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Article

Restoration of Legacy Trees as Roosting Habitat for *Myotis* Bats in Eastern North American Forests

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Abstract: Most eastern North American *Myotis* roost in forests during summer, with species forming maternity populations, or colonies, in cavities or crevices or beneath the bark of trees. In winter, these bats hibernate in caves and are experiencing overwinter mortalities due to infection from the fungus *Pseudogymnoascus destructans*, which causes white-nose syndrome (WNS). Population recovery of WNS-affected species is constrained by the ability of survivors to locate habitats suitable for rearing pups in summer. Forests in eastern North America have been severely altered by deforestation, land-use change, fragmentation and inadvertent introduction of exotic insect pests, resulting in shifts in tree distributions and loss of large-diameter canopy-dominant trees. This paper explores patterns in use of tree roosts by species of *Myotis* across Canada and the United States using meta-data from published sources. *Myotis* in western Canada, the Northwest, and Southwest selected the largest diameter roost trees and also supported the largest maximum exit counts. *Myotis lucifugus*, *M. septentrionalis* and *M. sodalis*, three species that inhabit eastern forests and which are currently experiencing region-wide mortalities because of WNS, selected roosts with the smallest average diameters. Recovery efforts for bark- and cavity-roosting *Myotis* in eastern North American forests could benefit from management that provides for large-diameter trees that offer more temporally-stable structures for roosting during the summer maternity season.

Keywords: bark and cavity-roosting bats; leave trees; legacy structures; maternity colony; *Myotis*; roost longevity; roost switching; white-nose syndrome

1. Introduction

Alterations to forested landscapes across eastern North America from shifting land use practices, fire suppression, and inadvertent introduction of exotic forest pests have led to reduced forest land cover, younger stand ages, and changes in the composition of canopy-dominant trees. Most forests in eastern North America now represent lands recolonized through secondary succession following cessation of agricultural activities [1]. In the Northeast, there has been a large-scale shift to early- and mid-successional tree species away from late-seral canopy dominants [2]. Eastern oak (*Quercus*) forests have seen a widespread increase in shade-intolerant hardwoods and a decline in shade-intolerant oaks resulting from decades of fire exclusion [3]: an ecological response termed “mesophication” [4]. These forests are further threatened by outbreaks of gypsy moths (*Lymtria dispar*), which cause mortality of both overstory and young trees in oak species [5]. Several other large, canopy-dominant tree species in eastern North America have experienced mortalities and declines due to introduced forest pests including Canadian hemlock (*Tsuga canadensis*), American beech (*Fagus grandifolia*), ash (*Fraxinus* spp.), and American chestnut (*Castanea dentata*) [6]. Shifts away from historically available tree species and canopy structures are likely to be accompanied by changes in behavior of bark- and cavity-roosting bats, particularly in selecting roosting and maternity habitats during summer months.

The importance of tall large-diameter dead trees to bark- and cavity-roosting bats in coniferous forests of western North America is well documented [7–9]. These “legacy” trees, i.e., roosting sites that remain available on the landscape for generations of bats, are believed: to confer thermal advantages from increased solar exposure [10], to be recognizable to foraging bats within habitat patches while in flight [11], and to persist for longer periods of time than smaller-diameter dead trees [12]. Selection for larger-diameter trees by bats in eastern North American forests is less evident [13], and it is likely that loss of canopy-dominant trees has influenced existing patterns in roost selection by these bat species. Use of multiple roosts with variable patterns of roost-switching, i.e., fission-fusion behavior, has been described in tree-roosting bats [14,15], including *Myotis* [16–18], with evidence for reliance on “central-node” roosts in some populations [18–20]. Loss of canopy-dominant tree species from eastern North American forests has likely decreased the availability of large-diameter, long-standing trees, that otherwise could serve as long-lived roosts which provide stability across time and landscape position for summer populations of bark- and cavity-roosting bats.

