

SELECTION OF DAY-ROOSTS BY KEEN'S MYOTIS (*MYOTIS KEENII*) AT MULTIPLE SPATIAL SCALES

JULIA L. BOLAND,* JOHN P. HAYES, WINSTON P. SMITH, AND MANUELA M. HUSO

Department of Forest Science, Oregon State University, 321 Richardson Hall, Corvallis,
OR 97330, USA (JLB, JPH, MMH)

United States Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory,
2770 Sherwood Lane, Suite 2A, Juneau, AK 99801-8545, USA (WPS)

Present address of JLB: Division of Fish and Wildlife, Commonwealth of the Northern Mariana
Islands, P.O. Box 1397, Rota, MP 96951, CNMI

Present address of JPH: Department of Wildlife Ecology and Conservation, University of Florida,
110 Newins-Ziegler Hall, P.O. Box 110430, Gainesville, FL 32611, USA

Present address of WPS: United States Forest Service, Pacific Northwest Research Station,
Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850, USA

Keen's myotis (*Myotis keenii*) has one of the most limited geographic distributions of any species of bat in North America. Because there is little knowledge of its roosting ecology, we examined selection of day-roosts in trees by male and female Keen's myotis at 3 spatial scales (tree, tree plot, and landscape) on Prince of Wales Island, southeastern Alaska, from May to September 2006. We selected variables known to influence roost selection by other tree-roosting bats for logistic regression models. We used Akaike's information criterion to rank all models within and between scales according to their ability to differentiate between characteristics of used and available roosts and we determined the effect of each variable with model-averaged coefficient estimates and associated odds ratios. We tracked 13 females and 6 males to 62 and 24 roosts in trees, respectively. Selection of day-roosts by males and females was most strongly influenced by characteristics of trees. The odds a tree was used for roosting by female Keen's myotis increased with the presence of defects, increasing diameter, and decreasing bark; increasing quadratic mean diameter in the tree plot; and decreasing distance to the nearest stream and increasing proportion of old growth in the landscape. Male Keen's myotis exhibited flexibility in types of roosts chosen, but the odds of a tree being used increased with decreasing bark, the presence of defects, and increasing slope-height. The odds a tree was used as a roost by males also increased with the increasing proportion of trees in early to late decay stages in the tree plot. Some habitat features differed between males and females at each spatial scale and differences are likely a reflection of the energetic demands associated with reproduction. We suggest that maintaining structural components characteristic of old-growth rain forest will promote conservation of Keen's myotis in southeastern Alaska.

Key words: Alexander Archipelago, bats, Keen's myotis, *Myotis keenii*, Prince of Wales Island, roosting, roost selection, southeastern Alaska, spatial scales, temperate rain forest

Animals respond to their environment at multiple spatial scales, and habitat associations at 1 scale may influence and constrain relationships at broader or finer scales (Gorresen et al. 2005; Orians and Wittenberger 1991; Wiens 1989). The spatial scales at which habitat characteristics influence selection of day-roosts by forest-dwelling bats can range from several

square centimeters (e.g., the entrance to a roost—Pysyllakis and Brigham 2006; Sedgeley and O'Donnell 2004) to hundreds of hectares (e.g., the area encompassing potential foraging areas and roost sites—Brigham et al. 1997; Broders et al. 2006; Miles et al. 2006; Waldien and Hayes 2001).

For a given species, habitat characteristics that influence selection of day-roosts by bats may vary by sex (Broders and Forbes 2004; Perry and Thill 2007), age, and reproductive status (Barclay and Kurta 2007; Kunz and Lumsden 2003; Solick and Barclay 2007; Tuttle 1976). Availability of roosts may limit populations of forest-dwelling bats (Barclay and Kurta 2007; Hayes and Loeb 2007), and dependence of bats on

* Correspondent: julia.boland88@gmail.com

the availability and abundance of suitable roosts and suitable habitat surrounding roosts may magnify sensitivity to structural alteration created by forest management (Hayes 2003; Hayes and Loeb 2007). Understanding the sex-specific roosting ecology of bats at all relevant spatial scales is fundamental for evaluating the impacts of habitat alteration and to effectively prioritize conservation efforts (Barclay and Kurta 2007; Broders et al. 2006; Racey and Entwistle 2003).

The putative geographic distribution of Keen's myotis (*Myotis keenii*) is one of the smallest of any species of bat in North America and the species appears to be restricted to coniferous forests of western Washington, southern British Columbia, Canada, and southeastern Alaska (Nagorsen and Brigham 1993; Parker and Cook 1996; van Zyll de Jong and Nagorsen 1994). Very little is known about the habitat associations and roosting ecology of this species. Although Keen's myotis are reported to roost in trees, houses, caves, rock crevices, and under boulders in British Columbia (Burles 2000, 2001; COSEWIC 2003; Firman et al. 1993; Mather et al. 2001), data are few and primarily anecdotal and virtually nothing is known about the roost requirements of Keen's myotis in southeastern Alaska.

Our primary objective was to determine the influences of habitat characteristics on selection of day-roosts by adult male and female Keen's myotis on Prince of Wales Island. We assessed selection of day-roosts in trees at 3 spatial scales: the tree, immediate vicinity around the tree (tree plot), and the landscape. For each scale, we examined variables predicted to be influential based on current knowledge of roosting ecology of forest-dwelling bats in North America (e.g., Barclay and Kurta 2007; Kalcounis-Rüppel et al. 2005; Kunz and Lumsden 2003).

Bats in temperate coniferous forests frequently roost under sloughing bark and inside structural defects (i.e., cracks, cavities, and broken tops) of live trees and snags that are larger in diameter and taller than surrounding vegetation (Barclay and Kurta 2007; Brigham et al. 1997; Campbell et al. 1996; Hayes 2003; Vonhof and Barclay 1996; Weller and Zabel 2001). Decay in live coniferous trees and snags influences the creation of potential roost sites such as cavities, cracks, and sloughing bark (Hennon 1995; Kimmey 1956). Structural characteristics and decay processes vary among species of tree and certain species may be preferentially chosen by bats for roosting (Barclay and Kurta 2007; Kunz and Lumsden 2003; Vonhof and Barclay 1996). We hypothesize that structural characteristics of a tree ultimately determine the energetic benefits it provides to roosting bats and that the energetic requirements of Keen's myotis are driving roost selection throughout their range. Therefore, at the scale of individual trees, we predicted that the presence of defects, bark coverage, diameter, height, decay stage, and tree species influence selection of trees for day-roosting by Keen's myotis.

Bats often roost in areas with an abundance of trees with similar size and decay characteristics as the roost tree (Campbell et al. 1996; Erickson and West 2003; Waldien et al. 2000; Weller and Zabel 2001). This may indicate a preference for roosts that are surrounded by an abundance of potential roost sites, but suitable roost habitat may have an

upper threshold to the density of surrounding trees regardless of roost potential (Hayes and Loeb 2007). Stem density is often associated with use of habitat by forest-dwelling bats (Brigham et al. 1997; Erickson and West 2003; Humes et al. 1999; Loeb and O'Keefe 2006; Psyllakis and Brigham 2006; Vonhof and Barclay 1996). We hypothesized that the selection of day-roosts in trees by Keen's myotis is influenced by the mean diameter, density, and stage of decay of trees in the immediate vicinity of the roost.

Characteristics of the landscape that influence roost selection by some forest-dwelling bats include the distance of the roost to the nearest stream (Ormsbee and McComb 1998; Waldien and Hayes 2001) and the age of the forest surrounding the roost (Grindal 1998; Perry and Thill 2007; Psyllakis and Brigham 2006). We predicted that the distance to the nearest stream and the proportions of old-growth and clear-cut habitat in the surrounding landscape influence selection of trees for day-roosting by Keen's myotis.

We hypothesized that male and female Keen's myotis differ in selection of roosts based on the ecological characteristics of the roosts, and that these differences are consistent with sex-based differences in energetic requirements (as suggested by Altringham and Senior 2005; Barclay and Kurta 2007; Broders et al. 2006). We further hypothesized that selection of summer day-roosts is influenced by multiple factors operating at multiple spatial scales. We proposed that bats simultaneously respond to several factors at different spatial scales and that the requirements at 1 scale may affect and constrain selection at broader or finer scales.

MATERIALS AND METHODS

Study area.—This study was conducted from 18 May to 1 September 2006 on Prince of Wales Island in southeastern Alaska. Prince of Wales Island, with an area of 6,675 km², is the largest island in the Alexander Archipelago and spans from 54°41' to 56°22'N latitude (Carrera et al. 2003). From May to September, mean monthly temperature ranges between 8°C and 14°C and mean monthly precipitation is between 17.8 and 29.7 cm (www.noaa.gov, 2007). We selected Prince of Wales Island for our study because of the extensive road system, diversity of habitats, and apparent higher abundance of Keen's myotis relative to other areas in the region (J. L. Boland, pers. obs.). Prince of Wales Island is mountainous with a mosaic of coastal coniferous old-growth rain forest, muskeg bogs, peatland mixed-conifer forest, alpine areas, and managed landscapes (van Hees 2003). Old-growth forests in southeastern Alaska typically contain a dense and structurally diverse understory, and an uneven-aged, vertically stratified canopy. Old-growth forests are dominated by western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), and to a lesser extent western red cedar (*Thuja plicata*) and Alaska cedar (*Chamaecyparis nootkatensis*), and red alder (*Alnus rubus*) is often present in riparian areas (Alaback 1982; van Hees 2003). Clear-cuts and regenerating forests <25 years old are comprised primarily of slash remaining from harvest activities, regenerating conifers, and a dense shrubby layer of *Vaccinium*.

