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Maternity roost site selection of big brown bats in ponderosa pine forests of the Channeled Scablands of northeastern Washington State, USA

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Abstract

Bats play a variety of ecological roles in forest ecosystems and forest management can impact habitat conditions for forest-dwelling bats. We examined the use and characteristics of roosts selected by reproductive female big brown bats (*Eptesicus fuscus*) in the Channeled Scablands of northeastern Washington. We radio-tracked 14 bats to locate 36 roosts. Bats were found in colonies averaging 27 and these colonies switched roosts about every 3.7 days. Habitat variables were measured for the roost itself and at a 0.1-ha microplot and 78-ha macroplot surrounding each roost. We measured habitat variables at random 0.1-ha microplots in the vicinity of each roost and at general random 0.1-ha microplots and 78-ha macroplots. Of the 36 roosts located, 34 were in natural tree cavities; 28 were in ponderosa pine (*Pinus ponderosa*) and eight in quaking aspen (*Populus tremuloides*). Dead tops of live pine trees were used significantly more as roosts than pine snags. Although there were significantly more roosts in trees >30 cm in diameter and >12 m high than what was available, roosts were not always the tallest tree in the stand. A significantly greater proportion of big brown bat roosts were found in open pine, aspen and mixed-aspen pine forests and less in grasslands and closed pine than expected. Forest management strategies should protect both large diameter snags and existing dead top live trees and maintain natural population levels of biological agents that create dead tops. Restoration of historic open conditions in ponderosa pine and aspen stands will provide improved habitat for big brown bats.
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Keywords: Big brown bat; *Eptesicus fuscus*; Dead top live trees; Maternity roosts; Ponderosa pine; Quaking aspen; Porcupine; Snags

1. Introduction

Bats play a variety of ecological roles in forest ecosystems (Marcot, 1996) and by altering habitat conditions, different forest management approaches have the potential to impact the abundance and distribution of forest-dwelling bats (O'Connell and Hallett, 2000). Maternity roost sites are an important resource for bats and their availability can be a major determinant of population size and distribution in temperate latitudes (Kunz, 1982). Roost selection is mediated by factors that vary regionally reflecting differences in availability, climate, potential predators, thermoregulatory requirements, and proximity to foraging habitat and water (Barbour and Davis, 1969; Brigham, 1991; Nagorsen and Brigham, 1993; Barclay and Brigham, 1996; Campbell et al., 1996; Chruszcz and Barclay, 2002; Rancourt et al., 2005). Therefore, examining factors determining roost selection throughout a species' geographic distribution is important for understanding the potential impact of forest management on forest-dwelling bats.

Big brown bats (*Eptesicus fuscus*) are distributed throughout North and Central America. While known to use a variety of natural and human-made roost types, big brown bats exhibit site-specific selection of roosts in different locations. Big brown bat maternity colonies were found exclusively in ponderosa pine (*Pinus ponderosa*) snags in northern Arizona (Rabe et al., 1998), in yellow-bellied sapsucker cavities in live and dead aspen in southwestern Saskatchewan (Kalcounis and Brigham, 1998), in rock crevices in southeastern Alberta (Lausen and Barclay, 2003), and in human-made structures in Ontario (Brigham, 1991). Although big brown maternity colonies are often found in buildings (Showalter and Gunson, 1979;

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Brigham and Fenton, 1986; Cope et al., 1991; Williams and Brittingham, 1997), Brigham (1991) found colonies only in ponderosa pine snags in south-central British Columbia, despite the availability of buildings. In contrast, Lausen and Barclay (2006) concluded that female big brown bats gain certain benefits with respect to predation risks, juvenile growth rates, and energy savings by selecting maternity roosts in buildings over rocks. These observations support Brigham's (1991) suggestion that additional studies of roost-site selection of reproductive big brown bats were necessary to determine if their use of buildings is a result of loss of natural roosting habitat.

Moreover, similar to many other species of bats (e.g., Lewis, 1995; Sherwin et al., 2000; Kunz and Lumdsen, 2003), individual big brown bats are known to switch roost sites periodically (e.g., Rabe et al., 1998; Willis and Brigham, 2004). As Barclay and Brigham (2001) noted, frequent roost-switching behavior means that conservation of roosting habitat must be on a larger scale than an individual roost site.

We examined maternity roost selection of the big brown bat in the Channeled Scablands of eastern Washington. The Scablands area with its stands of ponderosa pine and quaking aspen (*Populus tremuloides*) forests intermixed with basalt rock outcrops and cliffs, numerous wetlands, shrub-steppe, and human habitation provides the full spectrum of roost and foraging sites. This juxtaposition of potential roosting and foraging habitat provides an opportunity to investigate the basis for selection of specific roost types and sites. Specifically, our objectives were to identify the types of roosts selected by reproductive female big brown bats, examine patterns of use, and determine site and habitat characteristics of these roosts.

2. Methods

2.1. Study area

Our research was conducted on Turnbull National Wildlife Refuge (TNWR) in northeastern Washington State. The 6307 ha refuge is located amidst the Channeled Scablands on the eastern edge of the Columbia Basin Plateau. Elevations range from 670 to 720 m. A modified maritime climate of warm, dry summers ($\bar{x} = 27\,^{\circ}$C) and cool moist winters (-4 to $-1\,^{\circ}$C) is typical of the region. Topographic variations across TNWR result in a 10–15 °C difference among microclimatic pockets. Average annual precipitation is 42 cm, occurring primarily as rain or snow in winter and early spring (National Oceanic and Atmospheric Association, 1997).