Most *Myotis* in eastern North America form maternity populations in cavities or crevices or beneath the bark of trees during the growing season, making these bats ideal species for occupying legacy trees in forests [13]. These bats make migrations of up to several hundred kilometers from maternity sites in late summer/early autumn to caves and mines, where they mate and then overwinter to wait out the period of food shortage by entering deep torpor, i.e., a state of reduced body temperature, to minimize energy loss and stretch energy reserves through the winter. Many cave-hibernating *Myotis* have experienced recent catastrophic losses in population numbers due to an introduced fungal pathogen, *Pseudogymnoascus destructans* [21–24], with range-wide extinction of some species predicted [25–27]. The fungus causes structural damage to bat tissues, especially wings, with hyphae that penetrate hair follicles, apocrine glands, and sebaceous glands [28]. The fungus attacks bats while torpid, increasing the frequency of arousal and leading to energy loss, dehydration, emaciation, and immune responses to fungal infection that are lethal to the bats [29–31]. Collectively, these effects on hibernating bats have been termed white-nose syndrome (WNS), with recovery efforts of WNS-impacted *Myotis* now reliant on the ability of overwinter survivors to reproduce and successfully rear young bats to volancy during summer months [32]. The extent to which increased availability of large-diameter trees in eastern North American forests could facilitate reproductive success and recovery in these bats has not been explored. This study examines patterns in use of tree roosts by species of *Myotis* across Canada and the United States, using meta-data from published sources, and compares use of roosts across species and geographic regions. Two hypotheses were evaluated: *Myotis* in western North America select larger-diameter and taller trees for roosting than do *Myotis* in eastern regions due to a greater abundance of older-age forests and, thus, higher availability of larger-diameter live and dead trees; and, tree roosts of *Myotis* in western North America support larger-numbers of bats in maternity populations than do tree roosts of *Myotis* in eastern forests, due to a longer temporal stability of roosts combined with a greater volume of available roosting space within roosts.

2. Materials and Methods

To assess geographic patterns in use of tree roosts by *Myotis*, I surveyed the published literature from 1970 to 2015 for articles referring to tree roosting in North American *Myotis*. I limited my search to studies occurring north of Mexico. I used Web of Science as the primary search engine to identify relevant literature. I also extracted information from articles in two published symposia, one on forest bats [33] and another specific to the Indiana bat, *M. sodalis* [34]. I located 63 published sources that had data useful for analysis (Appendix A). Within each article I searched for population-level data on: mean diameter of roost trees (cm), mean height of roost trees (m), and mean size of exit counts from roost trees (No. bats/count). When data were provided on random or adjacent stand conditions, I compared these with values for mean roost-tree diameter and mean roost-tree height. I also identified studies specific to a single roost tree and studies in which the maximum exit count was reported from among a set of roost trees sampled, and collected information on tree diameter (cm), tree height (m),

and species of tree from which the maximum exit count was observed. I screened studies to minimize use of data for analysis from populations likely affected by WNS impacts.

Data were partitioned by geographic regions (Figure 1). Western Canada included British Columbia, Alberta, Yukon, Northwest Territories, and the U.S. state of Alaska. Central Canada included Saskatchewan, Manitoba, Nunavut, and Ontario, and eastern Canada covered the remaining provinces east of Ontario. For the U.S., the northwest region was bordered by Montana, Wyoming, and northern California. The southwest region covered southern California to Colorado, and south to Texas. The Midwest region included the states from North Dakota to Oklahoma, northeast to Ohio and Michigan. The southeast region was bordered on the west by Louisiana and Arkansas and to the north by Kentucky and Virginia. The northeast region included all states north of Virginia and east of Ohio. Data were also partitioned among 11 species of *Myotis* for analysis, including: *M. auricolus* (southwestern myotis), *M. austroriparius* (southeastern bat), *M. californicus* (California myotis), *M. evotis* (western long-eared bat), *M. keenii* (Keen's myotis), *M. lucifugus* (little brown myotis), *M. septentrionalis* (northern long-eared bat), Indiana bat, *M. thysanodes* (fringed myotis), *M. volans* (long-legged myotis), and *M. yumanensis* (Yuma myotis).



Figure 1. Schematic map of North America minus Mexico, with regional groupings of states and provinces used for analyses of tree roosts of *Myotis* bats. Abbreviations for regions are: WCAN (western Canada), CCAN (central Canada), ECAN (eastern Canada), NW (Northwest), SW (Southwest), MW (Midwest), NE (Northeast), and SE (Southeast).