TABLE 1.—Variables measured at each spatial scale to determine their influence on selection of day-roosts in trees by Keen's myotis (*Myotis keenii*) on Prince of Wales Island, 2006.

Scale	Variable	Description
Tree	Bark	Bark remaining on tree stem (%)
	DBH	Diameter at breast height (cm)
	Defects	Presence of cavities, cracks, or broken top
	Slope-height	Height of tree given the slope (m)
Tree plot	Decadence	Proportion of canopy trees that are in decay classes >1
	Density	Number of canopy trees
	QMD	Quadratic mean diameter (cm)
Landscape	Stream	Distance (m) to nearest flowing waterway
	Clear-cut	Proportion of unit that is recently clear-cut (<25 years old)
	Old growth	Proportion of unit that is old-growth forest

More than 31% of original productive old-growth forest in North Prince of Wales Island and nearly 10% on South Prince of Wales Island has been harvested (Albert and Shoen 2006; United States Department of Agriculture Forest Service 1996). Peatland mixed-conifer forests are gently sloping and interspersed with patches of muskeg bog (DeMeo et al. 1992; Smith et al. 2004). Canopy species in peatland mixed-conifer forests include western hemlock, Alaska cedar, western red cedar, mountain hemlock (*Tsuga mertensiana*), and lodgepole pine (*Pinus contorta*).

Captures and species identification.—The locations where bats are captured can influence the assessment of habitat relationships (Waldien et al. 2000). To minimize this bias, we attempted captures of bats in muskeg bogs, peatland mixed-conifer forest, and coniferous rain forests with varying management histories throughout Prince of Wales Island. However, because of logistical constraints, we limited sites to those within 0.5 km of a road or trail. We captured bats in mist nets suspended over creeks, rivers, and ponds and across roads and trails. We recorded the location of each capture site with a global positioning system (GPSMAP 60CS; Garmin International, Inc., Olathe, Kansas) and imported coordinates into a geographical information system (ArcGIS; Environmental Systems Research Institute, Redlands, California).

We identified species based on characteristics of pelage and external morphology (Nagorsen and Brigham 1993). To confirm identifications made in the field, we collected tissue with a 2-mm biopsy punch from the wing of each individual identified as Keen's myotis for DNA analysis. Analysis of character data from double-stranded mitochondrial sequences of the cytochrome-*b* gene (Dewey 2006) was conducted by T. Dewey and confirmed our field identifications.

Telemetry.—We attached 0.27-g (Blackburn Transmitters, Nacogdoches, Texas) or 0.36-g (LB-2N; Holohil Systems Ltd., Carp, Ontario, Canada) radiotransmitters to 13 adult female and 6 adult male Keen's myotis; radiotagged animals weighed 5–8 g ($\bar{X}$ = 6.3 g) and transmitters comprised 3–7% of body mass. We did not tag bats in late stages of pregnancy; however, we may have inadvertently tagged females early in pregnancy if the fetus could not be detected with abdominal palpations. We clipped a small

amount of fur between the scapulae and attached the transmitter with a nontoxic, nonirritant surgical adhesive (Torbot Bonding Cement; Torbot Group, Inc., Cranston, Rhode Island). Bats were wrapped in a cloth and held for 30 min while the adhesive dried. All protocols were approved by the Animal Care and Use Committee of Oregon State University and met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

We used PLL synthesized tracking receivers (model TRX-1000S; Wildlife Materials, Inc., Murphysboro, Illinois) and handheld 3- and 6-element yagi antennas to track bats to roosts. We tracked bats to day-roosts each day for a minimum of 10 days unless equipment failed, the battery in the transmitter died, or the transmitter was shed by the bat.

Roosts and available trees.—To avoid disturbing roosting bats, measurements at roost structures were made during days when tagged bats were not present. For each roost, we randomly selected 2 (and in 1 case, 3) available trees within 200 m in the same forest type. We defined available trees as those with diameters ≥ 20 cm. From the location of each roost tree we determined a transect by randomly selecting a compass bearing and a distance between 100 and 200 m. Once we reached the selected distance, 1 observer selected a random number between 1 and 60. A 2nd observer continued walking in the same direction counting all trees that were ≥ 20 cm in diameter 1.5 m above the ground (DBH) and within 5 m of the transect until the tree with the randomly selected number was reached.

For each roost or available tree, we noted presence of cracks, hollows, and a broken top (defects) and measured the DBH (cm), the proportion of bark remaining on the stem (bark), and the height of the tree relative to the slope it was on (slope-height, m; Table 1). The proportion of bark remaining on the stem was calculated as the mean of estimates made by 2 or 3 observers. Slope affects the relative height of trees and trees located upslope project above trees that occur down slope. At 10 m, a 10% slope is equivalent to approximately 1 m of vertical height. Therefore, slope-height was calculated for each tree by adding 1 m of height for every 10% of slope. We measured height (m) and slope (%) using a clinometer and slope was measured from a point 10 m down slope from the tree. Trees were classified into 1 of 3 decay stages (stage 1, live with no signs of decay; stage 2, live with at least 1 defect; stage 3, dead with defects, or missing bark, or both). We documented the species of each roost and available tree. Although Alaska cedar and western red cedar were present, we could not confidently distinguish between the 2 species if foliage was out of reach or absent. Therefore, the 2 species were grouped together and identified as "cedars." Dead conifers that could not be identified because they lacked bark and branches were categorized as "unknown." Location of each roost and available tree was recorded with a global positioning system and imported into ArcGIS.

Tree plot.—We recorded species and decay stage and measured DBH for every tree within a 0.1-ha (17.8-m-radius) circular plot (tree plot) centered on each roost and available tree. We defined plot density to be the number of canopy trees

(≥ 20 cm DBH) per plot (density; Table 1). We calculated the quadratic mean diameter (QMD) of canopy trees to determine the average size of canopy trees within each plot. We calculated the proportion of canopy trees in the plot that were in decay stages >1 (decadence).

Landscape unit.—We calculated the mean of maximum distances between 2 roosts used by individual males and females and used these values as diameters for defining the area of a circular landscape unit (Miles et al. 2006). The mean maximum distance between roosts was approximately 1.1 km for females and males; the corresponding area of the landscape unit was 96 ha.

We performed analyses of landscape characteristics with ArcGIS using digital maps of terrestrial ecosystems, roads (The Nature Conservancy, Terrestrial Ecosystems—Albert and Schoen 2006), and streams on Prince of Wales Island. To avoid overlap, we did not center landscape units on available trees. Instead, random points were generated using ArcGIS and landscape units were centered on roost and random points. Because capture locations were located within 0.5 km of a road or trail and all roosts were within 2.7 km of capture sites, we restricted the selection of random points to those within 3.2 km of a road or trail. Within each unit, we measured distances to nearest streams (stream) and calculated proportions of productive old-growth forest (old growth—Albert and Schoen 2006) and clear-cut area (harvested forests <25 years old; clear-cut; Table 1). Land that is currently producing or capable of producing stands of industrial timber is classified as "productive" and includes stands that typically have $>50\%$ crown canopy cover and are capable of producing >1.4 m³/ha of annual growth (van Hees 2003; Viereck et al. 1992). Forests classified as "unproductive" are forested lands not meeting the criteria of commercial or high-volume forests (Julin and Caouette 1997) and include open-canopy forest types such as peatland mixed-conifer woodlands and forested peatlands. Large-scale, industrial timber harvest in southeastern Alaska began in the early 1950s (Harris and Farr 1974). Although harvested forests >25 years old are present on the island, the proportionate area of these forests is small and was not included in statistical models because it was too highly correlated ($r \geq 0.55$) with the proportion of clear-cut area.

Statistical analyses.—This was a retrospective, observational, confirmatory study and therefore we used an information-theoretic approach for the analysis of all data (Burnham and Anderson 2002). Information-theoretic methods use an extension of likelihood theory to imply inference and estimate parameters from multiple models. This approach avoids null hypothesis testing (which often performs poorly for observational studies), subjective data dredging, and overfitting of models (Burnham and Anderson 2002). We used prior knowledge of habitat associations of other species of forest-dwelling bats (e.g., Barclay and Kurta 2007; Hayes 2003; Kunz 1982; Kunz and Lumsden 2003) to select variables predicted to be influential on roost-site selection by adult male and female Keen's myotis for analyses using logistic regression and model selection. We evaluated DBH, defects, bark, and slope-height at the tree scale; decadence, density, and QMD at the tree-plot

scale; and old growth, clear-cut, and stream at the landscape scale. We reported the mean $\pm$ SE and 95% confidence intervals (95% CIs) for each continuous variable. We developed a set of candidate models with all possible additive combinations of predictor variables at each spatial scale. To enhance interpretability of models, control for spurious effects, and maintain parsimony and precision of estimators, we limited the number of candidate models by restricting the number of predictor variables at each scale to ≤ 4 (Burnham and Anderson 2002). Model fitting with logistic regression is sensitive to multicollinearity among independent variables in the model (Hosmer and Lemeshow 2000). Therefore, before including variables in models we tested for linear correlations using Pearson's product-moment correlation (PROC CORR—SAS Institute 2003); variables that were highly correlated ($r \geq 0.55$) were not included in the same model. Decay stage and tree species were not included in logistic regression models because of correlation with 1 or more variables or predefined limitations on the number of variables that could be examined at the scale of the tree. However, we examined associations of decay stage and tree species with roost selection using 2×2 contingency tables and we report the likelihood ratio chi-square statistic and associated degrees of freedom and *P*-values (Gotelli and Ellison 2004).