Numerous wetlands comprised of vernal pools, pothole basins, and larger permanent ponds constitute 20% of the landscape (USFWS, 1999). The 130 wetland basins within the refuge were formed by volcanic activity and several massive floods that occurred at the end of the Pleistocene Epoch (Allen et al., 1986). Two important ecological zones make up TNWR, a Ponderosa Pine Zone and a remnant of the Palouse Zone. Second-growth pine forests cover approximately 40% of TNWR and are represented by two plant associations. Ponderosa pine–Idaho fescue (*Festuca idahoensis*) association is found on shallower, drier soil with a more open canopy and ponderosa pine–snowberry (*Symphoricarpos albus*) association typically occurs in topographic depressions and near wetlands (Daubenmire, 1952). The 2307 ha of Palouse habitat on TNWR is dominated by meadow and shrub-steppe plant communities within a landscape consisting of shallow rocky soils interspersed with regularly occurring soil mounds (Daubenmire, 1970). Edges of wetland basins, channels, and meadows, that constitute <2% of TNWR, are dominated by quaking aspen with an understory of red-osier dogwood (*Cornus stolonifera*), thinleaf alder (*Alnus tenuifolia*), water birch (*Betula occidentalis*), black hawthorne (*Crataegus douglasii*), and snowberry.

2.2. Bat capture and telemetry

We trapped bats at 17 harp trap (constructed following Tidemann and Woodside (1978) and 50 mist net (Avinet Inc., Dryden, New York, USA) sites at different wetland, road, and forest areas distributed throughout TNWR from June through September of 1996 and 1997. We identified all bats to species, and recorded their sex, age, and reproductive condition (Anthony, 1988; Racey, 1988).

Radiotransmitters (LB-2, Holohil Systems Ltd., Carp, Ontario, Canada) weighing approximately 0.45–0.51 g were attached to 14 pregnant or lactating big brown bats. Following a 1-day waiting period, a 3-element Yagi antenna and a TRX-2000S (Wildlife Materials Inc., Carbondale, Illinois, USA) receiver were used to locate radio-marked bats at day roosts. Bats were located daily until the transmitter terminated (10–21 days). Individual roost sites were revisited at night, using night vision equipment to reduce potential disturbance, to determine specific location of the roost, verify its status as a maternity colony, and record emergence time and number of individuals in the colony. If a radio-tagged bat switched roosts, we revisited the old roost site for three consecutive nights to verify that no bats left the old roost. We visited the new roost sites nightly while they were in use to count individuals emerging. Although not all bats were radio tagged, the switch was assumed to include the entire colony when no individuals were observed emerging from the old colony and the number emerging from the new roost was the same as that emerging from the old roost.

2.3. Sampling scale for roost and habitat characteristics

To characterize the roost site, we measured habitat variables at three different spatial scales: (1) the roost itself, (2) a 0.1 ha (17.8 m radius) circular microplot centered on the roost (hereafter termed roost microplot), and (3) a 78 ha (500 m radius) landscape-level macroplot (hereafter termed roost macroplot). We selected 500 m because it is approximately one-half the longest recorded distance between roosts of individual big brown bats in this study.

To examine whether habitat characteristics of roost sites and randomly selected areas differed, we measured habitat variables at two categories of plots: vicinity and general. The first category was a plot randomly selected in the roost

vicinity, hereafter referred to as vicinity-random plots. We selected vicinity-random plots by measuring 50 m from the roost in a randomly selected direction. We identified a tree (=focal tree) within the size class of the roost tree as the center point of the vicinity-random microplot. To locate the general-random plots, we selected 64 points throughout the forested portions of TNWR using a random number generator and plotted them using ARCVIEW GIS (ESRI, Redlands, California, USA). We used these 64 points as the center for 0.1-ha microplots and 78-ha landscape-level macroplots. We refer to these plots as general-random microplots and general-random macroplots, respectively.

2.4. Habitat variables

We measured 35 variables to characterize each identified roost. To characterize the roost microplots we measured 34 habitat variables; 33 of these were measured at the vicinity-random microplots and 32 were measured at the general-random microplots. We estimated the percent composition of seven habitat types to characterize the roost and general-random macroplots (Appendix A).

2.5. Statistical analysis

We used Chi-square goodness of fit tests to compare the observed frequency of three roost characteristics with expected frequencies based on their availabilities at different spatial scales. First, we compared observed frequencies of tree species and configuration (i.e., live, dead top live trees, snag) of roosts to expected values based on their availabilities at general-random microplots. We restricted tallies for tree species to snags or trees with the configuration and minimum dbh and height of roosts we observed used by the bats. For tree configuration and stem type, we restricted tallies only by minimum dbh. Second, we compared observed frequencies of roost trees in three dbh and three height classes with expected values based on their availabilities at the roost microplot, vicinity-random microplot, and general-random microplot. Third, we compared frequencies of roost entrance exposures to expected values based on a uniform distribution.

We used two approaches to compare habitat characteristics between roost and random plots. First, we used a Chi-square goodness of fit test to compare the frequency of roosts in each of the five upland habitat categories to expected values based on their availability in the general-random microplots. Second, we compared habitat variables between (1) roost microplots and vicinity-random microplots, (2) roost microplots and general-random microplots, and (3) roost macroplots and general-random macroplots using a Kruskal–Wallis test.

