; mean transmitter retention time was 4.1 days. Overall, we tracked these bats to 105 day roosts that comprised 21 tree species (Table 2) for a total of 270 relocation events. Number of tagged bats within a single day roost ranged from 1 to 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 to 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 ± 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 ± 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 m²*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 we 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 (67%; $W = 19$, $P < 0.001$). We detected no difference in dbh ($W = 1334$, $P = 0.46$), gap fraction ($W = 1062$, $P = 0.27$), LAI ($W = 1273$, $P = 0.75$) PPF ($W = 1250$, $P = 0.87$), 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 were significantly shorter ($W = 1576$, $P = 0.02$) and had significantly less remaining bark than live trees ($W = 2205$, $P < 0.001$; Table 3).

Our best supported model differentiating day roosts by maternity status was a site-specific canopy condition model containing gap fraction, LAI, and PPF (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 PPF (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, while 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

TABLE 2: Female *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 × 100 m belt transects oriented at random azimuths from each day roost.

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

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. Our best supported model differentiating sassafras day roosts from other species was a tree-specific model containing dbh and 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%).

4. Discussion

The limited day roost documentation of northern bats mostly has shown maternity colony use of snags and live trees larger and more decadent than neighboring boles. It is widely 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 [18, 36], particularly during lactation [34]. 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 [36]. 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 $m^2 \cdot m^{-2}$, mean = 5.41 $m^2 \cdot m^{-2}$) our observed LAI was low [37]. Nonetheless, our LAI value is greater than those reported for nonshrubby forest understory conditions (range 0.2–13.3 $m^2 \cdot m^{-2}$, mean 1.81 $m^2 \cdot m^{-2}$; [37]) supporting the supposition that northern bats roost in relatively dense forest at Fort Knox.

Many studies have used canopy closure as a surrogate measure for solar radiation. We found that our 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 [4] and Menzel et al. [5] as well as to Johnson et al. [36]. However, canopy closures at our day roosts were substantially greater than those reported by Garroway and Broders [33] in Nova Scotia, Canada, and Carter and Feldhamer [38] in southern Illinois bottomland hardwoods. Additionally, while the use of day roosts that were larger than surrounding trees in our study would generally support the solar radiation hypothesis, the majority of day roosts (71.4%) we observed were suppressed and under substantial canopy cover.

Our analysis of day roost selection by maternity status indicates that gap fraction and solar radiation best differentiate day roosts used during lactation and nonlactation periods. However, the overall poor performance of the model suggests that female northern bats at our study sites did not strongly differentiate between day roosts used during different reproductive conditions. This contrasts with Garroway and Broders [33] who found that female northern bats selected larger day roosts during the lactation period relative to non-lactation periods and suggests that selection of larger day roosts is a function of increased solar radiation.

TABLE 3: Mean \pm SD values of day-roost characteristics for all trees, live and snag trees, and the two tree species most commonly used by female *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	<i>Sassafras albidum</i>	<i>Acer saccharum</i>
<i>N</i>	105	35	70	51	10
dbh (cm)	30.19 \pm 18.59	31.69 \pm 18.06	29.44 \pm 18.94	20.96 \pm 7.69	26.09 \pm 10.92
Height (m)	14.56 \pm 7.07	17.39 \pm 8.14	13.15 \pm 6.05	11.86 \pm 4.65	13.48 \pm 5.79
Decay (stage)	3.53 \pm 1.59	1.71 \pm 0.46	4.44 \pm 1.10	4.02 \pm 1.48	3.6 \pm 1.65
Live (<i>N</i>)	33	NA	NA	11	4
Remaining bark (%)	64.57 \pm 36.11	93.00 \pm 4.47	50.36 \pm 36.61	52.82 \pm 39.10	76.00 \pm 28.36
Suppressed (%)	71.4	51.4	81.4	92.2	70.0
Gap fraction (%)	8.37 \pm 2.26	7.98 \pm 1.96	8.57 \pm 2.38	8.13 \pm 2.25	9.42 \pm 1.81
Slope (%)	13.46 \pm 11.10	11.67 \pm 9.42	14.35 \pm 11.81	12.05 \pm 10.65	16.68 \pm 11.35
Aspect ($^{\circ}$)	222.90 \pm 90.84	211.08 \pm 93.09	227.51 \pm 90.34	223.80 \pm 92.15	241.91 \pm 79.22
Elevation (m)	217 \pm 18.26	219.92 \pm 16.38	216.96 \pm 19.17	219.35 \pm 16.96	216.92 \pm 11.78
LAI (m ² *m ⁻²)	2.55 \pm 0.37	2.74 \pm 0.34	2.71 \pm 0.43	2.71 \pm 0.38	2.68 \pm 0.34
PPFD (μ mol*m ⁻² *s ⁻¹)	1.65 \pm 0.76	1.68 \pm 0.82	1.63 \pm 0.72	1.65 \pm 0.89	1.71 \pm 0.59