We used Akaike's information criterion adjusted for small sample sizes and overdispersed data (QAIC_c—Burnham and Anderson 2002) to rank all models within and between scales according to their ability to differentiate between characteristics of used and available roosts. To determine the relative level of empirical support for each model, we calculated the difference between the QAIC_c value for that model and the minimum QAIC_c value of all models considered in the analysis (Δ QAIC_c—Burnham and Anderson 2002). Models with Δ QAIC_c < 2 are highly competitive; models with Δ QAIC_c > 10 have essentially no support for being the best model given the set of models being considered. We report results for null models and all models with Δ QAIC_c < 4 . We calculated the Akaike weight (w_i) of each model *i* as an index of the weight of evidence in favor of that model being the actual best model given the candidate set of models (Burnham and Anderson 2002). Also, we report a generalization of the coefficient of determination (R_G^2) as an index of the ability of the model to predict whether the sampling unit is used by Keen's myotis (Nagelkerke 1991). This value generalizes the concept of R^2 to generalized linear models and can be roughly interpreted as similar to R^2 in classic regression models.

We calculated model-averaged coefficient estimates and associated odds ratios with 95% CIs to determine the direction and magnitude of effect for each predictor variable on selection of day-roosts in trees by Keen's myotis (Burnham and Anderson 2002). Model-averaged estimators are calculated based on inference from all candidate models and weighted by the strength of evidence for each model. Model-averaged estimators are often less biased and more precise because they are not conditional on the inference of a single best model. We calculated the sum of Akaike weights ($\sum w_i$) for each predictor variable from the subset of models that included that variable.

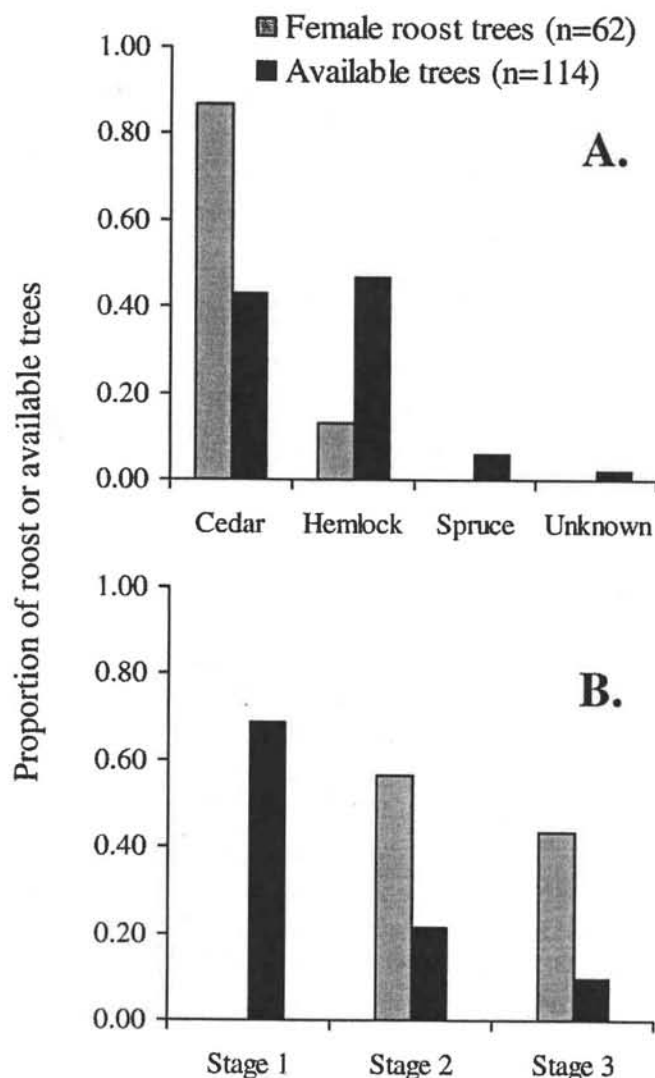


FIG. 1.—The proportion of roost and available trees for female Keen's myotis (*Myotis keenii*) that were A) within each category of conifer tree species and B) within each category of decay stage on Prince of Wales Island, southeastern Alaska, 2006.

$\sum w_i$ is the evidence of the importance of a variable, given the set of candidate models and variables (Burnham and Anderson 2002). Model-averaged coefficient estimates cannot be accurately determined for categorical variables. Therefore, for the categorical variable of defects, we calculated estimates of odds ratios given a case-control method and a 2×2 contingency table (PROC FREQ—SAS Institute 2003).

In all analyses, if multiple bats were found using the same tree on the same day, we assumed that their decisions to use that tree were not made independently and the tree was counted only once. If a tree was used by different bats on different days it was assumed their decisions to use that tree were made independently and the tree was counted once for each day it was used by a different bat. Each time a tree was used as a roost by a different bat, 2 available trees and plots were selected for comparison.

RESULTS

We tracked female Keen's myotis for a mean of 11.5 ± 0.7 days (range 7–17 days) and males for 10.8 ± 1.9 days (range 5–19 days). We tracked 13 females to 62 roosts in trees; 1 female was also tracked to a roost in a house. We tracked 6 males to 24 roosts in trees; 2 of these bats were tracked to roosts in 6 stumps, 1 to the space under 3 loose rocks in a quarry, and 1 to a rock crevice. Five roost trees were used on different occasions by different tagged female bats and on 6 occasions, 2–4 tagged female bats were found roosting simultaneously in the same tree. Including all nontree roosts and roosts shared by multiple bats, each female used an average of 6.6 ± 0.7 (95% CI 5.2, 8.0) different roosts every 10 days and males used an average of 5.7 ± 0.8 (95% CI 4.2, 7.2) different roosts every 10 days. One female was excluded from these calculations because she was only tracked for 2 days because of equipment failure.

We removed 7 available trees and their associated plots from all analyses because those species of tree (red alder and ponderosa pine) were never used as roosts by Keen's myotis and because their structural dissimilarity would have made comparisons using these trees uninformative. We removed 3 roost trees used by females from multiscale analyses because we did not have associated data for characteristics at the tree-plot scale, and validity and interpretability of model selection using QAIC is dependent on analysis of a fixed data set (Burnham and Anderson 2002). The final data set for females included 62 used and 114 available samples at the tree scale and 59 used and 114 available samples at the tree-plot and landscape scales. The final data set for males included 24 used and 44 available samples for all spatial scales.

Tree characteristics.—Trees used as roosts by females were cedars (87% of roosts) or hemlocks (13% of roosts); cedars comprised 43% and hemlocks comprised 47% of available trees sampled within 200 m of roost trees used by females (Fig. 1A). Because females were never recorded using any other species, we included only hemlock and cedar in chi-square analysis and found that females roosted in cedars significantly more than in hemlocks and more than expected given their availability ($\chi^2 = 27.6$, $df = 1$, $P < 0.0001$). The mean diameter of trees used as roosts by females was 106.5 ± 4.4 cm (95% CI 97.7, 115.2 cm) and the mean diameter of available trees was 50.7 ± 3.3 cm (95% CI 44.2, 57.2 cm). Average slope-height was 43 ± 1.9 m (95% CI 39.3, 46.7 m) for roost trees used by females and 36.9 ± 1.5 m (95% CI 33.9, 39.9 m) for available trees. Roost selection was dependent on decay stage ($\chi^2 = 98.3$, $df = 2$, $P < 0.0001$) and 56% of roosts selected by females were in decay stage 2 and 44% were in decay stage 3 (Fig. 1B); 94% of these roost trees contained defects. Females were never found roosting in a live tree without defects (decay stage 1), although the vast majority of available trees (70%) were in this category. The mean percent of bark remaining was $63\% \pm 3.7\%$ (95% CI 55.7%, 70.3%) on roost trees and $90.6\% \pm 2.9\%$ (95% CI 85.0%, 96.2%) on available trees.

The model with the lowest QAIC_c included the variables DBH, defects, and bark (Table 2). High cumulative Akaike

TABLE 2.—Logistic regression models with $\Delta\text{QAIC}_c < 4$ and null models from the set of candidate models predicted to influence selection of day-roosts by female Keen's myotis (*Myotis keenii*) at 3 spatial scales. Shown are variables; number of parameters (K); difference between the Akaike's information criterion adjusted for small sample sizes and overdispersed data (QAIC_c) value for that model and the minimum QAIC_c value of all models considered in the analysis (ΔQAIC_c); Akaike weights (w_i); and Nagelkerke's coefficient of determination (R_G^2). DBH = diameter at breast height; QMD = quadratic mean diameter.

Scale	Model	K	ΔQAIC_c	w_i	R_G^2
Tree	DBH, defects, bark	4	0	0.72	0.63
	DBH, defects, bark, slope-height	5	2.12	0.25	0.63
	Null	1	102.09	0	0
Tree plot	Decadence, QMD	3	0	0.48	0.13
	QMD	2	1.50	0.23	0.11
	Decadence, QMD, density	4	2.04	0.18	0.13
	QMD, density	3	3.55	0.08	0.11
	Null	1	13.48	0	0
Landscape	Old growth, stream	5	0	0.74	0.38
	Old growth, stream, clear-cut	4	2.08	0.26	0.38
	Null	1	51.23	0	0

weights ($\sum w_i$) for DBH, defects, and bark indicate strong evidence for the importance of these variables on roost selection by females (Table 3). The odds that a tree was used as a roost by females increased by 1.33 times (95% CI 1.15, 1.54 times) for every 10-cm increase in DBH. For every 10% decrease in bark, the odds of a tree being a roost site for females increased by 1.30 times (95% CI 1.10, 1.53 times). However, only 12% of roost trees had less than 20% bark cover, indicating there may be a lower threshold for the amount of bark preferred on roost trees used by females. The odds of a tree being used as a roost by females increased by 37.16 times (exact 95% CI 12.02, 148.82 times) if the tree had at least 1 defect (i.e., a cavity, crack, or broken top). Confidence limits for the coefficient estimate of slope-height included 0, meaning the effect of slope-height on roost selection by females was not detectable given the data; this is supported by the low value for $\sum w_i$.