We used two approaches to examine possible selection criteria for roost sites at the landscape level. Following Nur et al. (1999), we used logistic regression to determine the relative importance of habitat variables in discriminating between roost sites and random sites at both the microplot and macroplot scales. Initially we included each variable separately in the model. Those variables with $P < 0.20$ were then included in a step-wise logistic regression with a backwards selection of variables that best predicted selected roosts. Variables were included in the model at $P = 0.05$. We did this separately for vicinity-random, general-random microplots and macroplots. We also compared the proportion of habitats in the roost macroplot to the general-random macroplot using a method described by Johnson (1980). The procedure used distributional properties of differences in ranks between usage (roost macroplots) and availability (random macroplots) to order habitats from most to least selected and to test the null hypothesis that all habitats are equally selected. The Waller Duncan multiple range test was then used to determine difference in selection between individual habitats.

All statistical tests were conducted with Statistical Analysis System (Statistical Analysis System, 2003). We used $P \leq 0.05$ for all statistical tests.

3. Results

We captured 42 big brown bats (31 adult females, 7 adult males, and 4 juvenile females) and tracking 14 radio-tagged females, we located 36 big brown bat roosts. The mean colony size in the 15 colonies for which we could obtain accurate counts was 27 ± 5.2. All radio-marked bats switched roosts at least once. When a radio-marked bat switched roost, our follow-up observations of that roost indicated that all individuals had vacated it. When we located radio-marked bats' new roost sites the numbers of individuals emerging from these roost were similar to those of the previous roosts. The average number of roosts switches for the 10 female big brown bat colonies that were tracked for >10 days was 3.6 ± 0.62 and days between roost switches averaged 3.7 ± 0.34 days. On two occasions in 1996 and on three in 1997, big brown bats returned to a previous roost site. The average distance traveled between day roosts was 614.3 ± 46.1 m ($n = 36$).

3.1. Roost characteristics

We located 19 roosts in dead tops of live ponderosa pine trees (hereafter referred to as dead tops), 7 in ponderosa pine snags, 4 in aspen snags, 4 in cavities of live aspen trees, and 2 under fascia of buildings. For analyses of roost characteristics, we did not include the two buildings.

Roosts were more commonly found in dead tops of live pine trees, and were larger and taller than expected (Table 1). Fifteen of the 19 dead tops used as roosts were in decay classes >6. The seven roosts in ponderosa pine snags were equally distributed in decay classes 4–7, and all four in aspen snags were in decay class 4. The mean (53.4 ± 3.3 cm) dbh of roost trees and mean height (18.3 ± 1.31 m) were not significantly different than the average dbh and height of the four near trees in the roost site. The mean diameter of dead tops near the base was 33.3 ± 2.75 cm. The length of dead tops averaged 4.3 ± 0.58 m. The mean height of dead tops was 14.6 ± 1.21 m.

Fifteen roosts were in primary cavity excavator holes, 17 in cracks, and 4 under exfoliating bark. The mean height of roost entrances was 8.95 ± 0.72 m, which was greater than 70% of

Table 1
Chi-square comparisons of observed (n_o) frequencies of trees used as roosts by female big brown bats with expected (n_e) frequencies of roost tree species, condition, dbh classes, and height classes at indicated spatial scales in the Channeled Scablands of northeastern Washington, 1996–1997

Characteristic	n_o	n_e	Roost microplot	n_e	Vicinity-random microplot	n_e	General-random microplot
Roost tree species							
Ponderosa pine	26		–		–	24	$\chi^2 = 0.56$; d.f. = 1; $P = 0.5$
Aspen	8		–		–	10	
Roost tree condition							
Snag	7		–		–	11	$\chi^2 = 9.08$; d.f. = 1; $P = 0.02$
Dead top	19		–		–	15	
Roost tree dbh class (cm)							
0 to >30	4	28	$\chi^2 = 35.2$; d.f. = 2; $P < 0.001$	28	$\chi^2 = 36.86$; d.f. = 2; $P < 0.001$	26	$\chi^2 = 31.29$; d.f. = 2; $P < 0.001$
30–60	15	5		6		7	
>60	15	1		0		1	
Roost tree height class (m)							
0 to <3	2	28	$\chi^2 = 46.67$; d.f. = 2; $P < 0.001$	28	$\chi^2 = 49.62$; d.f. = 2; $P < 0.001$	26	$\chi^2 = 45.05$; d.f. = 2; $P < 0.001$
3–12	5	5		6		7	
>12	27	1		0		1	

the trees in the roost microplot, but less than one-half the mean height of the nearest trees ($\bar{x} = 20.5 \pm 1.4$ m). Entrance holes averaged 6.2 ± 0.5 cm in width and 25.3 ± 2.4 cm in height. The inside diameter of the cavity at the entrance hole averaged 16.2 ± 1.0 cm. The total cavity depth averaged 101.2 ± 15.2 cm. Exfoliated bark used as roosts ranged in thickness of 0.85–3.5 cm. The space under the bark occupied by bats ranged from 2.5 to 10 cm. The mean height of the bark flake used as a roost site was 5.2 ± 0.4 m. The distance to cover above and below the roost entrance averaged 2.5 ± 0.3 and 2.5 ± 0.4 m, respectively.

Fewer roost entrances faced north than expected ($\chi^2 = 4.9$, d.f. = 2, $P = 0.027$). Measurements of roost obstruction (distances to first obstruction, canopy edge, and nearest neighboring tree canopy) taken in front of the roost entrance were not different from the average of measurements taken at 90° left and right and 180° from the entrance.

