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Day-roost tree selection by northern long-eared bats—What do non-roost tree comparisons and one year of data really tell us?

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ABSTRACT

Bat day-roost selection often is described through comparisons of day-roosts with randomly selected, and assumed unused, trees. Relatively few studies, however, look at patterns of multi-year selection or compare day-roosts used across years. We explored day-roost selection using 2 years of roost selection data for female northern long-eared bats (Myotis septentrionalis) on the Fort Knox Military Reservation, Kentucky, USA. We compared characteristics of randomly selected non-roost trees and day-roosts using a multinomial logistic model and day-roost species selection using chi-squared tests. We found that factors differentiating day-roosts from non-roosts and day-roosts between years varied. Day-roosts differed from non-roosts in the first year of data in all measured factors, but only in size and decay stage in the second year. Between years, day-roosts differed in size and canopy position, but not decay stage. Day-roost species selection was non-random and did not differ between years. Although bats used multiple trees, our results suggest that there were additional unused trees that were suitable as roosts at any time. Day-roost selection pattern descriptions will be inadequate if based only on a single year of data, and inferences of roost selection based only on comparisons of roost to non-roosts should be limited.

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1. 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), belt transects (Ford et al., 2006; Silvis et al., 2012) or are paired randomly selected trees (Johnson et al., 2009; Miles et al., 2006; Perry and Thill, 2007). Statistical analysis of selection generally is conducted using a set of candidate models representing combinations of measured tree and/or landscape characteristics that may distinguish day-roosts from non-roosts. In information theoretic approaches, either the best supported model or a model containing model-averaged parameters are reported (Burnham and Anderson, 2002). Less common in recent studies as in the past, individual characteristics of day-roosts and non-roosts, such as height and diameter at breast height (dbh),

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are compared using univariate null hypothesis tests such as parametric and non-parametric t-tests, and chi-squared tests (Ford et al., 2006; Menzel et al., 2002). 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 ideally provides a basis for assessment of roost selection that are useful in guiding bat habitat management activities at both the forest stand and landscape levels. Such research suggests that bats select roosts based on a number of possible criterion 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 (Boyles, 2007; Kerth et al., 2001; Lourenço and Palmeirim, 2004), cavity volume (Parsons et al., 2003; Willis et al., 2006), surrounding landscape condition and quality (Ruczyński et al., 2010), and weather (Kerth et al., 2001; Lewis, 1996). However, when comparing multiple studies of a single species, there are commonly differences in roost selection that are observed. As factors such as weather vary from year to year, differences in roost selection may not be attributable to a known cause. Relatively few studies have assessed patterns of bat day-roost selection using multi-year datasets. Miller et al. (2003) recognized that the use of short-term datasets in assessing patterns of bat habitat use clearly is problematic, as variability in day-roost selection criteria may be underestimated. For land managers, bias in estimates of local day-roost selectivity may have practical implications for forest management.

The roosting ecology of the northern long-eared bats has been extensively studied (Ford et al., 2006; Menzel et al., 2002; Perry and Thill, 2007; Silvis et al., 2012). Range-wide, a minimum of understanding of northern long-eared bat day-roost selection criteria is now available that can be used to guide coarse-scale habitat management. Nonetheless, within local landscapes and regions, limited numbers of studies on day-roost selection by northern long-eared bats are available to adequately account for potential variation in the selection process. Accordingly, important questions remain regarding fine-scale differences in the types of roosts used. Both for northern long-eared bats and other tree-roosting bats, adapting current practice of assessing day-roost selection to add comparisons among roosts themselves has the potential to provide advances in understanding of roost selection criteria that are not easily gleaned from comparisons with non-roosts alone. For example, both Garroway and Broders (2008) and Silvis et al. (2012) compared day-roosts used by female northern long-eared bats in different reproductive conditions and discovered that lactating females selected for larger, more exposed roosts than did non-lactating bats. Johnson et al. (2012) compared primary roosts used by groups of female northern long-eared bats and discovered that primary roosts were of smaller diameter and shorter 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). With continuing population declines of northern long-eared bats and other tree-roosting bat species in the face of White-nose Syndrome (WNS), fuller understanding of the ecology of WNS-impacted bats is critical for assessment of recovery strategies and management options. Fuller understanding of the ecology of these species will provide managers with guidance on avoiding "take" of individuals or important habitat components under the aegis of the United States Endangered Species Act and will aid in promoting optimal habitat conditions.