Male Keen's myotis roosted primarily in cedars (42% of roosts) followed by hemlocks (33% of roosts), unknown conifers (21% of roosts), and spruce (4% of roosts). Cedars comprised 25%, hemlocks 48%, unknown conifers 7%, and spruce 20% of all available trees sampled within 200 m of roost trees used by males (Fig. 2A). A statistical relationship between roost selection and tree species could not be determined because 25% of cells had expected counts < 5 and exact P -values could not be computed because row and column totals were not fixed a priori (Gotelli and Ellison 2004). The mean diameter of trees used for roosting by males was 65.6 ± 7.1 cm (95% CI 51.6, 79.6 cm) and the mean diameter of available trees was 49.9 ± 5.0 cm (95% CI 40.0, 59.8 cm). Mean slope-height was 35.6 ± 3.0 m (95% CI 29.6, 41.6 m) for roosts and 31.5 ± 2.3 m (95% CI 26.8, 36.1 m) for available trees. Roost selection by males was dependent on decay stage ($\chi^2 = 32.7$, $d.f. = 2$, $P < 0.0001$) and 83% of roost trees were snags. In

TABLE 3.—The influence of habitat characteristics at multiple spatial scales on selection of day-roosts by female Keen's myotis (*Myotis keenii*) as indicated by model-averaged coefficient estimates and their 95% confidence intervals (LCL = lower confidence limit; UCL = upper confidence limit), odds ratios, and cumulative Akaike weights ($\sum w_i$). A coefficient estimate was not calculated for defects because its odds ratio was calculated with estimates of relative risk from a 2×2 contingency table. DBH = diameter at breast height; QMD = quadratic mean diameter.

Scale	Variable	Relationship ^a	Estimate	LCL	UCL	Odds ratio	$\sum w_i$
Tree	Bark	10% (–)	0.26	–0.43	–0.10	1.30	0.99
	DBH	10 cm (+)	0.29	0.14	0.43	1.33	1.00
	Defects	(+)	—	—	—	37.16	0.99
	Slope-height	5 m ^b	0	–0.05	0.04	1.00	0.25
Tree plot	Decadence	10% (+)	0.26	0.07	0.45	1.30	0.68
	Density	5 trees ^b	0.01	–0.06	0.03	1.01	0.28
	QMD	5 cm (+)	0.22	0.07	0.38	1.25	0.97
	Clear-cut	10% ^b	0.02	–0.10	0.06	1.02	0.26
Landscape	Stream	20 m (–)	0.13	–0.21	–0.05	1.14	1.00
	Old growth	10% (+)	0.40	0.24	0.56	1.50	1

^a The value and sign indicate unit change in the independent variable resulting in the estimated odds ratio.

^b The effect was not detectable given inclusion of 0 in 95% confidence limits for the coefficient estimate.

contrast, most available trees were without signs of decay (stage 1; 52%; Fig. 2B). Seventy-nine percent of roost trees used by males and 39% of available trees contained defects. Mean percent bark remaining on trees was $37.4\% \pm 6.0\%$ (95% CI 25.6%, 49.1%) for roosts and $78.2\% \pm 4.4\%$ (95% CI 69.6%, 86.8%) for available trees.

The best model for males at the tree scale included defects, bark, and slope-height (Table 4). However, there were 2 other strongly competing models with $\Delta\text{QAIC}_c < 2$ and the w_i values for each of the top models were relatively low; indicating a high level of model uncertainty at this scale (Table 4). Calculations of $\sum w_i$ for model-averaged coefficient estimates ranked bark and slope-height as the most important variables on selection of roost trees by males, followed by defects and DBH (Table 5). The odds of a tree being used as a roost increased 1.52 times (95% CI 1.22, 1.90 times) with every 10% decrease in bark. Roost trees used by males did not appear to have a minimum threshold for the amount of bark given the high proportion of roost trees with less than 20% bark (42% of roosts). The odds a tree was used increased 1.48 times (95% CI 1.14, 1.91 times) for every 5-m increase in slope-height. A tree with at least 1 defect was 6 times (exact 95% CI 1.74, 23.52 times) more likely to be used as a roost than a tree without defects. The odds a tree was used by males increased by 1.09 times (95% CI 1.03, 1.15 times) with every 10-cm decrease in DBH, but the low $\sum w_i$ for DBH (0.25) suggests the evidence for the importance of this effect is low.

Tree-plot characteristics.—Mean QMD was 55.6 ± 1.7 cm (95% CI 52.3, 58.9 cm) in plots surrounding roosts of females and 46.8 ± 2.6 cm (95% CI 41.6, 52.0 cm) in available plots. The mean proportion of trees in early to advanced stages of decay (decadence) was 0.38 ± 0.02 (95% CI 0.34, 0.42) in

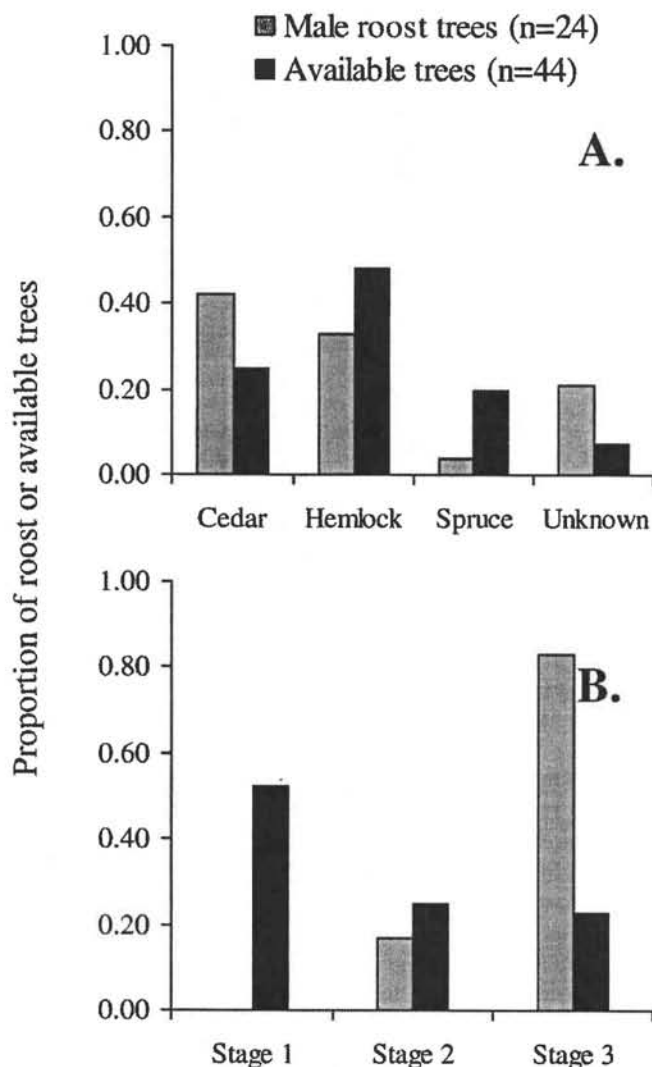


FIG. 2.—The proportion of roost and available trees for male Keen's myotis (*Myotis keenii*) that were A) within each category of conifer tree species and B) within each category of decay stage on Prince of Wales Island, southeastern Alaska, 2006.

plots surrounding roosts and 0.36 ± 0.01 (95% CI 0.33, 0.39) in plots surrounding available trees. The mean density of trees was 36.1 ± 1.8 (95% CI 32.6, 39.7) in plots surrounding roosts of females and 38.8 ± 1.4 (95% CI 36.0, 41.7) in plots of available trees. The best model contained the variables decadence and QMD, but a model containing only QMD was strongly competing ($\Delta\text{QAIC}_c = 1.50$; Table 2). The relatively low w_i s for each model indicate a high degree of model uncertainty. Quadratic mean diameter was the most important variable influencing selection of roosts by females at this scale ($\sum w_i = 0.97$) and the odds that a tree was used as a roost by females increased 1.25 times (95% CI 1.07, 1.45 times) for every 5-cm increase in QMD (Table 3). Odds a tree was a roost increased 1.30 times (95% CI 1.07, 1.57 times) with every 10% increase in decadence, but the evidence for the importance of this effect was relatively weak ($\sum w_i = 0.68$). There was no

TABLE 4.—Logistic regression models with $\Delta\text{QAIC}_c < 4$ and null models from the set of candidate models predicted to influence selection of day-roosts by male Keen's myotis (*Myotis keenii*) at 3 spatial scales. Shown are variables, number of parameters (K), difference between the Akaike's information criterion adjusted for small sample sizes and overdispersed data (QAIC_c) value for that model and the minimum QAIC_c value of all models considered in the analysis (ΔQAIC_c), Akaike weights (w_i), and Nagelkerke's coefficient of determination (R_G^2). DBH = diameter at breast height; QMD = quadratic mean diameter.