3.2. Habitat

Our comparison of the frequency of roost microplots in each of the five upland habitat categories to expected values based on their availability in general-random microplots revealed that roosts were more frequently found in open ponderosa pine, aspen, and mixed ponderosa pine/aspen forests (Fig. 1; $\chi^2 = 15.51$, d.f. = 4, $P = 0.004$). In contrast, grasslands and closed ponderosa pine forests were avoided (Fig. 1).

Comparison of habitat characteristics between roost microplots and vicinity-random microplots revealed that roosts were located on more level ground and in shorter trees (Table 2). When habitat characteristics were compared between roost microplots and general-random microplots, roosts were again found on more level ground. Additionally, distance to water was greater, density of saplings was less, nearby shrubs were taller, nearest trees were larger but farther from the roost or focal tree, and there was more coarse woody debris but less moss ground cover at the roost as compared to the general-random microplots (Table 3). Comparing roost macroplots with general-random macroplots, the area surrounding the roosts had a lower proportion of seasonal and semi-permanent wetlands than general-random macroplots (Table 3).

At roost-vicinity scale, we found slope and tree height best discriminated big brown bat roost sites from vicinity-random sites (Table 4). Odds of a tree being used as a roost increased with decreasing slope and tree height (Table 4). When roost microplots were compared to general-random microplots slope, nearest tree dbh, percentage of forb ground cover, and percentage of coarse woody debris cover were the best predictors (Table 4). Odds of a tree being used as a roost increased with decreasing slope, forb cover, tree height, and increasing size of nearest tree and amount of woody debris cover (Table 4). At the landscape level, likelihood of roost selection decreased with proportion of grassland habitat and the proportion of permanent water in the 78-ha plots (Table 4).

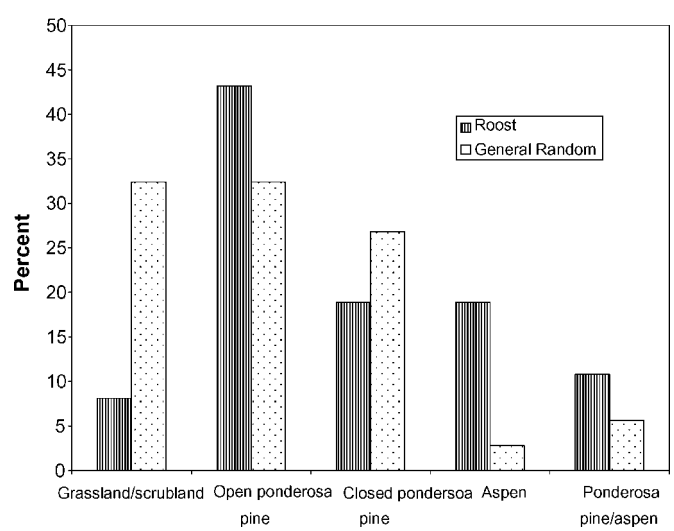

Fig. 1. . The percentage of five habitat types observed in the roost-vicinity microplots of big brown bats and general-random microplots in the Channeled Scablands of northeastern Washington.

Table 2
Comparison of habitat variables between 0.1-ha plots at 34 big brown roost sites and vicinity-random plots in the Channeled Scablands of northeastern Washington

Variable	Roost, mean (±S.E.)	Random, mean (±S.E.)	Kruskal–Wallis, χ^2	P
Slope	**3.71 ± 1.08**	**6.74 ± 1.63**	4.222	0.040
Distance to any water	182.40 ± 27.65	166.41 ± 27.43	0.159	0.690
Distance to permanent water	266.32 ± 32.46	240.56 ± 36.67	0.578	0.477
Roost or focal tree dbh	53.08 ± 3.25	50.93 ± 3.51	0.305	0.581
Roost or focal tree height	**17.98 ± 1.26**	**22.67 ± 1.27**	7.557	0.006
Canopy edge	2.01 ± 0.34	2.69 ± 0.26	1.941	0.164
Nearest canopy	19.36 ± 3.36	23.29 ± 4.29	0.159	0.690
Average stem dbh	23.23 ± 2.08	22.92 ± 2.20	0.025	0.873
Average stem height	12.20 ± 0.74	12.55 ± 0.84	0.012	0.912
Basal area	18.65 ± 2.00	16.59 ± 1.80	0.506	0.477
Seedlings (# per ha)	1373.24 ± 321.53	1312.35 ± 479.82	3.387	0.066
Saplings (# per ha)	321.47 ± 127.01	383.24 ± 171.98	0.134	0.715
Canopy cover (%)	47.85 ± 3.83	47.21 ± 4.43	0.195	0.659
Large shrub cover (%)	27.80 ± 5.61	33.60 ± 5.72	0.341	0.559
Distance nearest shrub	26.69 ± 5.68	23.66 ± 6.75	0.667	0.414
Nearest shrub height	0.71 ± 0.10	0.96 ± 0.37	0.385	0.535
Distance nearest tree	20.49 ± 3.56	16.40 ± 2.39	0.447	0.504
Nearest tree dbh	45.79 ± 2.98	43.73 ± 2.32	0.716	0.397
Nearest tree height	20.05 ± 1.39	21.03 ± 0.82	1.192	0.275
Moss ground cover (%)	8.71 ± 1.70	9.20 ± 1.46	1.116	0.291
Grass/sedge ground cover (%)	32.78 ± 2.68	32.00 ± 2.95	0.005	0.941
Forbs ground cover (%)	5.10 ± 1.01	7.67 ± 1.41	0.817	0.366
Small shrub ground cover (%)	7.18 ± 1.70	9.26 ± 1.74	1.116	0.291
Litter ground cover (%)	33.76 ± 2.57	33.58 ± 1.79	0.067	0.796
Coarse woody debris (%)	6.82 ± 1.61	3.93 ± 0.72	0.993	0.319
Rock cover (%)	1.84 ± 0.53	1.66 ± 0.68	0.588	0.443
Bare ground (%)	2.52 ± 0.81	1.42 ± 0.45	0.824	0.364

Values in bold are significantly larger than corresponding value for habitat variable.