Our objective was to explore whether characterization of female northern long-eared bat roost selection using only a single year of data could result in different management recommendations between years. We did this by assessing day-roost selection by female northern long-eared bats derived using comparisons among day-roosts used between years and randomly selected non-roost trees. We hypothesized that day-roost selection would differ between years, but that overall characteristics of roosts relative to randomly selected non-roosts would be similar.

2. Methods

We conducted our study on the Fort Knox military reservation in Meade, Bullitt, and Hardin counties, Kentucky, USA from May through July 2011 and 2012. Our sites predominantly are of 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). We captured northern long-eared bats over small woodland pools or at known roosts using mist nets and attached radiotransmitters (LB-2, 0.31 g: Holohil Systems Ltd., Woodlawn, ON, Canada[1]) between the scapulae of female bats using Perma-Type surgical cement (Perma-Type Company Inc., Plainville, CT, USA). A uniquely numbered lipped band (Porzana Ltd., United Kingdom) was attached to the forearm of all captured bats. Captured bats were released within 30 min 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). 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).

We attempted to locate radio-tagged bats daily for the life of the transmitter or until the unit dropped from the bat. For each located day-roost, we recorded tree species, 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), and canopy openness. We measured canopy openness at each roost tree in the 4 cardinal directions using

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

Table 1

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

	Non-roost	2011 roost	2012 roost	Pooled roost
Height (m)	15.0 ± 7.1	14.8 ± 7.1	17.0 ± 8.7	15.9 ± 8.0
DBH (cm)	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 $\geq$ 6 (% in stage)	1.9	13.9	2.8	8.4

a hemispherical densitometer and used the averaged values to represent the percent of canopy not closed. We recorded these same measurements for one randomly located non-roost tree for each day-roost located during the first year of our study. Non-roost tree locations were identified using randomly generated points within roosting areas used by bats with the nearest tree to the point location selected as the measurement tree; roosting areas previously were identified in Silvis et al. (2014).

We performed a chi-squared test of independence to assess differences in tree species composition among our groups and examined standardized Pearson residuals from that analysis to determine which species were used more or less than expected. We compared characteristics of day-roosts (dbh, height, canopy position, decay stage, canopy openness) used in different years and non-roosts using multinomial logistic regression. The use of multinomial logistic regression, rather than three 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 such as reduced error propagation and more precise estimates of regression parameters. To use the multinomial modeling method, we assumed that the odds of a tree being in any one class (non-roost or day-roost in either year) were independent of the presence or absence of the other classes as alternatives. Prior to modeling, we tested for correlations among continuous variables, and, where strong correlations existed, conducted a principal components analysis (PCA) to create orthogonal synthetic variables. We used eigenvectors accounting for >75% of the observed variation as predictors in our multinomial model. We centered and scaled our independent continuous variables so that we could directly assess effect sizes (Schielzeth, 2010), and treated crown and decay class as ordinal variables. When a day-roost was used in multiple years, we included it in our analysis only 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, we included each day-roost only once in our dataset regardless of the number of times that tree was used. Because we were conducting an exploratory analysis, we used an all subsets regression approach rather than a comparison of *a priori* hypotheses. We 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 *i*th model (Δ_i) and Akaike's weights (w_i) (Burnham and Anderson, 2002). We considered models with $\Delta_i \leq 2$ to have strong empirical support among all models. We 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 percent 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 be relatively large (Hensher and Johnson, 1981; Hosmer and Lemeshow, 2004). All analyses were performed in the R statistical program (R. Development Core Team, 2014). We fit multinomial models using neural networks with the package *nnet* (Venables and Ripley, 2002).