I compared maximum exit counts, mean exit counts, mean roost tree diameter, and mean roost tree height by geographic region using one-way analysis of variance, with an LSD procedure to identify differences when ANOVAs were significant (PROC GLM, SAS Institute, Cary, NC, USA). Comparisons across *Myotis* were evaluated similarly for mean roost-tree diameter and mean roost-tree height. To assess the extent to which different *Myotis* selected roost trees from among those available in the habitat, I calculated the percent difference from surrounding stand-level-conditions for each species, when reported, for both mean roost-tree diameter and mean roost-tree height. Percent differences were then arcsine transformed and evaluated using one-way analysis of variance with an LSD procedure (PROC GLM, SAS Institute, Cary, NC, USA). To assess relationships of maximum exit counts with

associated roost tree diameter and roost tree height, and mean exit counts with mean roost tree diameter and mean roost tree height, I performed simple linear and multiple linear regressions combining data across the continent (PROC REG, SAS Institute, Cary, NC, USA). Statistical tests were considered significant when $p < 0.05$.

3. Results

Mean diameter of tree roosts of *Myotis* demonstrated longitudinal trends from west to east of decreasing roost size in both Canada and the United States (Figure 2). Differences among regions were significant ($F_{7,66} = 6.64$, $p < 0.0001$), with largest average roost diameters for bats in western Canada, the northwest, and southwest regions. Tree roosts of *Myotis* also exhibited a decreasing trend for height of roost trees from west to east across the United States ($F_{7,54} = 5.39$, $p < 0.0001$); however, data for Canadian populations were reversed with the tallest roost trees recorded in eastern Canada (Figure 3). Variation in roost-tree height was much wider for populations of *Myotis* in eastern Canada than for all other regions.

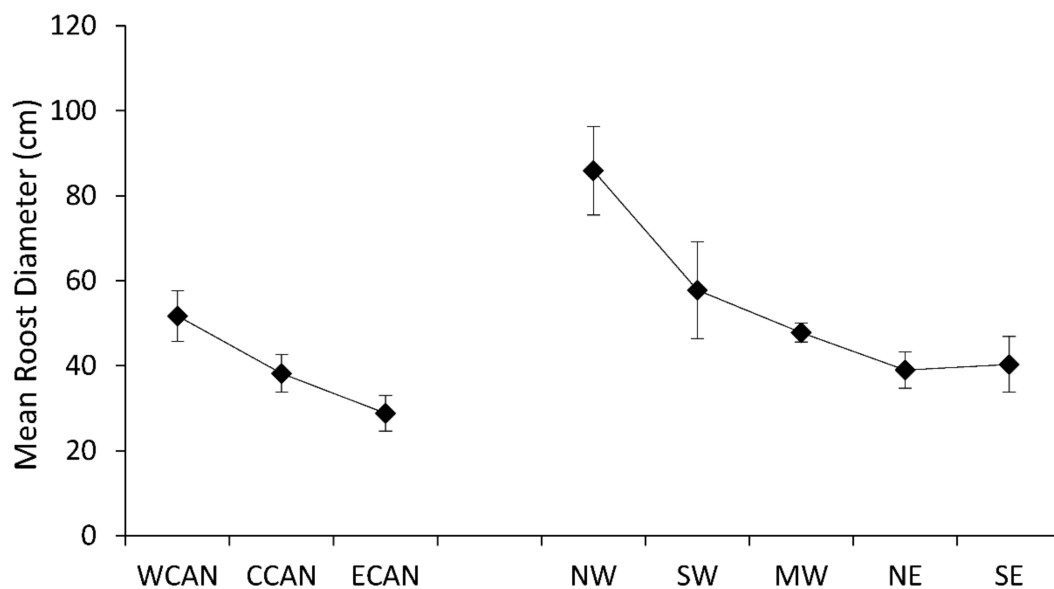


Figure 2. Mean diameter (SE) of roost trees of *Myotis* by region across Canada and the United States.

Comparisons among species of *Myotis* demonstrated differences in mean roost diameter ($F_{10,61} = 7.63$, $p < 0.0001$), but not mean height of roost trees ($F_{9,50} = 1.5$, $p = 0.1755$). Species with the largest roost diameters were *Myotis auriculus*, *M. keenii*, *M. thysanodes*, *M. volans*, and *M. yumanensis* (Figure 4); all of these species occur only in western North America. Conversely, populations of *M. lucifugus*, *M. septentrionalis*, and *M. sodalis*, primarily inhabiting eastern forests, used roost trees with the smallest diameters.