The ranking procedure used for comparison of habitats between roost and random macroplots showed that the proportion of habitats were not equal ($F = 36.19$, d.f. = 6,31, $P < 0.05$). Big brown bat roost macroplots contained a greater proportion of aspen and open ponderosa pine and less closed pine, grasslands and permanent wetlands (Fig. 2). Seasonal and semi-permanent wetlands were nearly equal in rank in the roost and random macroplots.

4. Discussion

4.1. Roost selection

As reported from other geographic regions, we observed that reproductive female big brown bats exhibited site-specific selection of roosts. Although big brown bats have been associated with snags elsewhere in their geographic range (Brigham, 1991; Kalcounis and Brigham, 1998; Rabe et al., 1998), the almost exclusive selection of dead top live trees appears to be specific to this region. The site-specific selection of this roost type reflects forest conditions in the Channeled Scablands and points to important forest management considerations.

Despite the variety of human-made structures (houses, barns, bridges, and outbuildings) available to reproductive female big brown bats, the nearly exclusive use of cavities in dead tops or snags supports Brigham's (1991) suggestion that use of human-made structures results from the loss of natural roost habitat. Our findings are in contrast to Lausen and Barclay's (2006) conclusion that these bats select buildings over natural roosts, however big brown bats in their study were roosting in rock crevices rather than trees.

The selection of dead top live trees by big brown bats reflects both the availability in the landscape and specific characteristics of this roost type. Although dead tops used as roosts retained a hardened shell of sapwood, the heartwood was in an advanced stage of decay creating a substantial cavity that sometimes extended into the living part of the tree bole. Willis et al. (2006) observed that big brown bats selected roost trees with larger cavities and that maternity colony size was positively correlated with cavity size. Past refuge inventories of snags indicate that snags may not be retained long enough to obtain the advanced stage of decay needed to provide for suitable roosting cavities. Less than 18% of snags ($n = 332$) inventoried were in decay class 6 or 7 (U.S. Fish and Wildlife Service, unpublished data). Reported fall rates for ponderosa pine snags are relatively high. Harrington (1996) found that 75–80% of trees dying within the first post-burn year will fall within 10 years. Keen (1955) found that on average 60% of beetle-killed ponderosa pine trees fell within 10 years and <20% were still standing after 15 years. Fire and insects are the primary agents of snag creation in the study area. Observations of snags on the refuge also indicate that the study area may experience fall rates higher than those previously reported. Ponderosa pine with its large tap root normally has a deep rooting habit which makes it more resistant to windthrow

Table 3
Comparison of habitat variables at 34 big brown bat roost micro- and macroplots and 64 general-random micro- and macroplots in the Channeled Scablands of northeastern Washington

Scale/variable	Roost, mean (±S.E.)	Random, mean (±S.E.)	Kruskal–Wallis, χ^2	*P*
Microplot				
slope	**3.70 ± 1.08**	**7.67 ± 0.85**	12.351	0.0004
Distance toedge	10.85 ± 4.31	10.14 ± 2.07	0.508	0.8216
Distance to any water	**182.40 ± 27.64**	**96.47 ± 7.79**	6.654	0.0310
Distance to permanent water	266.32 ± 32.47	197.11 ± 16.47	1.938	0.1639
Average stem dbh	23.23 ± 2.08	22.48 ± 1.52	0.062	0.803
Average stem height	12.20 ± 0.74	12.01 ± 0.73	0.70	0.791
Basal area	18.65 ± 2.00	18.29 ± 1.62	0.089	0.765
Seedlings (# per ha)	1373.24 ± 321.53	2274.53 ± 526.32	0.309	0.578
Saplings (# per ha)	**312.51 ± 127.49**	**371.72 ± 69.73**	4.300	0.038
Canopy cover (%)	47.85 ± 3.83	45.85 ± 3.30	0.162	0.687
Large shrub cover (%)	27.80 ± 5.61	26.18 ± 3.47	0.289	0.591
Distance nearest shrub	26.69 ± 5.68	16.97 ± 3.51	1.237	0.266
Nearest shrub height	**0.71 ± 0.10**	**0.51 ± 0.09**	5.000	0.025
Distance nearest tree	**20.49 ± 3.56**	**9.58 ± 1.45**	17.159	<0.0001
Nearest tree dbh	**47.24 ± 2.64**	**30.68 ± 1.64**	21.517	<0.0001
Nearest tree height	**20.57 ± 1.25**	**14.98 ± 0.80**	13.348	0.0003
Moss ground cover (%)	**8.73 ± 1.89**	**16.78 ± 2.06**	7.888	0.005
Grass/sedge ground cover (%)	32.70 ± 2.69	28.52 ± 2.09	2.037	0.154
Forbs ground cover (%)	5.01 ± 1.01	8.36 ± 1.19	2.384	0.123
Small shrub ground cover (%)	7.17 ± 1.72	4.34 ± 0.71	0.182	0.679
Litter ground cover (%)	33.86 ± 2.57	33.00 ± 2.21	0.229	0.632
Coarse woody debris (%)	**6.74 ± 1.61**	**2.80 ± 0.51**	6.230	0.0126
Rock cover (%)	1.77 ± 0.51	3.16 ± 0.57	2.485	0.1149
Bare ground (%)	2.51 ± 0.82	1.89 ± 0.44	0.159	0.689
Macroplot				
Seasonal wetland	**6.95 ± 0.85**	**9.72 ± 0.69**	7.238	0.007
Semi-permanent wetland	**2.68 ± 0.58**	**3.99 ± 0.40**	7.480	0.006
Permanent wetland	3.74 ± 1.04	4.47 ± 0.72	2.624	0.105
Grassland	42.81 ± 3.76	34.41 ± 1.57	3.026	0.082
Ponderosa >50% cover	24.96 ± 2.03	24.26 ± 1.31	0.247	0.619
Aspen	1.32 ± 0.19	1.58 ± 0.18	0.315	0.575
Ponderosa <50% cover	21.31 ± 2.09	21.98 ± 1.42	0.104	0.740