TABLE 4: Rankings of models used to compare female *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	<i>K</i>	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

TABLE 5: Parameter summary of the best supported model comparing female *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	$P > \chi^2$	Odds ratio
Intercept	-4.32	4.12	1.1	0.29	—
Gap fraction	0.56	0.22	6.4	0.01	1.75
LAI	0.9	1.09	0.69	0.41	2.47
PPFD	-1.15	0.38	9.3	0.002	0.32

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 our sites relative to generally cooler northern sites [33] is not surprising, nor

is comparable canopy cover between our sites and sites along similar latitudinal gradients [4, 5, 36]. A latitudinal temperature gradient would explain differences between our analysis of day roost selection by maternity status and that of Garraway and Broders [33].

We found that day roosts were consistently located on ridge tops and plateaus primarily on south facing aspects similar to the observations of other researchers working with northern bats [4, 36, 39]. 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 [40]. Historic cycles of repeated natural stand disturbance and increased snag presence rather than increased solar radiation might be the primary influence on northern 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 play a role in northern bat day roost selection.

TABLE 6: Rankings of models used to compare *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 i th 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 + PPF	17	122.38	5.71	0.04
Decay + percent bark + gap fraction + LAI + PPF	11	136.32	19.65	<0.001
Decay + percent bark	8	141.22	24.55	<0.001
Gap fraction + LAI + PPF	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 + PPF	9	152.20	35.53	<0.001
Percent slope + sin (aspect) + cos (aspect) + elevation	6	153.56	36.88	<0.001

TABLE 7: Parameter summary of the best supported model comparing *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 χ^2	$P > \chi^2$	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

We documented a wider use of tree species by northern bats than reported elsewhere [4, 5, 7, 36], including the first recorded use of eastern redcedar (*Juniperus virginiana*). Northern bats in our study displayed a marked preference for sassafras as day roosts. Black locust, a preferred day roost species by both male and female northern bats in the central Appalachians of West Virginia [5, 15, 36], was rarely used at Fort Knox. Despite overwhelming selection by northern bats, our inability to reliably differentiate sassafras day roosts from other day roost using logistic regression was surprising. As suggested by Ford et al. [15], 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 our sites clearly provided appropriate roosting structure, preference for this tree species is probably ecologically novel at the scale we observed. In the context of forest succession, this fast-growing shade-intolerant species [41] would not historically

have been a large component of closed canopy forests in our study region under small disturbance gap-phase dynamics [42–45]. Much of the extant sassafras at Fort Knox is almost certainly a product of extensive timber harvest from the late 1700s to 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 [46, 47].

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 bats [4, 5, 17, 33, 36] and the lack of differences between species used as day roosts in this study, we believe that ecological processes of forests may play a greater role in bat day roost selection than is currently recognized. Because our original intent was not to analyze the effects of forest succession on day roost selection, we are unable to test this hypothesis directly using our data. However, we 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 bats in Arkansas [7] largely were snags created following pine beetle (*Ips* spp.) outbreaks (R. Perry, personal communication). Ford et al. [15] suggested that northern 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 we 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 [48].

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. We are 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. We believe the following questions should be considered relative to understanding day roost ecology of tree-roosting bats such as the northern 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 have drastically 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?