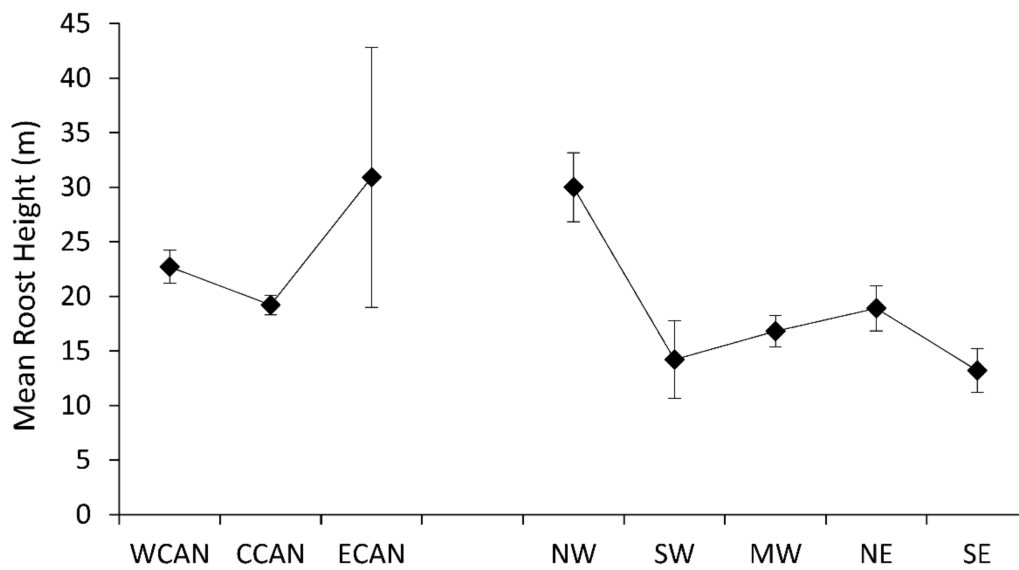


Figure 3. Mean height (SE) of roost trees of *Myotis* by region across Canada and the United States.

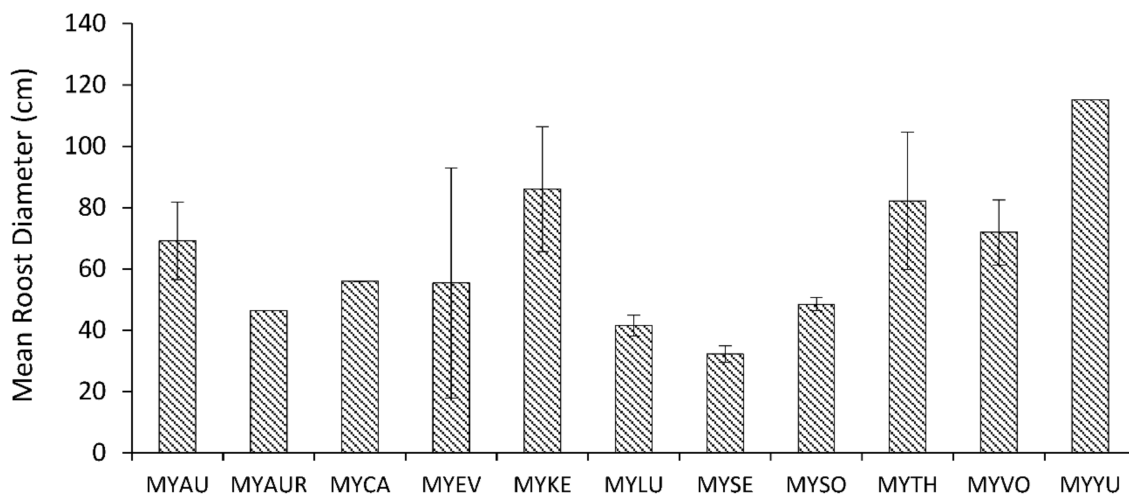


Figure 4. Mean diameter (SE) of tree roosts of *Myotis* in Canada and the United States. Abbreviations for species are: MYAU (*Myotis auriculus*), MYAUR (*M. austroriparius*), MYCA (*M. californicus*), MYEV (*M. evotis*), MYKE (*M. keenii*), MYLU (*M. lucifugus*), MYSE (*M. septentrionalis*), MYSO (*M. sodalis*), MYTH (*M. thysanodes*), MYVO (*M. volans*), and MYYU (*M. yumanensis*).