Values in bold are significantly larger than corresponding habitat variable.

(Brayshaw, 1965; Agee, 1993). The thin soils and underlying basalt over much of the study area often prevent the formation of a tap root and the lateral roots remain just below the soil surface. The result is an ineffective anchor against the high winds in the spring and fall that can reach >80 km/h (National Oceanic and Atmospheric Association, 1997).

In addition, snags, especially those resulting from fire kill, have a tendency to break off at various heights from the ground (Kimmey, 1955; Lowell et al., 1992) which could result in a shorter roost site than preferred. The height of the breakage results from differential decay of the bole which is related to volume of sapwood and moisture levels. Sapwood decays more

Table 4
Parameter coefficients for logistic regression on habitat variables at three spatial scales for big brown bat maternity roosts in the Channeled Scablands of northeastern Washington

Scale	Variable	d.f.	*P*	Estimate	95% CI	Odds ratio
Microplot: roost vicinity-random	Slope	1	0.038	−0.1168	0.797–0.991	0.890
	Tree height	1	0.018	−0.0999	0.833–0.983	0.905
	Intercept	1	0.016	2.6525		
Microplot: roost general-random	Slope	1	0.0240	−0.1849	0.708–0.976	0.831
	Nearest tree dbh	1	0.0003	0.1867	1.090–1.333	1.205
	% Forbs ground cover	1	0.0028	−0.1732	0.751–0.942	0.841
	% Coarse woody debris	1	0.0038	0.2672	1.090–1.566	1.306
	Intercept	1	0.0161	−4.7795		
Macroplot: roost general-random	Proportion of seasonal wetland	1	0.0210	−0.117	1.017–1.229	1.118
	Proportion of grassland	1	0.0212	−0.0306	0.945–0.995	0.970
	Intercept	1	0.011	62.82		

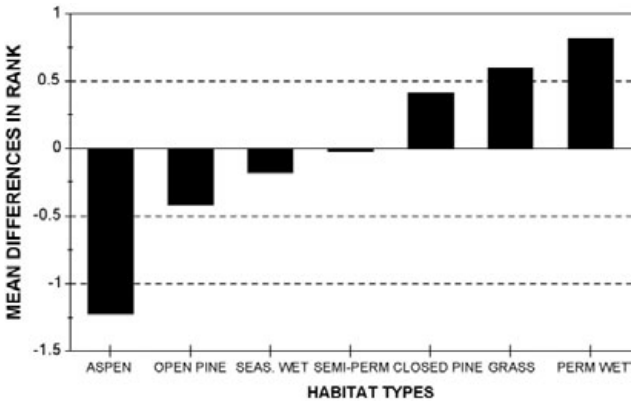

Fig. 2. . Mean differences in rank of habitat types between big brown bat roost and general-random macroplots. Ranks based on proportions of each habitat in macroplot. Habitats are ordered from most selected on the left to least selected.

rapidly than heartwood and sapwood volume and diameter decreases with height (Lowell et al., 1992). The lack of moisture, especially in dry sites, can be a factor in limiting decay in the upper bole (Kimmey, 1955). The thicker bark of ponderosa pine especially near the base can maintain moisture levels conducive to fungal decay (Kimmey, 1955). The end result is that many ponderosa pine snags often break off near the ground and fall intact rather than slowly decomposing from the top down.

The larger size of cavities in dead tops likely provided a greater range of microclimates. We found guano in different areas of the dead top and within the live bole. With dead top cavities averaging 1 m in depth, bats likely moved up or down the cavity for thermoregulation. Big brown bats are sensitive to high temperatures and may leave a roost when temperatures exceed 34 °C (Davis et al., 1968). Thirty-eight percent of the cavities in the dead tops extended into the living portion of the bole. This area of the tree bole retained all of its outer bark, which could have provided greater insulation.

4.2. Habitat selection

The big brown bats' site-specific selection of dead top live trees influenced, to a large extent, the general habitat conditions with which the bats were associated. The relatively large body size and low frequency echolocation calls of big brown bats have led to the suggestion that these bats require more open habitats and easily accessible roost sites (Norberg and Rayner, 1987) than smaller Vespertilionid bats. Our results suggest that the habitat selected by the bats met these conditions.

