

CHARACTERISTICS OF FRINGED MYOTIS DAY ROOSTS IN NORTHERN CALIFORNIA

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Abstract: Understanding habitat relationships; of forest dwelling bats has become a wildlife management priority during the past decade. We used radiotelemetry to examine the use of day roosts by fringed myotis (*Myotis thysanodes*) in a Douglas-fir (*Pseudotsuga menziesii*) forest in northern California. We located 52 roosts in 23 trees and compared the characteristics of roost sites and structures to random sites and structures. All roost trees were snags in early to medium stages of decay. Bats switched roosts often, and the number of bats exiting roosts varied from 1-88. The most important factor that discriminated roost sites from random sites was 5.4 more snags ≥ 30 cm dbh at roost sites. Roost sites also had 11% less canopy cover and were 41 m closer to stream channels than random sites. Roost snags were 27 m taller and had diameters 42 cm larger than random snags in the watershed and were 21 m taller and had diameters 30 cm larger than snags nearby the roost. Our results are comparable to findings for other forest-dwelling bat species which conclude that management of day roost habitat requires large numbers of tall snags in early to medium stages of decay.

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During the summer, temperate-zone bats spend over half of their time in day roosts (Kunz 1982). The availability of roosts is an important factor in determining bat population sizes and distributions (Humphrey 1975, Kunz 1982, O'Donnell and Sedgely 1999). Recent studies have demonstrated the use of large snags and quantified roost-site characteristics for several bat species in coniferous forests of British Columbia and the Pacific Northwest (Campbell et al. 1996, Vonnhof and Barclay 1996, Brigham et al. 1997, Betts 1998, Ormsbee and McComb 1998, Waldien et al. 2000). However, additional information is required to understand roost use and selection by forest-dwelling bats. The needs of fringed myotis have not been addressed specifically in any previous studies.

The fringed myotis is a species of special concern in California. The U.S. Fish and Wildlife Service listed it as a federal, Category 2 species, and it is on the British Columbia Provincial Blue List. This species is widely distributed throughout western North America in habitats from low desert scrub to montane evergreen forests (O'Farrell and Studier 1980). However, the species is considered rare in the northern portion of its range (Barbour and Davis 1969, U.S. Department of Agriculture and U.S. Department of the

Interior 1993). Most documented roosts of fringed myotis have been in rock crevices (Cryan 1997), caves, or anthropogenic structures (O'Farrell and Studier 1980). However, Chung-MacCoubrey (1996) and Rabe et al. (1998) reported day roosts in ponderosa pine (*Pinus ponderosa*) snags in the southwestern United States. The fringed myotis is not considered a tree-roosting bat in the Pacific Northwest (Christy and West 1993, Nagorsen and Brigham 1993).

As part of the Northwest Forest Plan, the Forest Ecosystem Management Assessment Team (FEMAT) identified fringed myotis as a species associated with old-growth forests in the Pacific Northwest that needed further study (U.S. Department of Agriculture and U.S. Department of the Interior 1993). FEMAT panelists considered fringed myotis to be particularly vulnerable to forest fragmentation because they were rare and thought to have strong site fidelity (U.S. Department of Agriculture and U.S. Department of the Interior 1993).

Bats tend to exhibit roost site fidelity when roost structures are permanent or rare (Kunz 1982, Brigham 1991, Lewis 1995). Conversely, roost switching appears common among tree-roosting bats (Vonnhof and Barclay 1996, Brigham et al. 1997, Ormsbee and McComb 1998, Waldien et al. 2000), which may be partly because of the impermanence and/or abundance of roost trees. Caves and anthropogenic structures were rare in our

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study area, while live trees and snags were abundant. This lead us to hypothesize that fringed myotis would not have high roost-site fidelity.

We designed our study to characterize day roosts and determine which habitat features were important for day roost selection by fringed myotis. We evaluated 2 orders of habitat selection (Johnson 1980) by comparing roost sites to random sites (3rd order) and roost snags to random snags (4th order).