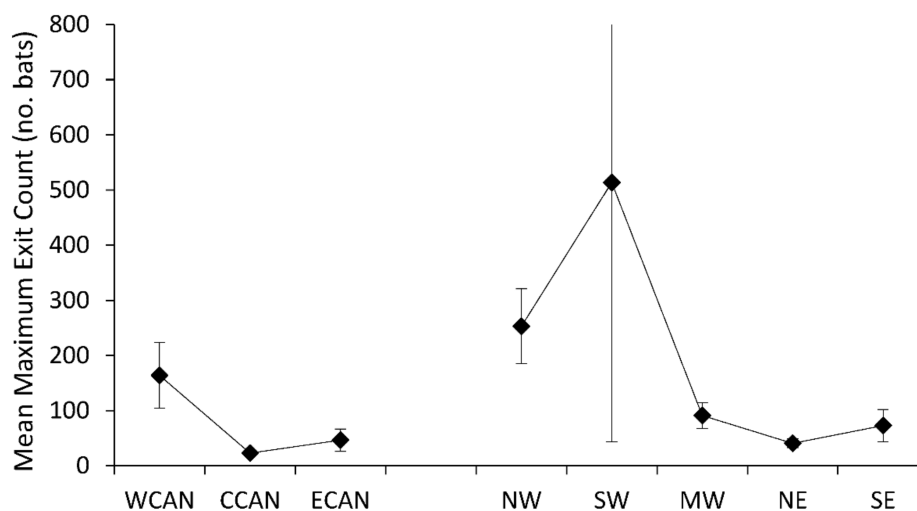
Evaluation of differences in roost-tree diameter from surrounding stand conditions demonstrated variation among *Myotis* ($F_{10,33} = 3.87, p < 0.0015$), with the greatest difference observed for *M. yumanensis* and the least differences observed for *M. austroriparius* and *M. evotis* (Table 1). Detectable patterns in difference from stand conditions for height of roost trees were not observed among *Myotis* ($F_{9,21} = 0.14, p = 0.9979$).

Table 1. Mean (\pm SE) difference in diameter (%) and height (%) of roost trees from surrounding stand-level conditions for populations of *Myotis* bats in North America.

Bat Species	<i>n</i> ^a	% Difference		
		in Diameter	in Height	
<i>M. austroriparius</i>	4	0.9 (0.25)	2	0.85 (0.6)
<i>M. auriculus</i>	1	1.06 (–)	1	1.3 (–)
<i>M. californicus</i>	2	1.77 (0.23)	2	1.58 (0.005)
<i>M. evotis</i>	1	0.83 (–)	1	0.75 (–)
<i>M. keenii</i>	2	1.7 (0.4)		
<i>M. lucifugus</i>	4	1.12 (0.06)	3	1.1 (0.06)
<i>M. septentrionalis</i>	14	1.33 (0.12)	11	2.02 (0.84)
<i>M. sodalis</i>	8	1.72 (0.23)	3	1.73 (0.38)
<i>M. thysanodes</i>	3	1.41 (0.08)	3	1.62 (0.51)
<i>M. volans</i>	4	1.29 (0.09)	4	1.69 (0.26)
<i>M. yumanensis</i>	1	3.74 (–)	1	2.02 (–)

^a Indicates number of populations.

Seventeen species of trees were associated with maximum exit counts of *Myotis* (Supplementary Table S1), with the largest population sizes recorded for a *Myotis* sp. in a *Pseudotsuga menziesii* (Douglas fir, $n = 984$), for *M. volans* in a *Pinus ponderosa* (Ponderosa pine, $n = 459$), and for *M. sodalis* in a *Populus deltoides* (eastern cottonwood, $n = 384$). Mean maximum exit counts varied regionally ($F_{7,39} = 3.23$, $p < 0.0084$), with highest maximum counts for tree-roosting populations of *Myotis* in western Canada, the northwest, and southwest regions (Figure 5). Variation in maximum exit counts from tree roosts was greatest for *Myotis* in southwestern U.S. Mean exit counts of tree-roosting *Myotis* did not show discernible patterns by geographic region ($F_{5,26} = 0.34$, $p = 0.8868$); however, there were limited data for this metric in two regions, central Canada and southwestern U.S. (Figure 6).