3. Results

We captured 58 female northern long-eared bats in 2011 and 71 in 2012 representing 4 separate colonies (Silvis et al., 2014). We obtained relocation data for 54 individuals (16 gestating, 29 lactating, 3 post-lactation, 6 non-reproductive) in 2011 and 67 (5 gestating, 48 lactating, 10 post-lactation, 4 non-reproductive) in 2012. We located 108 day-roosts from 271 relocations in 2011 and 112 day-roosts (5 of which were used in 2011) from 334 relocations in 2012. We recorded a mean (±SD) of 5.0 (±1.9) locations per bat in 2011 and 5.1 (±2.9) in 2012. We recorded measurements for 108 non-roosts (Table 1). A total of 3 roosts were located under loose bark, all others were in cavities.

Our non-roost trees comprised 27 species, whereas day-roosts represented 21 and 17 species in the first and second years of our study, respectively. In total, we recorded the presence of 30 tree species within the day-roost- and immediately adjacent forest stands. Tree species were not equitably distributed among non-roosts or day-roosts (*chi-square* = 103.04, *d.f.* = 58, *P* = 0.003). Sugar maple (*Acer saccharum*) and sassafras (*Sassafras albidum*) were the most common non-roost tree species, accounting for 25% and 15% of all non-roosts, 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

Table 2

Standardized Pearson's residuals for chi-squared analysis comparing abundance of non-roost tree species, and species used as day-roosts by female northern long-eared bats (*M. septentrionalis*) on the Fort Knox Military Reservation, Kentucky, USA in 2011 and 2012. Values close to 2 are considered influential (values > |1.75| bolded). Negative and positive values indicate less than and greater abundance than expected, respectively. Overall *chi-squared* = 103.04 (*d.f.* = 58, *P* = 0.003).

Species	Non-roost	2011	2012
Boxelder (*Acer negundo*)	−0.71	1.41	−0.70
Sugar maple (*Acer saccharum*)	**3.14**	**−2.55**	−0.60
Tree of heaven (*Ailanthus altissima*)	1.41	−0.71	−0.70
Pignut hickory (*Carya glabra*)	**2.52**	−1.27	−1.26
Shagbark hickory (*Carya ovata*)	1.13	0.45	−1.58
Eastern redbud (*Cercis canadensis*)	0.71	0.71	−1.42
Hackberry (*Celtis occidentalis*)	0.50	0.50	−1.00
Flowering dogwood (*Cornus florida*)	**2.46**	−1.23	−1.22
Common persimmon (*Diospyros virginiana*)	**2.46**	−1.23	−1.22
American beech (*Fagus grandifolia*)	−0.64	1.27	−0.63
White ash (*Fraxinus americana*)	−0.32	−0.78	1.09
Blue Ash (*Fraxinus quadrangulata*)	−0.71	1.41	−0.70
Black walnut (*Juglans nigra*)	−0.36	0.71	−0.35
Eastern redcedar (*Juniperus virginiana*)	0.31	−0.64	0.33
Sweet gum (*Liquidambar styraciflua*)	1.41	−0.71	−0.70
Yellow poplar (*Liriodendron tulipifera*)	**1.76**	**−2.03**	0.27
Blackgum (*Nyssa sylvatica*)	0.50	0.50	−1.00
Loblolly pine (*Pinus taeda*)	1.41	−0.71	−0.70
American sycamore (*Planatus occidentalis*)	−1.01	0.50	0.51
Black Cherry (*Prunus serotina*)	0.00	−1.23	1.24
White oak (*Quercus alba*)	−1.95	**1.75**	0.20
Chinkapin oak (*Quercus muhlenbergii*)	**2.16**	−1.09	−1.07
Northern red oak (*Quercus rubra*)	−1.43	−0.36	**1.79**
Black oak (*Quercus velutina*)	−0.01	−0.88	0.89
Black locust (*Robinia pseudoacacia*)	1.01	−0.51	−0.49
Sassafras (*Sassafras albidum*)	**−5.82**	**2.74**	**3.08**
Basswood (*Tilia americana*)	**2.00**	−1.01	−1.00
Winged elm (*Ulmus alata*)	−0.01	**1.74**	**−1.74**
American elm (*Ulmus americana*)	1.41	−0.71	−0.70
Slippery elm (*Ulmus rubra*)	0.00	1.23	−1.22

Table 3

Best supported multinomial models comparing non-roosts and female northern long-eared bat (*M. septentrionalis*) day-roosts on the Fort Knox Military Reservation, Kentucky, USA 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	AIC$_c$	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

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 non-roost tree pool.