Scale	Model	K	ΔQAIC_c	w_i	R_G^2
Tree	Defects, bark, slope-height	4	0.00	0.52	0.50
	Defects, bark, slope-height, DBH	5	1.55	0.24	0.51
	Bark, slope-height	3	1.73	0.22	0.45
	Null	1	26.11	0	0
	Decadence	2	0	0.51	0.16
Tree plot	Decadence, QMD	3	1.79	0.21	0.16
	Decadence, density	3	2.17	0.17	0.16
	Decadence, QMD, density	4	3.94	0.07	0.16
	Null	1	6.51	0.02	0
	Stream, clear-cut	3	0	0.22	0.10
Landscape	Clear-cut	2	0.10	0.21	0.06
	Null	1	1.00	0.13	0
	Clear-cut, old growth	3	1.31	0.11	0.07
	Stream, clear-cut, old growth	4	1.50	0.10	0.11
	Old growth	2	1.68	0.09	0.03
	Stream	2	2.09	0.08	0.02
	Stream, old growth	3	2.96	0.05	0.04
	Stream, old growth	3	2.96	0.05	0.04

detectable effect of density on selection of roosts by female Keen's myotis.

Mean QMD was 46.8 ± 2.6 (95% CI 41.6, 52.0) in plots surrounding roost trees of males and 46.1 ± 2.3 (95% CI 41.6, 50.6) in available plots. The mean proportion of trees in early to late decay stages was 0.49 ± 0.03 (95% CI 0.44, 0.55) in roost plots and 0.38 ± 0.02 (95% CI 0.33, 0.42) in available plots. The mean density of trees in plots surrounding roosts of males was 34.0 ± 2.8 (95% CI 28.4, 39.6) and mean density in plots of available trees was 32.7 ± 2.2 (95% CI 28.3, 37.0). The model with the lowest QAIC_c value contained only the variable decadence, but a strongly competing model contained the variables decadence and QMD (Table 4). The $\sum w_i$ indicate that decadence was the most important variable influencing selection of roost sites by males at this spatial scale (Table 5). The odds of a tree being used as a roost increased 1.66 times (95% CI 1.15, 2.40 times) for every 10% increase in decadence. There was no detectable effect of density or QMD on roost selection by males.

Landscape characteristics.—Roosts of females were on average 101 ± 18 m (95% CI 66, 137 m) from the nearest stream and random points were 179 ± 13 m (95% CI 153, 204 m) from the nearest stream. The mean proportion of old-growth forest was 0.73 ± 0.03 (95% CI 0.67, 0.80) in the landscape surrounding roost trees used by females and 0.48 ± 0.02 (95% CI 0.44, 0.53) in the landscape surrounding random points. The mean proportion of area that was clear-cut was 0.06 ± 0.02 (95% CI 0.02, 0.11) in the landscapes surrounding roosts and

0.13 $\pm$ 0.02 (95% CI 0.10, 0.17) in the landscapes surrounding random points. The top model contained the variables stream and old growth and there were no other models with $\Delta\text{QAIC}_c < 2$ (Table 2). The relative importance of old growth and stream on roost selection by females was equally high (Table 3). For every 10% increase in old growth, the odds of a tree being used as a roost by females increased 1.50 times (95% CI 1.28, 1.75 times). For every 20-m decrease in the distance to nearest stream, the odds of a tree being used as a roost by females increased by 1.14 times (95% CI 1.05, 1.24 times). There was no detectable effect of the proportion of clear-cut area on roost selection by females, as indicated by the inclusion of 0 in the confidence interval for the coefficient estimate of that variable.

The mean distance to the nearest stream from trees used as roosts by males was 219 $\pm$ 28 m (95% CI 164, 275 m) and the mean distance from random points was 182 $\pm$ 20 m (95% CI 143, 221 m). In the landscape surrounding roosts of males, the mean proportion of old growth was 0.39 $\pm$ 0.05 (95% CI 0.28, 0.48) and the mean proportion of clear-cut area was 0.22 $\pm$ 0.04 (95% CI 0.14, 0.29). In landscapes surrounding random points the mean proportion of old growth was 0.46 $\pm$ 0.04 (95% CI 0.39, 0.53) and the mean proportion of clear-cut area was 0.12 $\pm$ 0.03 (95% CI 0.07, 0.17). Six models, including the null model, had $\Delta\text{QAIC}_c < 2$ (Table 4) and all variables had a relatively low $\sum w_i$ (Table 5). These results suggest that the variables, and consequently the models, selected at this scale were not useful for differentiating between landscapes surrounding roosts of males and landscapes surrounding random points.

Multiscale comparisons.—We compared all models across spatial scales to determine at which spatial scale relationships between habitat characteristics and use of roosts are strongest. The top models for females and for males were from the tree scale, suggesting that characteristics at the tree scale were most influential on roost selection by Keen's myotis.

DISCUSSION

We found that habitat characteristics at multiple spatial scales influenced selection of day-roosts by Keen's myotis on Prince of Wales Island, but characteristics that influenced selection by females often differed from those of males. Associations were strongest for males and females at the tree scale with some degree of selection at the plot level. We found relationships at the landscape scale for females, but not males.

Females.—Female Keen's myotis primarily roosted in live trees or trees that had recently died with large diameters, sloughing bark, and structural defects. We suspect that the tendency for females to roost in trees with these characteristics is likely related to availability and suitability of roost sites, given energetic strategies used by females in the cool, wet climate of southeastern Alaska. Warm roost sites with stable microclimates are selected by females of some species of bats for day-roosting in temperate climates (Sedgeley 2001; Solick and Barclay 2007), which likely reduces the metabolic demands of thermoregulation, facilitating fetal development

TABLE 5.—The influence of habitat characteristics at multiple spatial scales on selection of day-roosts by male Keen's myotis (*Myotis keenii*) as indicated by model-averaged coefficient estimates and their 95% confidence intervals (LCL = lower confidence limit; UCL = upper confidence limit), odds ratios, and cumulative Akaike weights ($\sum w_i$). A coefficient estimate was not calculated for defects because its odds ratio was calculated with estimates of relative risk from a 2 $\times$ 2 contingency table. DBH = diameter at breast height; QMD = quadratic mean diameter.

Scale	Variable	Relationship ^a	Estimate	LCL	UCL	Odds ratio	$\sum w_i$
Tree	Bark	10% (–)	–0.42	–0.64	–0.20	1.52	1.00
	DBH	10 cm (–)	–0.09	–0.14	–0.03	1.09	0.25
	Defects	(+)	—	—	—	6.00	0.77
	Slope-height	5 m (+)	0.39	0.13	0.65	1.48	0.99
Tree plot	Decadence	10% (+)	0.51	0.14	0.87	1.66	0.96
	Density	5 trees ^b	0.02	–0.03	0.07	1.02	0.25
	QMD	5 cm ^b	0.06	0	0.11	1.06	0.29
Landscape	Clear-cut	10% (+)	0.22	0.06	0.38	1.25	0.65
	Stream	20 m (+)	0.05	0.02	0.08	1.05	0.45
	Old growth	10% (–)	0.11	–0.19	–0.03	1.11	0.36

^a The value and sign indicate unit change in the independent variable resulting in the estimated odds ratio.

^b The effect was not detectable given inclusion of 0 in 95% confidence limits for the coefficient estimate.

and growth of juveniles by allowing reproductive females to avoid or reduce the use of torpor (Barclay and Kurta 2007; Kunz and Lumsden 2003; Sedgeley 2001). Bats often enter torpor during inclement weather to conserve energy, but this delays juvenile and fetal development and inhibits milk production (Racey and Swift 1981; Tuttle and Stevenson 1982; Wilde et al. 1999). The use of torpor by reproductive females and juveniles in southeastern Alaska is likely selected against because the growing season is short and bats need time to accumulate fat reserves for hibernation (Barclay and Kurta 2007; Solick and Barclay 2007). Insufficient reserves before hibernation likely cause higher mortality of juveniles over winter (Grindal et al. 1992; Kunz et al. 1998) and lower fecundity for species at higher latitudes (Kunz et al. 1998). The insulating properties of a tree increase with thickness of tree walls (Kurta 1985; Maeda 1974; Nicolai 1986), thus trees with larger diameters have greater potential to provide well-insulated roost sites. Large-diameter trees likely provide larger cavities and crevices where bats can cluster to further reduce costs of thermoregulation (Brigham et al. 1997; Barclay and Kurta 2007; Kurta 1985, 1986; Willis and Brigham 2007). Although sloughing bark does not necessarily provide roost sites with stable microclimates, tree-dwelling bats often roost under loose bark (Barclay and Kurta 2007; Kunz and Lumsden 2003) and bats may require a suite of roost sites with a range of internal temperatures depending on their reproductive state and the range of ambient temperatures that occur throughout the active season (Smith and Racey 2005). We hypothesize that females select roost sites in large-diameter trees with defects because they provide stable microclimates and space where bats can cluster and that selection of day-roosts by females is likely dictated by energetics.