**Figure 5.** Mean maximum exit counts from tree roosts of *Myotis* across Canada and the United States.

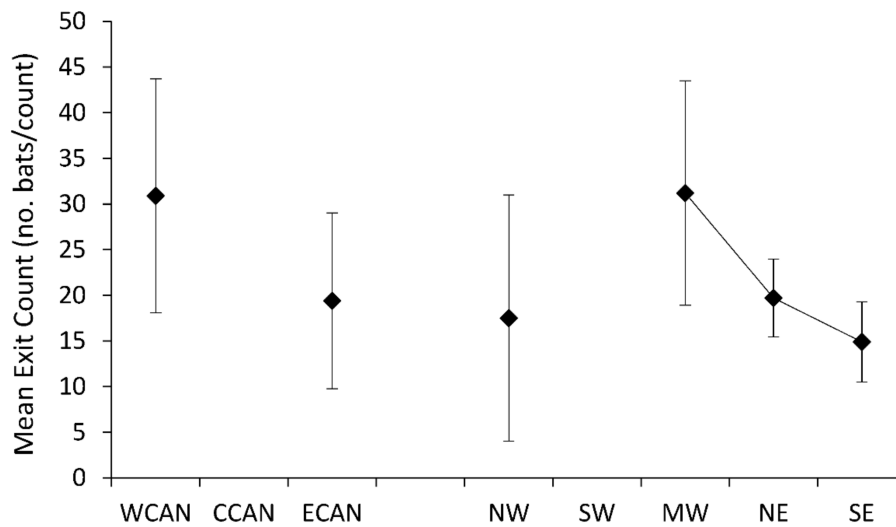


Figure 6. Mean number of bats exiting tree roosts of *Myotis* across Canada and the United States.

Continent-wide trends in mean maximum exit counts and average exit counts of tree-roosting populations of *Myotis* demonstrated no clear relationships with roost tree diameter, roost tree height or for models incorporating both characteristics simultaneously (Table 2). Adjusted R^2 -values failed to exceed 0.13 for any model comparison.

Table 2. Linear regressions of maximum exit counts (No. bats) and mean exit counts (No. bats/count) with characteristics of tree roosts of *Myotis* across Canada and the United States.

	Adj- R^2	Parameter	β	SE	F	p
Maximum	0.0162	Roost diameter	-1.347	1.23	1.2	0.297
	0.0771	Roost height	8.748	7.35	1.42	0.299
	0.1221	Roost diameter	-1.825	1.66	1.1	0.352
		Roost height	12.061	7.78	1.55	0.218
Mean	-0.0021	Mean diameter	0.223	0.23	0.94	0.341
	-0.0155	Mean height	0.451	0.55	0.66	0.424
	-0.0662	Mean diameter	0.016	0.38	0.04	0.967
		Mean height	0.421	0.92	0.46	0.653

4. Discussion

Findings corroborated the importance of large-diameter trees for summer roosts of *Myotis* in western North America [7–9], with a distinct longitudinal trend from western to eastern populations of decreasing roost-tree diameter. Patterns for height of roost trees were more equivocal, with decreasing height of roost trees from west to east in more southern U.S. populations of *Myotis* contrasted by increasing height of roost trees from west to east in Canadian populations. Average roost-tree diameter differed among *Myotis* with western species occupying the largest roosts on average, and eastern species selecting the smallest diameter roosts, especially *M. sodalis*, eastern and Midwestern populations of *M. septentrionalis*, and populations of the eastern subspecies of *M. lucifugus lucifugus*. These three species are all cave-hibernators that are vulnerable to impacts from WNS [25,27,35]. Differences in roost-tree diameter from surrounding stand conditions varied among *Myotis*, but showed no consistent clinal variation across geographic regions. The geographic difference observed for roost-tree diameter in this study suggests two possibilities. Use of smaller-diameter roosts by eastern North American *Myotis* represents a difference in preferred roost condition from that of western species, or, is an indication that roost choice in eastern *Myotis* is constrained by a shortage of available large-diameter trees for roosting in eastern forests.