Tree dbh and height exhibited a strong, positive correlation ($r = 0.69$, $P < 0.001$). The first eigenvector from the PCA of these two variables explained 84.7% of the variation in tree size and was positively correlated with both dbh and height. Our global model was the best supported model differentiating day-roosts from non-roosts receiving 99% of the overall model support (Table 3). Because no other models had $\Delta_i < 2$, we did not model average parameters, but instead used estimates directly from our best supported model. Our model fit the data better than a null model (*chi-squared* = 235.98, *d.f.* = 20, $P < 0.001$), and explained a moderate 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 non-roosts, 2011 roosts and 2012 roosts, respectively. Model results indicated that 2011 day-roosts were larger than non-roosts with greater canopy openness, in later decay stages, and more likely to be in suppressed canopy positions, whereas day-roosts in 2012 were larger and in later stages of decay than non-roosts, but did not differ in canopy openness or position (Table 5). Between years, day-roosts differed in size, canopy openness and decay stage, with 2011 day-roosts being physically larger but in earlier decay stages, more suppressed canopy positions and with less canopy openness (Table 6).

Table 4
Predicted vs. observed tree status for the multinomial model comparing non-roosts and female northern long-eared bat (*M. septentrionalis*) day-roosts on the Fort Knox Military Reservation, Kentucky, USA in 2011 and 2012. Numbers are raw counts.

		Actual		
		Non-roost	2011 roost	2012 roost
Predicted	Non-roost	77	14	19
	2011 roost	12	77	22
	2012 roost	19	17	66

Table 5
Parameter estimates of the best supported multinomial model comparing non-roosts to female northern long-eared bat (*M. septentrionalis*) day-roosts on the Fort Knox Military Reservation, Kentucky, USA 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 (I = intermediate, CO = co-dominant, D = dominant) in the forest canopy.

	Estimates		Std. errors		*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 I	−3.22	0.48	0.59	0.49	<0.001	0.33
Position CO	−4.99	0.44	1.01	0.80	<0.001	0.58
Position D	−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 6
Parameter estimates comparing day-roosts used in 2011 and 2012 from the best supported multinomial model comparing non-roosts to female northern long-eared bat (*M. septentrionalis*) day-roosts on the Fort Knox Military Reservation, Kentucky, USA using 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 (I = intermediate, CO = co-dominant, D = dominant) in the forest canopy.

	Estimate	Std. error	*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 I	3.70	0.53	<0.001
Position CO	5.44	0.87	<0.001
Position D	5.42	1.03	<0.001
Openness	−0.44	0.17	0.01

4. Discussion

Our global model was the most parsimonious model differentiating day-roosts and non-roosts; each of the variables used consistently is an important predictor of roost status for many bat species (Kalcounis-Rüppell et al., 2005). Under our best supported model, as we predicted, and consistent with previous studies (Garroway and Broders, 2008; Johnson et al., 2009; Lacki and Schwierjohann, 2001; Perry and Thill, 2007), day-roosts used by female northern long-eared bats in both years of our study generally were larger, in later stages of decay, and in relatively more open canopies than randomly selected non-roosts. The effect sizes that we observed for canopy openness and overall difference in tree size between day-roosts and non-roosts were greater than the individual effect sizes of dbh and height reported in Kalcounis-Rüppell et al.'s (2005) review for cavity roosting bats in North America. The larger effect sizes that we observed 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 strongly from random trees in some cases.