Female Keen's myotis preferentially selected roosts in cedars, but also roosted in western hemlocks. Kimmey (1956) found that 86.7% of western red cedar, 50.9% of western hemlock, and 13.4% of Sitka spruce in southeastern Alaska were infected with decay-causing fungi associated with heartrot, which attack the cellulose or lignin content of wood and often contribute to the formation of cracks and cavities (Hennon 1995; Kimmey 1956) often used as roost sites by tree-roosting bats (Barclay and Kurta 2007; Kunz 1982; Kunz and Lumsden 2003). We suspect that cedar trees used as roosts by Keen's myotis were likely western red cedar given the relative low abundance of Alaska cedar and its high resistance to decay (Hennon et al. 2002; United States Department of Agriculture Forest Service 2001). Western red cedars may be preferentially selected as day-roosts by female Keen's myotis because they are more susceptible to fungal infections that facilitate formation of cavities; resulting in greater availability of potential roost sites (Vonhof and Barclay 1996).

Bats often roost in trees that are taller than surrounding vegetation (Campbell et al. 1996; Vonhof and Barclay 1996; Weller and Zabel 2001), potentially because roost sites may be easier to locate, enter, and exit. We predicted that selection of roosts by Keen's myotis is influenced by the relative height of the tree, but data for females did not support any relationship. With logistic regression, the estimated effect for a variable is determined after accounting for other variables in the model. The effects of DBH, defects, and bark were strong and after accounting for these variables, slope-height contributed little to differentiating between roost and available trees.

Our results are consistent with other studies showing that plots surrounding roost trees have more large-diameter trees in later stages of decay (Campbell et al. 1996; Erickson and West 2003; Waldien et al. 2000; Weller and Zabel 2001). Plots with larger trees and more snags or live trees with defects may be selected by females because they have a greater abundance of potential roost sites. Our findings suggest that forest patches with greater availability of large-diameter trees with decay are important for female Keen's myotis on Prince of Wales Island.

The effect of stem density on habitat selection by bats has been attributed to structural limitations imposed on flight (Brigham et al. 1997; Humes et al. 1999). The lack of a significant relationship with tree density in our plots surrounding roosts may reflect the fact that Keen's myotis is small with low wing loading and presumably high maneuverability (Brigham et al. 1997; Saunders and Barclay 1992; Swartz et al. 2003), and is adept at flying in forested environments. Alternatively, plots surrounding roosts and randomly selected structures may not have varied enough for us to detect influences of tree density on roost use. Given that all roosts used by females were found in old-growth forest and available trees and plots were selected in the same habitat type as each roost tree, our sampling design precluded detection of relatively large differences in tree densities, such as those that typically occur between old and young forests. Several studies have shown that bat activity in young forest is low relative to that in older forests (Erickson and West 2003; Humes et al. 1999; Law and Chidel 2002; Lloyd et al. 2006; Parker et al.

1996), consistent with our results that younger stands are not frequently used for roosting.

Females typically used trees closer to streams than available trees. Weller and Zabel (2001) found a relationship between roost selection by bats and distance to streams and suggest this may result from using riparian habitats for foraging and commuting. Riparian corridors also may represent good flyways for commuting between roosts and foraging areas because they provide protection from wind and predators (Verboom and Huitema 1997), but are structurally open relative to the forest interior (Grindal 1998; Law and Chidel 2002; Lloyd et al. 2006). Although costs of commuting from roosts to flight corridors and foraging areas may be trivial in relation to the long distances bats can travel each night (Barclay and Kurta 2007), there may still be a significant energetic advantage to roosting close to foraging and commuting areas. Also, large-diameter trees that provide potential roost sites for females may be more abundant near riparian areas because increased availability of water and nutrients.

Large-diameter conifers with defects are generally more abundant in older forests. The proportional abundance of old-growth forest in landscapes surrounding day-roosts of female Keen's myotis may reflect greater use of portions of the landscape with more potential roost sites. A bat's ability to select from an abundance of potential roosts in the landscape could provide the advantage of selecting roosts surrounded by optimal landscape features (Miles et al. 2006; Waldien and Hayes 2001) or that have a range of thermal characteristics suitable in variable weather conditions (Barclay and Kurta 2007; Kunz and Lumsden 2003).

We hypothesized that the area of clear-cut habitat in the landscape influences selection of roost sites by Keen's myotis, but our data were not consistent with this for females. In southeastern Alaska, wind is a predominant agent of disturbance (Nowacki and Kramer 1998) and owls have been observed preying on bats in several areas of the region (J. L. Boland, pers. obs.). We predicted Keen's myotis would select roosts in landscapes with proportionately less clear-cut area due to behavioral strategies aimed at reducing exposure to predators and wind (as suggested by Verboom and Huitema [1997]) and because potential roost sites (i.e., mature trees) are rare or absent in clear-cuts. The absence of a relationship between proportionate area of clear-cut and roost selection by females may be because suitable roost trees are not limited on Prince of Wales Island.

Males.—Selection of day-roosts by male Keen's myotis appears to be associated with the amount of bark remaining on the stem, relative height of the tree, and, to a lesser extent, the presence of defects. We found no detectable effect of tree diameter. Males also roosted solitarily in stumps, rock crevices, and under loose rocks. Male tree-dwelling bats in temperate regions of North America typically roost alone (Altringham and Senior 2005; Barclay and Kurta 2007; Kunz and Lumsden 2003) and consequently do not reap the thermal benefits associated with communal roosting. Males may be more flexible than females in roost selection because they are not burdened by the energetic constraints of pregnancy and

lactation and use torpor to effectively reduce thermoregulatory costs (Altringham and Senior 2005; Speakman and Thomas 2003; Turbill 2006). However, male Keen's myotis in southeastern Alaska must still meet the energetic demands of sperm production and thermoregulation despite the typically cool temperatures and frequent precipitation. Males may benefit energetically by choosing poorly insulated, sun-exposed roosts when they can switch between torpor and euthermia as ambient temperature fluctuates (Turbill 2006). Selecting roosts that facilitate torpor also may benefit bats by lowering energetic requirements during periods of low insect availability associated with inclement weather (Barclay and Kurta 2007; Turbill 2006). On Prince of Wales Island, males may select poorly insulated roosts (e.g., under loose bark or in cracks) that facilitate torpor use but still provide protection from rain.

Trees used by males were primarily in intermediate to late stages of decay. We suspect that males, like females, select forest stands with a high proportion of decayed trees because these forests provide an abundance of potential roost sites. There was no detectable effect of QMD and we speculate that this is further evidence of the unimportance of tree diameter on roost selection by male Keen's myotis.

The high level of model uncertainty for males at the landscape scale leads us to conclude that the variables we examined at this scale do not influence selection of roosts or else the effects were not detectable given our data. Even small samples may allow detection of strong associations, but weaker associations may not be detectable when the sample size is small. Although male Keen's myotis do exhibit some level of selection based on characteristics at the tree and plot scales, they appear to be more opportunistic than females, and we hypothesize that these differences are the result of reduced energetic constraints.

Scope and limitations.—Keen's myotis was listed as a species of special concern in 1988 by the Committee on the Status of Endangered Wildlife in Canada, but has since been down-listed to "data deficient" due in part to insufficient knowledge regarding its taxonomic status (COSEWIC 2003). Nagorsen and Brigham (1993) indicate that Keen's myotis cannot be differentiated from western long-eared bats (*M. evotis*) using external morphology, precluding identification in the field. Van Zyll de Jong and Nagorsen (1994) argue that it may be impossible to distinguish these 2 species morphologically, based on external or cranial morphology. Although the taxonomic status of this species is unclear, our study will contribute valuable information for use in future research and forest management.

The detailed characteristics of sites selected for study and the approach we used to select random points undoubtedly influenced our results. However, our basic findings are consistent with other studies of bat roosting ecology in coniferous forests (Barclay and Kurta 2007; Hayes 2003). Although site-specific variation may result in some quantitative differences in patterns of selection, we suspect our general findings regarding the influence of tree and landscape characteristics on selection of trees for day-roosts by Keen's myotis on Prince of Wales Island are generally applicable to selection of tree roosts by this species throughout its range.

Because of relatively small sample sizes, we followed standard protocols (e.g., Brigham et al. 1997; Broders and Forbes 2004; Broders et al. 2006; Miles et al. 2006; Ormsbee and McComb 1998; Perry and Thill 2007; Psyllakis and Brigham 2006; Sedgeley 2001; Vonnhof and Barclay 1996; Waldien et al. 2000; Weller and Zabel 2001) and treated each roost tree as an independent sample in our analyses despite the fact that multiple roosts were selected by each bat. Ideally bats should be treated as the independent sampling unit to account for variation in characteristics selected by individuals and among the species. However, we are unaware of any evidence that roosts selected by individuals lack independence or that this approach is biased.

We restricted the number of variables we examined to achieve parsimony and enhance inference given our relatively small data set and we were unable to include all variables measured within each scale in the same model given multicollinearity between some variables. Exploratory, univariate analyses suggested that some variables we did not include in our models may influence selection of day-roosts and warrant further examination.

Logistic regression models are often used when the response variable is binary (Ramsey and Shafer 2002), such as the presence or absence of animals from a habitat. Our analyses and interpretations do not depend on the assumption that bats were absent from available trees. Our conclusions depend on the availability of each roost or landscape characteristic at the time of the study. Additional characteristics likely influence roost selection, but low variability of those characteristics within each scale inhibits our ability to detect them. It may not be until habitat features become a limiting factor in the environment that their importance can be differentiated between used and available sites (Ford et al. 2006).

Conclusions and management implications.—The conservation status of Keen's myotis throughout its range is unclear. Its biology and habitat associations are poorly known and there are no data on population status or trends (COSEWIC 2003). Our results offer insight into factors affecting selection of day-roosts by Keen's myotis at multiple spatial scales. Day-roosts in trees are a critical resource for many forest-dwelling species of bat. Removal of large-diameter trees during timber harvest can reduce the number of potential roosts available to bats, and harvesting forests under short rotations can inhibit the development of suitable roosts over time (Hayes and Loeb 2007). Our findings suggest that maintaining coniferous forests with a diversity of decay stages and high proportions of large-diameter trees with defects in close proximity to riparian habitats provides critical roosting habitat for female Keen's myotis on Prince of Wales Island.