Average size of bat populations exiting tree roosts did not vary regionally, however, maximum exit counts observed were largest for populations of *Myotis* in the southwest region, the northwest, and western Canada. Counts of bats exiting tree roosts that exceeded 300 individuals were rare in studies of eastern and midwestern populations [36,37], but were frequently reported for western populations of *Myotis* [9,38–42]. Interestingly, all maximum counts exceeding 300 bats at roosts of *M. lucifugus*, a species whose range encompasses both eastern and western regions, occurred in populations from western Canada [41,42]. Thus, large maternity populations are rare in eastern *Myotis*, but potential exists for at least some species to form large maternity populations in eastern forests with sufficient availability of suitable roosting structures in the form of large-diameter live and dead trees.

Bark- and cavity-roosting *Myotis* reuse roost trees over multiple seasons [13,43,44], with populations of *Myotis* in Europe known to inhabit the same roost tree in summer for up to 16 years [45]. This longevity is constrained, however, by how long it takes for standing dead trees to fall [46]. Survivorship of standing dead trees varies by species and size [47,48], with trees larger in diameter and shorter in height persisting longer [47,49]. Half-lives of tree roosts of *M. volans* in coniferous forests in the northwest U.S. were <3 years, with only 4.3% of roosts remaining upright after 10-years post-discovery [12]. Suitability of tree roosts for reuse by *M. californicus* in western Canada also declined rapidly post-discovery [44]. These patterns would indicate that an increase in the availability of large-diameter trees could help in maintaining connectivity and persistence of maternity populations of *Myotis* at local scales, as these trees are more likely to persist and remain standing for longer periods [12,47,49]. Loss of roosts results in changes in behavior of some species of bats [50,51], with *M. lucifugus* known to abandon local roosting areas with loss of access to a significant building roost [52].

To an extent, bark- and cavity-roosting bats are preadapted to seasonal and annual shifts in availability of tree roosts. These species form social units of varying relatedness in which individual members move among roost trees and associated population sub-groups, or fission-fusion behavior [14,53]. Fission-fusion behavior is well documented in North American bats, including *Myotis* [16–18], with highly-centralized, scale-free roost networks centered around a central-node roost tree typical of some maternity populations [18,19]. A central-node roost serves as the focal site of a maternity population, within which all members of the colony roost at some point in time [54]. Central-node roosts are commonly enclosed on the landscape by a number of peripheral or satellite roosts, each used by only a subset of bats in the colony. In *Myotis*, loss of central-node or peripheral roosts has resulted in minimal impact to roosting patterns as bats remained in the same roosting areas [18,55]; however, increases in distances moved and changes in social behavior were observed in *M. septentrionalis* following removal of roosts [55].

Declines in the abundance and distribution of American chestnut, due to the introduced blight fungus (*Cryphonectria parasitica*), certainly represented a significant change to canopy structures and deadwood biomass in eastern North American forests where this species once thrived. American chestnut had a distribution from New England to the southern Appalachian Mountains where it represented >50% of the timber volume in stands on well-drained slopes [56,57]. The largest tree in eastern North American forests, American chestnut achieved heights of 40 m and diameters of 3 m, and lived as long as 600 years [58]. American chestnut has thick bark in older trees and decay-resistant wood [59–61], contributing to the potential of this tree as a long-term habitat structure for use by wildlife as shelter [62,63]. The extent to which bark- and cavity-roosting bats used American chestnut for roosting is unknown, however, the size and longevity of these trees likely made them a desirable choice of bats as roosting habitat. American chestnut trees occurred at an estimated historic population size of 4.2 billion trees [64]. Loss of American chestnut likely resulted in a pulse of dead wood legacy structures that have now all but disappeared from forested landscapes in eastern North America where the species occurred as a canopy dominant. Impacts to roosting bats were likely, as these trees may have served as temporally stable, central-node roost trees for populations of bark- and cavity-roosting *Myotis* bats. Chestnut trees were once distributed across >800,000 km² of eastern North American forests [60], and the disappearance of American chestnuts from the landscape may

have required populations of bats to roost more frequently in alternate trees, most of which do not achieve the same size or persist for as long as American chestnut did before population collapse.