Day-roost species selection patterns that we observed differed from those reported in Arkansas (Perry and Thill, 2007), Illinois (Carter and Feldhamer, 2005), West Virginia (Johnson et al., 2009; Menzel et al., 2002), central Ontario (Jung et al.,

2004), Prince Edward Island (Henderson and Broders, 2008), and eastern Kentucky (Lacki and Schwierjohann, 2001), as we observed a wider use of tree species. Differences in individual tree 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 our most common roost species, our patterns of roost selection are similar to those observed by Ford et al. (2006) and Menzel et al. (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 (Kerth et al., 2001; Lewis, 1996), it is possible that our observed difference in roost selection between years is related to temperature. Based upon previous literature, it is expected that relative to non-roosts, day-roosts would be smaller and less exposed under warmer conditions, or that variation in characteristics would be greater in response to decreased constraints on selection. Mean minimum temperature June–July was 1.78 °C higher in the first year of our study than in the second (National Oceanic and Atmospheric Administration station GHCND: USC00154955) and we therefore expected selection for larger and more exposed day-roosts in 2012 that would allow bats to remain within preferred thermal ranges. Contrary to our expectations, our model indicated that relative to non-roosts, day-roosts used in 2012 were actually smaller and in smaller canopy gaps than those used in 2011. Standard errors for model parameters differentiating day-roosts from non-roosts were almost universally larger in 2011, however. Interestingly, despite apparently overall greater size and canopy openness, day-roosts used in 2011 were also substantially more likely to still be in suppressed canopy conditions than those used in 2012. Because we 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 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 smaller dbh than those used in 2012, but, were also more variable in dbh. As such, we 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 our 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. Our 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 may be biased. Furthermore, our results suggest that day-roost selection by northern long-eared bats may be more variable than currently is thought, with variation potentially related to differences in environmental conditions.

Secondarily, it was surprising that we identified as many new roosts in the second year of our study as we located in our first. Roosts generally are considered a critical, potentially limiting, resource (Fenton, 1997; Kunz and Lumsden, 2003), although generally this is not found to be the case; our results suggest that this is not true in our mature temperate deciduous forest community study sites. Relative to assessment of day-roost selection, it is likely that some number of roosts with undetected use may be included in the non-roost category. Inclusion of these roosts in the non-roost category will introduce greater or lesser bias in parameter estimates depending upon the analysis type chosen. For example, contamination of the non-roost pool with roosts with undetected use will yield more biased parameter estimates in a case-control analysis framework than in a use-availability analysis framework with small sample sizes (Beyer et al., 2010; Keating and Cherry, 2004; Rota et al., 2013). From a conservation perspective, this is of concern if management and regulatory decisions for the northern long-eared bat are made from studies with small sample sizes and using only a single year of data (Miller et al., 2003). However, Kalcounis-Rüppell et al. (2005) found in their meta-analysis that for North American bats generally, conclusions drawn from individual studies largely were consistent with those from aggregated data. It currently is unclear how biased (or unbiased) estimates of day-roost selectivity for northern long-eared bats are. We believe that previous efforts have resulted in estimates of roost preferences that are not necessarily indicative of the species across its distribution, but rather the local conditions of a site and year combination.

5. Conclusions

Relative to sampling duration and size, past assessment of roost preferences for northern long-eared bats, and possibly many other species, likely has occurred at too limited a scale. Failure of past studies to assess multi-year patterns in day-roost selection may have yielded 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 if feasible. For example, multi-year studies will help ensure that weather-related variability in roost selection is not conflated with overall roosting preferences, and therefore also should provide important insight into the relative availability of roost trees in an area. As our 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 yields a probability of locating numerous roosts. Although the comparison of day-roosts with non-roosts clearly has utility for identifying and describing bat habitat, inferences from short-term studies should be tempered.

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 affected bats may no longer be practical, so we encourage the re-analysis of multi-year datasets, and datasets that include information on different classes of

day-roosts. In particular, we 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. These comparisons could have direct and timely conservation implications. As we have demonstrated, use of the multinomial logistic model is a parsimonious method for comparing >2 classes of trees, and we encourage researchers to use this modeling method for future multi-class comparisons. The use of centered and scaled variables also should be considered, as the use of such standardized variables 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 we encourage such hypothesis testing.

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