Big brown bat selection of a greater proportion of roosts in open pine, aspen and mixed pine/aspen forest and avoidance of grasslands undoubtedly relates to their use of pine and aspen trees as roosts. However, the selection of these more open forests over the closed pine forests might reflect avoidance of these dense, obstructed habitats. The reduced availability of larger trees in the suppressed stands that make up closed pine habitat is another possible explanation. Habitat conditions between grasslands and forests and between the open and closed forests explain observed differences between roost and random plots with respect to slope, nearest shrub height, sapling density, moss and woody debris cover. In contrast to the stands of closed pine forest, open pine forest stands occur on flat broad ridges and mixed pine/aspen and aspen stands occur on the flat edges of wetlands or in depressions. Tall shrubs are a component of the aspen and mixed pine habitats whereas many saplings characterize the closed forest habitat. Moss ground cover is more common in the grassland habitats whereas woody debris is obviously more common in forest habitat. Woody debris cover was greater in roost microplots than in other forested plots because of the tendency for branches and bark on the dead tops and snags to fall off.

Tree-roosting bats in other forests have been observed to select tall, 'super-emergent', trees (Campbell et al., 1996; Betts, 1998). Although big brown bats selected large dbh roost trees, they were not necessarily the tallest tree in the roost site. This relates to their use of dead tops which stunt the terminal growth of affected trees making them shorter than trees of similar diameter. Despite this, roosts appeared to be easily accessed due to several aspects of the stand conditions. Similar to findings by Kalcounis and Brigham (1998), the front of the roost entrance was no less obscured than the back of the roost. The growth characteristics of ponderosa pine might facilitate access to the roost. High crowns and a lack of branches on the lower bole increase the probability ponderosa pine will survive frequent, low intensity ground fires that were common in this dry forest (Agee, 1993). These characteristics create relatively open conditions under the canopy. Trees on the refuge in the same height class as roost trees had a canopy height that averaged 8.9 m which was equal to the mean height of roost entrances (U.S. Fish and Wildlife Service, unpublished data). During emergence, big brown bats were often first observed dropping below the cavity entrance and flying beneath the canopy.

In addition to roost accessibility, habitat selection might be mediated by prey abundance. The selection for aspen and mixed pine/aspen forests might also reflect selection of prey-rich habitats near the roost. Grindal et al. (1999) observed 10 times greater foraging activity in riparian areas than uplands and assumed this was the result of greater insect abundance.

Similarities in mean distance to water between roosts and random sites and the low selection of open, permanent wetlands at the landscape level indicated that water was not a limiting factor in the selection of roost sites by big brown bats on TNWR. This area had a high density of wetlands and distances to water were less than one-half that found in northern Arizona where water was a factor in identifying suitable roosts in one study area (Rabe et al., 1998).

4.3. Roost switching

Similar to other studies, we observed frequent roost switching by big brown bats. Roost switching in this species has been characterized by a fission–fusion model with individuals moving between sub-groups of a larger colony using multiple roost sites (Willis and Brigham, 2004). Unlike Willis and Brigham (2004), we did not observe a portion of the

individuals in a group remaining in a roost tree vacated by radio-marked bats. However, our methods did not allow us to follow more than an individual bat in a colony. Rabe et al. (1998) suggested that roost switching may result from the ephemeral nature of the roost (exfoliating bark of ponderosa pine). In contrast, our findings indicated that bats switched roosts frequently regardless of the permanency of the roosts. Roost switching by big brown bats on TNWR might improve access to foraging sites that varied both temporally and spatially. Insect densities are typically patchy in distribution and bats exploit these resource patches (Bell, 1980; Geggie and Fenton, 1985; Furlonger et al., 1987). The long-lived nature of roosts in dead tops may have allowed big brown bats over the years to investigate and inventory suitable maternity roosts. This knowledge would allow a colony to switch to a new roost near a newly discovered patch of insects. Although we did not look at insect abundance, insect flushes in seasonal wetlands are known to vary in response to wetland depth (Swanson et al., 1974; Fredrickson and Reid, 1988; Leeper and Taylor, 1998). The undulating topography of TNWR creates numerous wetlands that vary in size and depth that result in a patchy distribution of insects (Kulp and Rabe, 1984). Roost switching might have allowed big brown bats to exploit these insect patches and minimize traveling distance to roosts.

5. Management implications

Our findings that dead tops are an important roost resource for big brown bats coupled with our observations of smaller species of bats and several cavity-nesting birds occupying dead tops, elevates the need for consideration of dead top live trees and the agents that create these dead tops in forest management decisions. Dead tops of trees can be caused by porcupines (*Erethizon dorsatum*) insects (particularly the bark beetles *Pityophthorus confertus* and *Ips pini*), disease, lightning strikes or some combination of these agents (Gabrielson, 1928; Curtis, 1941; Rudolf, 1949; Harder, 1979; Roze, 1989; Sinclair et al., 1987; Rasmussen, 1992; Kegley et al., 1997). For example, we observed porcupines in the winter girdling the tops of large ponderosa pine trees similar to those used as roosts by big brown bats.

Because porcupines and insects are known causes of dead tops in ponderosa pine, they are considered harmful and destructive timber pests by many. Live trees with dead tops or trees that have sustained some other physical damage are often considered defective because they are often shorter and deformed compared to trees of similar age in the stand (Lawrence, 1957; Faulkner and Dodge, 1962; Rasmussen, 1992). Insect-damaged trees are often removed from stands to prevent a more extensive outbreak. Because of the U.S. Office of Safety and Health Administration restrictions on logging activities near 'danger' trees (snags and defective trees), they are often removed to allow workers access to a larger area (Egan, 1998). Cline et al. (1980) suggested killing large defective trees as a possible management strategy to replenish snags. In contrast, our results highlight the importance of protecting these large dead top live trees. Managing for natural populations of porcupines, insects, and disease in a forest community can play a vital role in the protection of the biodiversity of an area.