Limited data exist for survivorship of bark- and cavity-roosting bats [65,66], including North American *Myotis*, with existing studies of survivorship in these bats having focused primarily on populations inhabiting caves [67,68]. Implicit to benefits of large-diameter trees for roosting in bats is the assumption that use of these structures, especially by larger colonies, will lead to enhanced survival and fitness of individuals within the colony. Studies in New Zealand have demonstrated higher survival rates for populations of *Chalinolobus tuberculatus* roosting in large-diameter, well insulated, tree roosts, compared with bats occupying poorly insulated, roosts in smaller-diameter stems [69,70]. Loss of 97% of the original forest in some areas was responsible for a decline in large-diameter trees, leading to use of poor quality roosting habitat by this bat following disturbance [71]. Although limited in scope, these data would indicate that disease, fragmentation, and loss of forests in eastern North America, and the concomitant decline in availability of large-diameter trees, may have produced similar responses in summer populations of bark- and cavity-roosting *Myotis* bats. Regardless, a full understanding of the effects of roost trees on bark- and cavity-roosting bats also necessitates continued research into the importance or limitations of smaller-diameter trees as roosts for bats, focusing on reproductive and survivorship rates of both solitary-roosting individuals and small colonies, and the role of these smaller-diameter trees in maintaining connectivity of roost networks of bat colonies.

Maternity habitat that allows for gestation, parturition, and the successful rearing of young to sexual maturity is fundamental to the long-term conservation of tree-roosting *Myotis* affected by WNS [72,73]. Results from this study show that eastern *Myotis* currently rely on smaller-diameter trees for use as maternity roosts compared to western North American species and live in colonies that achieve smaller maximum population sizes. Through use of retention forestry methods, that provide for uncut forested habitats in varying patch sizes and spatial arrangements [74], development of landscapes supporting higher densities of large-diameter trees could lead to increased stability and long-term enhancements in available roosting habitat of bark- and cavity-roosting bats in forests of eastern North America. Natural disturbance-based silviculture is increasingly being applied with the intent of creating habitat conditions comparable to those resulting from natural disturbance events [75], while enhancing forest resilience and ability of forests to respond to environmental shifts [76,77]. Nevertheless, forest management which promotes large-diameter trees, with potential to remain standing for longer intervals, should create opportunities for formation of larger maternity populations of bats, potentially leading to improved survivorship, more favorable internal micro-climates, and increased benefits from social thermoregulation [70,78,79].

5. Conclusions

Concerted efforts are underway to develop blight resistant chestnut trees and restore this tree as a canopy dominant in eastern North American forests through genetic engineering, inter- and intra-specific breeding programs, and use of biocontrol with hypovirulence [80]. In turn, recent advances in the study of the *Pseudogymnoascus* fungus responsible for WNS have identified potential control strategies to reduce impacts to hibernating bats including use of ultraviolet light and microbial inhibitors [31,81]. Perhaps one day bark- and cavity-roosting bats in eastern North America will occupy American chestnut trees as roosting sites, but until then management efforts to increase availability of large-diameter trees via other canopy-dominant tree species could help facilitate reproduction and population recovery of bark- and cavity-roosting *Myotis* impacted by WNS. As a starting point, the U.S. Forest Service manages 6 million hectares of forests within the former range of the American chestnut [82], and silvicultural efforts to promote green-tree retention strategies on these public lands could begin the process of returning large-diameter trees to eastern forests. The positive impacts of legacy trees can be even more pronounced in plantation forests, where biological reserves occur within an expanse of exotic tree plantations [83], and in disturbed and fragmented forests [84,85]. Regardless, management that fosters development of large-diameter trees will not be implemented

without problems associated with balancing tree recruitment against mortality [86], and effects of climate change that could lead to geographic shifts in the distribution of canopy-dominant tree species over time [87].

Supplementary Materials: The following are available online at <http://www.mdpi.com/1424-2818/10/2/29/s1>, Table S1: Supplemental file of legacy structure data base.

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Conflicts of Interest: The author declares no conflict of interest.

Appendix Literature Sources Used in Analyses of Roosting Preferences of *Myotis* in North America

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