5. 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 [49]. 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 [40, 49] across the range of the northern bat may not be feasibly recreated by managers, or even desired in the light of other stewardship needs. Furthermore, current conditions do not necessarily 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.

Acknowledgments

This paper was supported by the US Army Environmental Quality and Installation Basic Research 6.1 program. The authors thank Jimmy Watkins, Mike Brandenberg, and Charlie Logsdon for their assistance in supporting this project. The Kentucky Department of Fish and Wildlife Resources graciously provided field housing for this project. Meryl Friedrich and Mark Lawrence provided invaluable field assistance on this project. Use of trade, product, or firm names does not imply endorsement by the US government.

References

- [1] D. S. Blehert, A. C. Hicks, M. Behr et al., "Bat white-nose syndrome: an emerging fungal pathogen?" *Science*, vol. 323, no. 5911, article 227, 2009.
- [2] R. W. Foster and A. Kurta, "Roosting ecology of the Northern bat (*Myotis septentrionalis*) and comparisons with the endangered Indiana bat (*Myotis sodalis*)," *Journal of Mammalogy*, vol. 80, no. 2, pp. 659–672, 1999.
- [3] M. C. Caceres and R. M. R. Barclay, "*Myotis septentrionalis*," *Mammalian Species*, no. 634, pp. 1–4, 2000.
- [4] M. J. Lacki and J. H. Schwieryjohann, "Day-roost characteristics of Northern bats in mixed mesophytic forest," *The Journal of Wildlife Management*, vol. 65, no. 3, pp. 482–488, 2001.
- [5] M. A. Menzel, S. F. Owen, W. M. Ford et al., "Roost tree selection by Northern long-eared bat (*Myotis septentrionalis*) maternity colonies in an industrial forest of the central Appalachian mountains," *Forest Ecology and Management*, vol. 155, no. 1–3, pp. 107–114, 2002.
- [6] H. G. Broders, G. J. Forbes, S. Woodley, and I. D. Thompson, "Range extent and stand selection for roosting and foraging in forest-dwelling Northern long-eared bats and little brown bats in the Greater Fundy Ecosystem, New Brunswick," *The Journal of Wildlife Management*, vol. 70, no. 5, pp. 1174–1184, 2006.
- [7] R. W. Perry and R. E. Thill, "Roost selection by male and female Northern long-eared bats in a pine-dominated landscape," *Forest Ecology and Management*, vol. 247, no. 1–3, pp. 220–226, 2007.
- [8] A. D. Morris, D. A. Miller, and M. C. Kalcounis-Rueppell, "Use of forest edges by bats in a managed pine forest landscape," *The Journal of Wildlife Management*, vol. 74, no. 1, pp. 26–34, 2010.
- [9] J. B. Johnson, W. Mark Ford, and J. W. Edwards, "Roost networks of Northern myotis (*Myotis septentrionalis*) in a managed landscape," *Forest Ecology and Management*, vol. 266, pp. 223–231, 2012.
- [10] T. S. Jung, I. D. Thompson, R. D. Titman, and A. P. Applejohn, "Habitat selection by forest bats in relation to mixed-wood stand types and structure in central Ontario," *The Journal of Wildlife Management*, vol. 63, no. 4, pp. 1306–1319, 1999.
- [11] S. F. Owen, M. A. Menzel, J. W. Edwards et al., "Bat activity in harvested and intact forest stands in the allegheny mountains," *Northern Journal of Applied Forestry*, vol. 21, no. 3, pp. 154–159, 2004.
- [12] R. T. Brooks and W. M. Ford, "Bat activity in a forest landscape of central Massachusetts," *Northeastern Naturalist*, vol. 12, no. 4, pp. 447–462, 2005.
- [13] S. C. Loeb and J. M. O'Keefe, "Habitat use by forest bats in South Carolina in relation to local, stand, and landscape characteristics," *The Journal of Wildlife Management*, vol. 70, no. 5, pp. 1210–1218, 2006.
- [14] M. A. Menzel, T. C. Carter, J. M. Menzel, W. Mark Ford, and B. R. Chapman, "Effects of group selection silviculture in bottomland hardwoods on the spatial activity patterns of bats," *Forest Ecology and Management*, vol. 162, no. 2–3, pp. 209–218, 2002.
- [15] W. M. Ford, S. F. Owen, J. W. Edwards, and J. L. Rodrigue, "*Robinia pseudoacacia* (black locust) as day-roosts of male *Myotis septentrionalis* (Northern bats) on the fernow experimental forest, West Virginia," *Northeastern Naturalist*, vol. 13, no. 1, pp. 15–24, 2006.
- [16] M. B. Fenton, "Science and the conservation of bats," *Journal of Mammalogy*, vol. 78, no. 1, pp. 1–14, 1997.