This is the 1st study to quantitatively characterize roost selection by Keen's myotis, and is one of few sex-specific, multiscale investigations of resource selection by bats in temperate forests. The apparent patterns and inferences that emanate from our models hopefully will encourage further investigation of the ecology of Keen's myotis. More importantly, our results will provide an ecological basis upon which to make policy decisions about the management of coastal

temperate forests, in particular, future efforts to restore forest conditions to meet the habitat requirements of Keen's myotis across highly modified landscapes.

ACKNOWLEDGMENTS

We thank R. M. Brigham and 2 anonymous reviewers for providing very helpful suggestions on the original manuscript. We thank J. Tharp, A. Miles, T. Gillen, A. Sjollem, L. Beard, and K. Thompson for their field assistance. Alaska Fish and Game and Oregon State University provided financial and administrative support and the United States Department of Agriculture Forest Service, Southeast Region, provided substantial logistical support and geographical information system data. Geographical information system data also were provided by David Albert and the Nature Conservancy and geographical information system technical assistance was provided by J. Thompson. We thank the communities on Prince of Wales Island for support and guidance.

LITERATURE CITED

- ALABACK, P. B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. *Ecology* 63:1932-1948.
- ALBERT, D., AND J. SCHOEN. 2006. A preliminary classification and conservation assessment of terrestrial ecosystems in southeast Alaska. The Nature Conservancy in Alaska. <http://www.nature.org>. Accessed 28 September 2006.
- ALTRINGHAM, J. D., AND P. SENIOR. 2005. Social systems and ecology of bats. Pp. 280-302 in *Sexual segregation in vertebrates: ecology of the two sexes* (K. E. Ruckstuhl and P. Neuhaus, eds.). Cambridge University Press, New York.
- BARCLAY, R. M. R., AND A. KURTA. 2007. Ecology and behavior of bats roosting in tree cavities and under bark. Pp. 17-59 in *Bats in forests: conservation and management* (M. J. Lacki, J. P. Hayes, and A. Kurta, eds.). Johns Hopkins University Press, Baltimore, Maryland.
- BRIGHAM, R. M., M. J. VONHOF, R. M. R. BARCLAY, AND J. C. WILLIAM. 1997. Roosting behavior and roost-site preferences of forest California bats (*Myotis californicus*). *Journal of Mammalogy* 78:1231-1239.
- BRODERS, H. B., AND G. J. FORBES. 2004. Interspecific and intersexual variation in roost-site selection of northern long-eared and little brown bats in the Greater Fundy National Park Ecosystem. *Journal of Wildlife Management* 68:602-610.
- BRODERS, H. G., G. J. FORBES, S. WOODLEY, AND I. D. THOMPSON. 2006. Range extent and stand selection for roosting and foraging in forest-dwelling northern long-eared bats and little brown bats in the Greater Fundy Ecosystem, New Brunswick. *Journal of Wildlife Management* 70:1174-1184.
- BURLES, D. W. 2000. Bats of Gand K'in. Pp. 321-326 in *Proceedings of a conference on the biology and management of species and habitats at risk* (L. M. Darling, ed.). British Columbia Ministry of Environment and University College of the Cariboo, Kamloops, British Columbia, Canada.
- BURLES, D. W. 2001. Influence of weather on life history characteristics of two bats, *Myotis lucifugus* and *Myotis keenii* at Gand K'in Gwaayaay, Haida Gwaii. M.S. thesis, University of Victoria, Victoria, British Columbia, Canada.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference, a practical information-theoretic approach. 2nd ed. Springer-Verlag New York, Inc., New York.
- CAMPBELL, L. A., J. G. HALLETT, AND M. A. O'CONNELL. 1996. Conservation of bats in managed forests: use of roosts by *Lasionycteris noctivagans*. *Journal of Mammalogy* 77:976-984.
- CARRERA, P. E., T. A. AGER, J. F. BAICHTAL, AND D. P. VANSISTINE. 2003. Map of glacial limits and possible refugia in the southern Alexander Archipelago, Alaska, during the late Wisconsin glaciation. United States Geological Survey, Miscellaneous Field Studies Map MF-2424. United States Geological Survey, Denver, Colorado. <http://pubs.usgs.gov/mf/2003/mf-2424/>. Accessed 11 December 2006.
- COSEWIC. 2003. COSEWIC assessment and update status report on Keen's long-eared bat *Myotis keenii* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada. www.sararegistry.gc.ca/status_e.cfm. Accessed 10 May 2006.
- DEMEO, T., J. MARTIN, AND R. A. WEST. 1992. Forest plant association guide: Ketchikan Area, Tongass National Forest. R10-MB-210. United States Department of Agriculture Forest Service, Alaska Region, Juneau.
- DEWEY, T. A. 2006. Systematics and phylogeography of North American myotis (Chiroptera: Vespertilionidae). Ph.D. dissertation, University of Michigan, Ann Arbor.
- ERICKSON, J. L., AND S. D. WEST. 2003. Associations of bats with local structure and landscape features of forested stands in western Oregon and Washington. *Biological Conservation* 109:95-102.
- FIRMAN, M., M. GETTY, AND R. M. R. BARCLAY. 1993. Status of the Keen's long-eared myotis in British Columbia. WR-59. British Columbia Ministry of Environment, Wildlife Branch, Victoria, British Columbia, Canada.
- FORD, W. M., J. M. MENZEL, M. A. MENZEL, J. W. EDWARDS, AND J. C. KILGO. 2006. Presence and absence of bats across habitat scales in the upper coastal plain of South Carolina. *Journal of Wildlife Management* 70:1200-1209.
- GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMOLOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809-823.
- GORRESEN, P. M., M. R. WILLIG, AND R. E. STRAUSS. 2005. Multivariate analysis of scale-dependent associations between bats and landscape structure. *Ecological Applications* 15:2126-2136.
- GOTELLI, N. J., AND A. M. ELLISON. 2004. A primer of ecological statistics. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.
- GRINDAL, S. D. 1998. Habitat use by bats in second- and old-growth stands in the Nimpkish Valley, Vancouver Island. *Northwest Science* 72:116-118.
- GRINDAL, S. D., T. S. COLLARD, R. M. BRIGHAM, AND R. M. R. BARCLAY. 1992. Influence of precipitation on reproduction by *Myotis* bats in British Columbia. *American Midland Naturalist* 128:339-344.
- HARRIS, A. S., AND W. A. FARR. 1974. The forest ecosystem of southeast Alaska: forest ecology and timber management. United States Department of Agriculture, Forest Service, General Technical Report PNW-GTR-25:1-116.
- HAYES, J. P. 2003. Habitat ecology and conservation of bats in western coniferous forests. Pp. 81-119 in *Mammal community dynamics: management and conservation in the coniferous forests of western North America* (C. J. Zabel and R. G. Anthony, eds.). Cambridge University Press, Cambridge, United Kingdom.
- HAYES, J. P., AND S. C. LOEB. 2007. The influences of forest management on bats in North America. Pp. 207-235 in *Bats in forests: conservation and management* (M. J. Lacki, J. P. Hayes, and