Due to previous logging and fire suppression practices, ponderosa pine forests in the region are often characterized by unnaturally dense stands of smaller-diameter trees. Efforts to restore ponderosa pine woodlands with the reintroduction of fire could result in the destruction of large diameter trees, dead tops, and snags. Management strategies should be implemented to preserve these large defective trees and snags during forest restoration. Selective thinning of dense ponderosa pine stands and removal of excess duff and debris around the base of the tree, dead top, or snag prior to burning may help protect these potential roost sites. We also recommend that the restoration and maintenance of aspen stands in this area be a management priority because of the disproportionate use of aspen/pine habitat by big brown bats.

Given regional differences in roost selection found in this and other studies, caution should be exercised in making generalizations about roost selection of bat species. Each area is unique in the availability of tree species, snags, rock and human-made structures. Roost site selection may be based upon that uniqueness and should be managed for accordingly.

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Appendix A

Definitions and methods of measurement of habitat variables used to characterize big brown bat roosts, roost- roost-vicinity- and general-random-microplots, and roost- and general-random-macroplots in Channeled Scablands of Washington State

Scale/habitat variable	Method
Roost	
Roost tree species	Roost tree identified to species
Roost tree condition	Classified into three categories: normal live tree, live tree with dead top, and snag
Decay class	Decay class of snags and dead tops of live trees were categorized into one of seven stages: 1, living; 2, dying; 3, dead; 4, loss of some bark with few branches; 5, no bark or branches; 6, broken; 7, decomposed (Thomas et al., 1979)

Appendix A (*Continued*)

Scale/habitat variable	Method
dbh of roost or focal tree	Diameter at breast height (cm)
Height of roost or focal tree	Measured with a clinometer (m)
Canopy edge of roost or focal tree	Distance (m) to edge of canopy or roost or focal tree measured in four quadrants
Nearest canopy to roost or focal tree	Distance (m) to edge of canopy of nearest tree to roost or focal tree measured in four quadrants
Height of roost entrance	Measured with a clinometer (m)
Configuration of cavity	Defined as round, crack, or bark flake
Cavity orientation	Cardinal direction of the cavity entrance
Dead top characteristics	Length, height, and dbh (cm) of dead top portions of live trees
Cavity characteristics	Height and width of entrance hole (cm); depth of cavity extending into live tree bole both above and below entrance (cm); inside diameter of cavity at entrance hole (cm); thickness of exfoliated bark (cm); space underneath bark (cm)
Horizontal obstruction	Distance to first obstruction (branch, overhang, shrub, tree, etc.) at 90° intervals from roost entrance (m)
Vertical obstruction	Distance (m) and type of cover above and below roost entrance
Distance between roosts	Distances (m) between roost sites for individual bats measured using GIS
Roost, vicinity-random, and general-random microplots	
Slope	Slope recorded using a clinometer
Upland habitat type	Microplots classified into one of five general upland habitat types: scrubland/grassland, closed ponderosa pine forest (≥50% cover), open ponderosa pine forest, aspen, or mixed ponderosa pine/aspen
Distance to edge	Distance (m) to change in habitat type. Not measured at vicinity-random microplots
Distance to water	Distances (m) to nearest available water and to permanent body of water determined from aerial maps of the study site and by using GIS
Water type	Nearest water type classified as vernal pool, seasonal wetland, semi-permanent wetland, permanent wetland, streambed, or channel
Shrub density and height	Shrub density and height (m) measured using the point center quarter method (Dix, 1961)
Nearest shrub characteristics	Distance (m) to and height (m) of nearest shrub from roost tree (roost microplot), focal tree (vicinity-random microplot) or center point (general-random microplot) in four quadrants
Shrub cover	Percentage of shrub cover estimated for each microplot by two observers; average used in analysis
Ground cover	Ground cover recorded for points at 1-m intervals along a transect extending from the center to the edge of the each microplot in each of the four cardinal directions. Categories of ground cover were: mosses, ferns, grasses and sedges, forbs, small shrubs (≤1 m tall), seedlings, litter, slash and logs, rocks, bare ground
Nearest tree characteristics	Distance (m) to, dbh (cm) and height (m) of nearest tree from roost tree (roost microplot), focal tree (vicinity-random microplot) or center point (general-random microplot) in four quadrants. Selection restricted to trees of comparable height and dbh of roost or focal tree
Seedling and sapling density	All seedlings (≤1 m tall) and saplings (>1–<2 m) counted within each plot. Densities converted to stems per hectare
Canopy cover	Percentage of canopy cover (measured with concave spherical densitometer) at 9 m (one-half radius of the microplot) from the center of both the roost and random plots in four cardinal directions (Lemmon, 1956). The four estimates averaged
Stand characteristics	Species, dbh, height, and configuration (i.e., dead top, dead top with lateral branches, forked top) of all stems within the microplot. Basal area (m^2/ha) calculated from stem data
Roost macroplot and general-random macroplot	
Cover of wetland and upland habitat type	GIS-overlays of vegetation cover used to determine the composition (%) of three wetland types: seasonal, semi-permanent, and permanent, and five upland habitat types: grassland/scrubland, open ponderosa pine, closed ponderosa pine, aspen, and mixed pine/aspen

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