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

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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—Psyllakis 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 Kurtz 2007; Kunz and Lumsden 2003; Solick and Barclay 2007; Tuttle 1976). Availability of roosts may limit populations of forest-dwelling bats (Barclay and Kurtz 2007; Hayes and Loeb 2007), and dependence of bats on...
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 1996). 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
(Grindle 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.
ob.). 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 land-
scapes (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 cedars
(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 com-
prised 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.

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

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 Shoem 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 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 (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 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 ≥ 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 ± 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 ≥ 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 (QAICc—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 QAICc value for that model and the minimum QAICc value of all models considered in the analysis (ΔQAICc—Burnham and Anderson 2002). Models with ΔQAICc < 2 are highly competitive; models with ΔQAICc > 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 ΔQAICc < 4. We calculated the Akaike weight (wi) 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 (R²) 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 R² to generalized linear models and can be roughly interpreted as similar to R² in classic regression models.

We calculated model-averaged coefficient estimates and associated odds ratios with 95% CIs for determining 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 (Σwi) for each predictor variable from the subset of models that included that variable.
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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% ± 3.7% (95% CI 55.7%, 70.3%) on roost trees and 90.6% ± 2.9% (95% CI 85.0%, 96.2%) on available trees.

The model with the lowest QAICc included the variables DBH, defects, and bark (Table 2). High cumulative Akaike
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 1.10, 1.53 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 (95% CI 10.2, 128.0 times) for every 5-m increase in slope-height. A tree with at least 1 defect was 6 times (exact 95% CI 2.5, 12.5 times) more likely to be used as a roost than a tree without defects. The odds a tree was used 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 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.

**Table 2.** Logistic regression models with $\Delta$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 ($\Delta$QAIC$_C$); Akaike weights ($w_i$); and Nagelkerke’s coefficient of determination ($R^2$). DBH = diameter at breast height; QMD = quadratic mean diameter.

<table>
<thead>
<tr>
<th>Scale</th>
<th>Model</th>
<th>K</th>
<th>$\Delta$QAIC$_C$</th>
<th>$w_i$</th>
<th>$R^2$</th>
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<tr>
<td>Tree</td>
<td>DBH, defects, bark</td>
<td>4</td>
<td>0.72</td>
<td>0.63</td>
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</tr>
<tr>
<td></td>
<td>DBH, defects, bark, slope-height</td>
<td>5</td>
<td>2.12</td>
<td>0.25</td>
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<tr>
<td></td>
<td>Null</td>
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<td>102.09</td>
<td>0</td>
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<tr>
<td>Tree plot</td>
<td>Decadence, QMD</td>
<td>3</td>
<td>0.48</td>
<td>0.13</td>
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<tr>
<td></td>
<td>QMD</td>
<td>2</td>
<td>0.23</td>
<td>0.11</td>
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<tr>
<td></td>
<td>Decadence, QMD, density</td>
<td>4</td>
<td>0.18</td>
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<tr>
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<td>0.00</td>
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<td>0.24</td>
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</table>

* The value and sign indicate unit change in the independent variable resulting in the estimated odds ratio.
* The effect was not detectable given inclusion of 0 in 95% confidence limits for the coefficient estimate.
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 (ΔQAICc = 1.50; Table 2). The relatively low ws 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 (Σw = 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 (Σw = 0.68). There was no 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 QAICc value contained only the variable decadence, but a strongly competing model contained the variables decadence and QMD (Table 4). The Σw 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.

### Table 4.—Logistic regression models with ΔQAICc < 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 (QAICc) value for that model and the minimum QAICc value of all models considered in the analysis (ΔQAICc). Akaike weights (w), and Nagelkerke's coefficient of determination (R2). DBH = diameter at breast height; QMD = quadratic mean diameter.

<table>
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<tr>
<th>Scale</th>
<th>Model</th>
<th>K</th>
<th>ΔQAICc</th>
<th>wi</th>
<th>R2</th>
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<tr>
<td>Landscape</td>
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<td>0.10</td>
<td>0.21</td>
<td>0.06</td>
</tr>
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<td>Null</td>
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<td>1.00</td>
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<td>0</td>
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<td>0.11</td>
</tr>
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<td>Stream, old growth</td>
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<td>2.96</td>
<td>0.05</td>
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</table>

**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.
0.13 ± 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 ΔQAICc < 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 ± 28 m (95% CI 164, 275 m) and the mean distance from random points was 182 ± 20 m (95% CI 143, 221 m). In the landscape surrounding roosts of males, the mean proportion of old growth was 0.39 ± 0.05 (95% CI 0.28, 0.48) and the mean proportion of clear-cut area was 0.22 ± 0.04 (95% CI 0.14, 0.29). In landscapes surrounding random points the mean proportion of old growth was 0.46 ± 0.04 (95% CI 0.39, 0.53) and the mean proportion of clear-cut area was 0.12 ± 0.03 (95% CI 0.07, 0.17). Six models, including the null model, had ΔQAICc < 2 (Table 4) and all variables had a relatively low Σwi (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.

**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 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.

**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 Σwi. 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.

<table>
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<td>1.25</td>
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<td></td>
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* The value and sign indicate unit change in the independent variable resulting in the estimated odds ratio.

* The effect was not detectable given inclusion of 0 in 95% confidence limits for the estimated odds ratio.
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 Huijtema 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 Huijtema [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; Vonhof 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.

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