- [17] J. M. Psyllakis and R. M. Brigham, "Characteristics of diurnal roosts used by female *Myotis* bats in sub-boreal forests," *Forest Ecology and Management*, vol. 223, no. 1–3, pp. 93–102, 2006.
- [18] T. H. Kunz and L. F. Lumsden, "Ecology of cavity and foliage roosting bats," in *Bat Ecology*, T. H. Kunz and M. B. Fenton, Eds., pp. 2–90, University of Chicago Press, Chicago, Ill, USA, 2003.
- [19] C. J. Garroway and H. G. Broders, "Nonrandom association patterns at Northern long-eared bat maternity roosts," *Canadian Journal of Zoology*, vol. 85, no. 9, pp. 956–964, 2007.
- [20] K. J. Patriquin, M. L. Leonard, H. G. Broders, and C. J. Garroway, "Do social networks of female Northern long-eared bats vary with reproductive period and age?" *Behavioral Ecology and Sociobiology*, vol. 64, no. 6, pp. 899–913, 2010.
- [21] C. L. Lausen, T. S. Jung, and J. M. Talerico, "Range extension of the Northern long-eared bat (*Myotis septentrionalis*) in the Yukon," *Northwestern Naturalist*, vol. 89, no. 2, pp. 115–117, 2008.
- [22] M. Rhodes, "Roost fidelity and fission-fusion dynamics of white-striped free-tailed bats (*Tadarida australis*)," *Journal of Mammalogy*, vol. 88, no. 5, pp. 1252–1260, 2007.
- [23] E. L. P. Arms, M. J. Mitchell, F. C. Watts, and B. L. Wilson, *Soil Survey of Hardin and Larue Counties, Kentucky*, USDA Soil Conservation Service, 1979.
- [24] E. L. Braun, *Deciduous Forests of Eastern North America*, Blakiston Company, Philadelphia, Pa, USA, 1950.
- [25] R. Cranfill, "Flora of Hardin County, Kentucky," *Castanea*, vol. 56, no. 4, pp. 228–267, 1991.
- [26] E. L. P. Anthony, "Age determination in bats," in *Ecological and Behavioral Methods for the Study of Bats*, T. H. Kunz, Ed., pp. 47–58, Smithsonian Institution Press, Washington, DC, USA, 1988.
- [27] M. A. Menzel, J. M. Menzel, S. B. Castleberry, J. Ozier, W. M. Ford, and J. W. Edwards, "Illustrated key to skins and skulls of bats in the Southeastern and mid-Atlantic states," Research Note NE-376, USDA Forest Service, Newton Square, Pa, USA, 2002.
- [28] R. D. Nyland, *Silviculture: Concepts and Applications*, McGraw-Hill, New York, NY, USA, 1996.
- [29] S. P. Cline, A. B. Berg, and H. M. Wight, "Snag characteristics and dynamics in Douglas-Fir forests, Western Oregon," *The Journal of Wildlife Management*, vol. 44, no. 4, pp. 773–786, 1980.
- [30] J. E. Brower and J. H. Zar, *Field and Laboratory Methods for General Ecology*, W. C. Brown, Dubuque, Iowa, USA, 1984.
- [31] J. R. Alldredge and J. Griswold, "Design and analysis of resource selection studies for categorical resource variables," *The Journal of Wildlife Management*, vol. 70, no. 2, pp. 337–346, 2006.
- [32] D. L. Thomas and E. J. Taylor, "Study designs and tests for comparing resource use and availability II," *The Journal of Wildlife Management*, vol. 70, no. 2, pp. 324–336, 2006.
- [33] C. J. Garroway and H. G. Broders, "Day roost characteristics of Northern long-eared bats (*Myotis septentrionalis*) in relation to female reproductive status," *Ecoscience*, vol. 15, no. 1, pp. 89–93, 2008.
- [34] K. P. Burnham and D. R. Anderson, *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, Springer, New York, NY, USA, 2002.
- [35] R. D. C. Team, *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria, 2011.