STUDY AREA

Our study area was within the Pilot Creek watershed in the Six Rivers National Forest in northwestern California (40°37', 123°36'). The watershed is approximately 55 km from the Pacific Ocean at an elevation range of 950-1320 m. This area is characterized by steep, rugged terrain, commonly gaining 200 m in elevation for each km of distance. This watershed has hundreds of small tributaries, but only Pilot Creek, its largest tributaries, and the lower reaches of its larger tributaries have water by the end of summer. Sixty percent of the 100-km² watershed was riparian habitat; and 60% was late-successional forest, >140 years old, including the headwaters area where our study took place. The vegetation was dominated by Douglas-fir, but oaks (*Quercus chrysolepis*, *Q. kelloggii*, and *Q. garryana*) and white fir (*Abies concolor*) were also common.

METHODS

We captured bats flying over stream channels using mist nets between 30 July and 8 September 1997 and between 8 June and 9 September 1998. We determined sex, relative age, and reproductive condition using external morphology (Anthony 1988, Racey 1988). We radiotagged 9 bats including 4 nonreproductive females, 2 post-lactating females, a lactating female, a juvenile female, and an adult male. We attached radio-transmitters (Type LB-2, mass = 0.5 g, Holohil Systems Ltd., Carp, Ontario, Canada) to bats using Skin Bond surgical adhesive (Smith and Nephew United, Inc., Largo, Florida, USA) after clipping the inter-scapular fur. The mass of all radio-tagged bats was ≥ 7 g, meaning that transmitters represented 5.6-7.1% of the bats' body mass.

We located roost snags during the day by tracking the transmitter signal using Telonics TR-2 receivers and RA-14 2-element flexible antennae (Telonics, Mesa, Arizona, USA). If we were not able to positively identify a roost snag using telemetry, we watched for bats to emerge at dusk

from beneath roost snags using a Generation III technology ITT Model 210 binocular night-vision viewer (ITT Night Vision, Roanoke, Virginia, USA) while monitoring radiosignals. Observations began 15 min prior to, sunset and ended 10 min after the last emerging bat was seen. We counted bats leaving confirmed roosts to determine the number of bats using snags.

Roost Site Characteristics

We measured habitat characteristics within 17.8-m radius circular plots (0.1 ha) centered on the roost snag (roost sites) and compared them to those of 2 random sites of the same dimension. We centered random sites on a snag ≥ 30 cm dbh and ≥ 3 m tall (focal snag) at a random distance (100-300 m) and direction from the roost tree. We defined snags as standing dead trees (Cline et al. 1980). We chose dimensions of focal snags from the minimum snag size used by bats in other western coniferous forests (Campbell et al. 1996, Ormsbee 1996). All random sites were located in forest habitat and were >50 m apart.

At all sites, we recorded slope, aspect, elevation, distance to nearest perennial water, distance to nearest stream channel (regardless of whether water was present), and species and dbh of all live trees and snags ≥ 10 cm dbh and ≥ 3 m height. We estimated canopy height from the mean height of 5 dominant trees in the immediate vicinity of the roost (or focal) tree. We measured height of all snags ≥ 30 cm dbh and assigned each snag to a decay class according to Cline et al. (1980). Class 1 snags were recently dead trees with intact bark and all limbs and bark remaining. Class 2 and 3 snags usually had broken tops, few branches, and sloughing bark. Class 4 and 5 snags exhibited advanced decay with few or no limbs and little or no bark. We used an Impulse 200 laser ranging instrument (Laser Technology Inc., Englewood, Colorado, USA) to measure tree heights. We measured percentage canopy cover at the cardinal directions 3 m from roost and focal snags using a concave densiometer. For roost snags where we counted exiting bats, we also measured canopy cover in the direction where bats exited. Thus, our value for canopy cover at a site was the mean of either 4 or 5 measurements.