- A. Kurta, eds.). Johns Hopkins University Press, Baltimore, Maryland.
- HENNON, P. E. 1995. Are heart rot fungi major factors of disturbance in gap-dynamic forests? *Northwest Science* 69:284–293.
- HENNON, P. E., M. H. MCCLELLAN, AND P. PALKOVIC. 2002. Comparing deterioration and ecosystem function of decay-resistant and decay-susceptible species of dead trees. Pp. 435–444 in *Proceedings of the symposium on the ecology and management of dead wood in western forests*. United States Department of Agriculture, Forest Service, General Technical Report PSW-GTR-181:1–949.
- HOSMER, D. W., JR., AND S. LEMESHOW. 2000. *Applied logistic regression*. 2nd ed. John Wiley & Sons, Inc., New York.
- HUMES, M. L., J. P. HAYES, AND M. COLLOPY. 1999. Activity of bats in thinned, unthinned, and old-growth forests in the western Oregon. *Journal of Wildlife Management* 63:553–561.
- JULIN, K. R., AND J. P. CAOUETTE. 1997. Options for defining old-growth timber volume strata: a resource assessment. Pp. 24–37 in *Assessments of wildlife viability, old growth timber volume estimates, forested wetlands, and slope stability*. United States Department of Agriculture, Forest Service, General Technical Report PNW-GTR-392:1–58.
- KALCOUNIS-RÜPPEL, M. C., J. M. PSYLLAKIS, AND R. M. BRIGHAM. 2005. Tree roost selection by bats: an empirical synthesis using meta-analysis. *Wildlife Society Bulletin* 33:1123–1132.
- KIMMEY, J. W. 1956. Cull factors for Sitka spruce, western hemlock, and redcedar in southeast Alaska. United States Department of Agriculture Forest Service, Alaska Forest Research Center Station Paper 6:1–31.
- KUNZ, T. H. 1982. Roosting ecology of bats. Pp. 1–55 in *Ecology of bats* (T. H. Kunz, ed.). Plenum Publishing Corporation, New York.
- KUNZ, T. H., AND L. F. LUMSDEN. 2003. Ecology of cavity and foliage roosting bats. Pp. 3–89 in *Bat ecology* (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.
- KUNZ, T. H., J. A. WRAZEN, AND C. D. BURNETT. 1998. Changes in body mass and fat reserves in pre-hibernating little brown bats (*Myotis lucifugus*). *Ecoscience* 5:8–17.
- KURTA, A. 1985. External insulation available to a non-nesting mammal, the little brown bat (*Myotis lucifugus*). *Comparative Biochemistry and Physiology* 82:413–420.
- KURTA, A. 1986. Factors affecting the resting and postflight body temperature of little brown bats, *Myotis lucifugus*. *Physiological Zoology* 59:429–438.
- LAW, B., AND M. CHIDEL. 2002. Tracks and riparian zones facilitate the use of Australian regrowth forest by insectivorous bats. *Journal of Applied Ecology* 39:605–617.
- LLOYD, A., L. BRADLEY, AND R. GOLDINGAY. 2006. Bat activity on riparian zones and upper slopes in Australian timber production forests and the effectiveness of riparian buffers. *Biological Conservation* 129:207–220.
- LOEB, S. C., AND J. M. O'KEEFE. 2006. Habitat use by forest bats in South Carolina in relation to local, stand, and landscape characteristics. *Journal of Wildlife Management* 70:1210–1218.
- MAEDA, K. 1974. Eco-ethologie de la grande noctule, *Nyctalus lasiopterus*, a Sapporo, Japon. *Mammalia* 38:461–448.
- MATHER, M., T. CHATWIN, M. DAVIS, AND A. VANDERBERG. 2001. Bat usage of the Weymer Creek cave systems on northern Vancouver Island. British Columbia Ministry of Environment, Lands and Parks, Nanaimo, HCTF Project 99/01/25:1–8.
- MILES, A. C., S. B. CASTLEBERRY, D. A. MILLER, AND L. M. CONNER. 2006. Multi-scale roost-site selection by evening bats on pine-dominated landscapes in southwest Georgia. *Journal of Wildlife Management* 70:1191–1199.
- NAGELKERKE, N. J. D. 1991. A note on a general definition of the coefficient of determination. *Biometrika* 78:691–692.
- NAGORSEN, D., AND M. BRIGHAM. 1993. *Bats of British Columbia*. University of British Columbia Press, Vancouver, British Columbia, Canada.
- NICOLAI, V. 1986. The bark of trees: thermal properties, microclimate and fauna. *Oecologia* 69:148–160.
- NOWACKI, G. J., AND M. G. KRAMER. 1998. The effects of wind disturbance on temperate rain forest structure and dynamics of southeast Alaska. United States Department of Agriculture, Forest Service, General Technical Report PNW-GTR-421:1–25.
- ORIAN, G. H., AND J. F. WITTENBERGER. 1991. Spatial and temporal scales in habitat selection. *American Naturalist* 137:S29–S49.
- ORMSBEE, P. C., AND W. C. MCCOMB. 1998. Selection of day roosts by female long-legged myotis of the central Oregon Cascade Range. *Journal of Wildlife Management* 62:596–603.
- PARKER, D. I., AND J. A. COOK. 1996. Keen's long-eared bat, *Myotis keenii*, confirmed in southeast Alaska. *Canadian Field-Naturalist* 110:611–614.
- PARKER, D. I., J. A. COOK, AND S. L. LEWIS. 1996. Effects of timber harvesting on bat activity in southeastern Alaska's temperate rain forests. Pp. 277–292 in *Bats and Forests Symposium* (R. M. R. Barclay and R. M. Brigham, eds.). British Columbia Ministry of Forests, Victoria, British Columbia, Canada.
- PERRY, R. W., AND R. E. THILL. 2007. Tree roosting by male and female eastern pipistrelles in a forested landscape. *Journal of Mammalogy* 88:974–981.
- PSYLLAKIS, J. M., AND R. M. BRIGHAM. 2006. Characteristics of diurnal roosts used by female *Myotis* bats in sub-boreal forests. *Forest Ecology and Management* 223:93–102.
- RACEY, P. A., AND A. C. ENTWISTLE. 2003. Conservation ecology of bats. Pp. 680–743 in *Bat ecology* (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.
- RACEY, P. A., AND S. M. SWIFT. 1981. Variations in gestation length in a colony of pipistrelle bats (*Pipistrellus pipistrellus*) from year to year. *Journal of Reproduction and Fertility* 61:123–129.
- RAMSEY, F. L., AND D. W. SCHAFER. 2002. *The statistical sleuth: a course in methods of data analysis*. 2nd ed. Duxbury Press, Pacific Grove, California.
- SAS INSTITUTE INC. 2003. *SAS/STAT user's guide*. Release 9.0. SAS Institute Inc., Cary, North Carolina.
- SAUNDERS, M. B., AND R. M. R. BARCLAY. 1992. Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. *Ecology* 73:1335–1345.
- SEdgeLEY, J. A. 2001. Quality of cavity microclimate as a factor influencing selection of maternity roosts by a tree-dwelling bat, *Chalinolobus tuberculatus*, in New Zealand. *Journal of Applied Ecology* 38:425–438.
- SEdgeLEY, J. A., AND C. F. J. O'DONNELL. 2004. Roost use by long-tailed bats in South Canterbury: examining predictions of roost-site selection in a highly fragmented landscape. *New Zealand Journal of Ecology* 28:1–18.
- SMITH, P. G., AND P. A. RACEY. 2005. The itinerant Natterer: physical and thermal characteristics of summer roosts of *Myotis nattereri* (Mammalia: Chiroptera). *Journal of Zoology (London)* 266:171–180.
- SMITH, W. P., S. M. GENDE, AND J. V. NICHOLS. 2004. Ecological correlates of flying squirrel microhabitat use and density in temperate rainforests of southeastern Alaska. *Journal of Mammalogy* 85:663–674.

- SOLICK, D. I., AND R. M. R. BARCLAY. 2007. Geographic variation in the use of torpor and roosting behaviour of female western long-eared bats. *Journal of Zoology* (London) 272:358–366.
- SPEAKMAN, J. R., AND D. W. THOMAS. 2003. Physiological ecology and energetics of bats. Pp. 430–490 in *Bat ecology* (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.
- SWARTZ, S. M., P. W. FREEMAN, AND E. F. STOCKWELL. 2003. Ecomorphology of bats: comparative and experimental approaches relating structural design to ecology. Pp. 257–300 in *Bat ecology* (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.
- TURBILL, C. 2006. Roosting and thermoregulatory behaviour of male Gould's long-eared bats, *Nyctophilus gouldi*: energetic benefits of thermally unstable tree roosts. *Australian Journal of Zoology* 54:57–60.
- TUTTLE, M. D. 1976. Population ecology of the gray bat (*Myotis grisescens*): factors influencing growth and survival of newly volant young. *Ecology* 57:587–595.
- TUTTLE, M. D., AND D. STEVENSON. 1982. Growth and survival of bats. Pp. 105–150 in *Ecology of bats* (T. H. Kunz, ed.). Plenum Press, New York.
- UNITED STATES DEPARTMENT OF AGRICULTURE FOREST SERVICE. 1996. Tongass land management plan revision: revised supplement to the draft environmental impact statement. United States Department of Agriculture, Forest Service, General Report R10-MB-314A: 1–567.
- UNITED STATES DEPARTMENT OF AGRICULTURE FOREST SERVICE. 2001. Forest insect and disease conditions in Alaska—2000. United States Department of Agriculture, Forest Service, and Alaska Department of Natural Resources, General Technical Report R10-TP-86:1–61.
- VAN HEES, W. S. 2003. Forest resources of Southeast Alaska: results of a single-phase systematic sample. United States Department of Agriculture, Forest Service, Research Paper PNW-RP-557:1–96.
- VAN ZYLL DE JONG, C. G., AND D. W. NAGORSEN. 1994. A review of the distribution and taxonomy of *Myotis keenii* and *Myotis evotis* in British Columbia and the adjacent United States. *Canadian Journal of Zoology* 72:1069–1078.
- VERBOOM, B., AND H. HUIJTEMA. 1997. The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. *Landscape Ecology* 12: 117–125.
- VIERECK, L. A., C. T. DYRNES, A. R. BATTEN, AND K. J. WENZLICK. 1992. The Alaska vegetation classification. United States Department of Agriculture, Forest Service, General Technical Report PNW-GTR-286:1–278.
- VONHOF, M. J., AND R. M. R. BARCLAY. 1996. Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. *Canadian Journal of Zoology* 74:1797–1805.
- WALDIEN, D. L., AND J. P. HAYES. 2001. Activity areas of female long-eared myotis in coniferous forests in western Oregon. *Northwest Science* 75:307–314.
- WALDIEN, D. L., J. P. HAYES, AND E. B. ARNETT. 2000. Day-roosts of female long-eared myotis in western Oregon. *Journal of Wildlife Management* 64:785–796.
- WELLER, T. J., AND C. J. ZABEL. 2001. Characteristics of fringed myotis day roosts in northern California. *Journal of Wildlife Management* 65:489–497.
- WIENS, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.
- WILDE, C. J., C. H. KNIGHT, AND P. A. RACEY. 1999. Influence of torpor on milk protein composition and secretion in lactating bats. *Journal of Experimental Zoology* 284:35–41.
- WILLIS, C. K. R., AND R. M. BRIGHAM. 2007. Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity dwelling bat. *Behavioral Ecology and Sociobiology* 62:97–108.

Submitted 6 November 2007. Accepted 29 June 2008.

Associate Editor was R. Mark Brigham.