- [36] J. B. Johnson, J. W. Edwards, W. M. Ford, and J. E. Gates, "Roost tree selection by Northern myotis (*Myotis septentrionalis*) maternity colonies following prescribed fire in a Central Appalachian Mountains hardwood forest," *Forest Ecology and Management*, vol. 258, no. 3, pp. 233–242, 2009.
- [37] L. Breuer, K. Eckhardt, and H. G. Frede, "Plant parameter values for models in temperate climates," *Ecological Modelling*, vol. 169, no. 2-3, pp. 237–293, 2003.
- [38] T. C. Carter and G. A. Feldhamer, "Roost tree use by maternity colonies of Indiana bats and Northern long-eared bats in Southern Illinois," *Forest Ecology and Management*, vol. 219, no. 2-3, pp. 259–268, 2005.
- [39] T. S. Jung, I. D. Thompson, and R. D. Titman, "Roost site selection by forest-dwelling male *Myotis* in central Ontario, Canada," *Forest Ecology and Management*, vol. 202, no. 1–3, pp. 325–335, 2004.
- [40] C. G. Lorimer and A. S. White, "Scale and frequency of natural disturbances in the Northeastern US: implications for early successional forest habitats and regional age distributions," *Forest Ecology and Management*, vol. 185, no. 1-2, pp. 41–64, 2003.
- [41] R. M. Burns and B. H. Honkala, *Silvics of North America*, vol. 2 of *Hardwoods, Agriculture Handbook*, no. 654, USDA Forest Service, Washington, DC, USA, 1984.
- [42] M. K. Trani, R. T. Brooks, T. L. Schmidt, V. A. Rudis, and C. M. Gabbard, "Patterns and trends of early successional forests in the Eastern United States," *Wildlife Society Bulletin*, vol. 29, no. 2, pp. 413–424, 2001.
- [43] M. Lemenih and D. Teketay, "Effect of prior land use on the recolonization of native woody species under plantation forests in the highlands of Ethiopia," *Forest Ecology and Management*, vol. 218, no. 1–3, pp. 60–73, 2005.
- [44] M. A. Albrecht and B. C. McCarthy, "Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests," *Forest Ecology and Management*, vol. 226, no. 1–3, pp. 88–103, 2006.
- [45] C. J. Schweitzer and D. C. Dey, "Forest structure, composition, and tree diversity response to a gradient of regeneration harvests in the mid-Cumberland Plateau escarpment region, USA," *Forest Ecology and Management*, vol. 262, no. 9, pp. 1729–1741, 2011.
- [46] C. C. Frost, "Presettlement fire frequency regimes of the United States: a first approximation," in *Fire in Ecosystem Management: Shifting the Paradigm from Suppression to Prescription: Proceedings, 20th Tall Timbers Fire Ecology Conference*, pp. 70–81, Tall Timbers Research Station, Tallahassee, Fla, USA, 1998.
- [47] R. W. McEwan, T. F. Hutchinson, R. P. Long, D. R. Ford, and B. C. McCarthy, "Temporal and spatial patterns in fire occurrence during the establishment of mixed-oak forests in Eastern North America," *Journal of Vegetation Science*, vol. 18, no. 5, pp. 655–664, 2007.
- [48] J. S. Ward and G. R. Stephens, "Influence of crown class and shade tolerance on individual tree development during deciduous forest succession in Connecticut, USA," *Forest Ecology and Management*, vol. 60, no. 3-4, pp. 207–236, 1993.
- [49] G. J. Nowacki and M. D. Abrams, "The demise of fire and "mesophication" of forests in the Eastern United States," *BioScience*, vol. 58, no. 2, pp. 123–138, 2008.