Roost Snag Characteristics

To examine roost selection at the level of structure (4th order selection), we compared roost snags to focal snags and to 2 random snags in the immediate vicinity of the roost tree (nearby snags). Nearby snags had to be $\leq 45^\circ$ on either

side of a random bearing from the roost snag. We selected the nearest snag (≥ 30 cm dbh and ≥ 3 m height) to this bearing within this 90° arc as the nearby snag. All nearby snags were < 30 m from the roost snag. We did not know whether focal or nearby snags were used by bats.

For each roost, focal, and nearby, snag we recorded species, decay class, dbh, height, distance to nearest tree, distance to nearest tree ≥ 30 cm dbh and ≥ 3 m tall, and distance to nearest tree $\geq$ height of the snag. We estimated percentage of bark on roost and focal snags (mean of estimates from 2 or 3 observers). We calculated height of roost and focal snags relative to canopy height by subtracting the snag's height from canopy height in the plot. This resulted in a negative number whenever the snag was shorter than canopy height.

Statistical Analyses

All data are presented as means $\pm$ SE. We determined correlation coefficients among habitat variables using SAS (SAS Institute 1990). We used log likelihood ratios to determine whether the distribution of roost snags among decay classes was independent of the distribution of snags ≥ 30 cm dbh among decay classes in roost or random sites (Zar 1984).

To determine which habitat variables best discriminated between roost and random habitat, we performed conditional logistic regression using a proportional hazards regression (PHREG) procedure (SAS Institute 1997). This type of analysis is recommended when using logistic regression in matched case-control studies (Hosmer and Lemeshow 1989, SAS Institute 1997). In this, context, the PHREG procedure estimates parameters and provides risk ratios but does not calculate the probability of a particular outcome. Thus, we could not determine percent correct classification of models. We computed risk ratios by taking the antilogarithm of parameter estimates. We calculated the difference in odds of use between sites (or snags) by raising the risk ratio to the power of the difference between covariate values for the sites (or snags).

For each comparison of roost to random habitat we ran a univariate PHREG analysis for discrete and continuous habitat variables (Hosmer and Lemeshow 1989). We did not include decay class or tree species as potential covariates in our models because categorical variables with zero cell counts produce undesirable outcomes (Hosmer and Lemeshow 1989).

We used a bias-corrected version of Akaike's Information Criteria, AIC_c to rank models and select a best approximating model (Burnham and Anderson 1998). Because there was limited published information on roost requirements of forest-dwelling bats, we could not construct a priori models (Burnham and Anderson 1998). The a priori portion of our modeling occurred when we selected variables to measure in the field. We selected habitat variables that were known to be important to other bat species in coniferous forests. We also measured other habitat variables that we believed had management significance for fringed myotis.

Univariate analyses were used to eliminate covariates from inclusion in multivariate models. If the deviance for a univariate model was within 2 points of the deviance for the model with no covariates, we eliminated that variable from inclusion in multivariate models. Variables that were highly correlated ($r \geq 0.7$) and that explained a similar biological phenomenon were not included together in multivariate models. We constructed bivariate models by combining the habitat variable with the lowest univariate AIC_c value with the other remaining variables. We constructed multivariate models using covariates from bivariate models that were ≤ 2.5 AIC_c points from the bivariate model that had the lowest AIC_c value. We selected the model with the lowest AIC_c value as the best approximating model at each spatial scale. We considered any model within 2 AIC_c points of the best approximating model to be a competing model (Burnham and Anderson 1998). We also calculated model selection uncertainty in terms of Akaike weights, which indicated the likelihood of the model given the data (Burnham and Anderson 1998).

RESULTS

Roosting Behavior

We radiotracked bats for 6.3 ± 1.2 days (range = 2-14 days) and located 3.1 ± 0.6 roosts per bat (range = 1-7 roosts) for a total of 52 day roosts in 23 different trees. All roost trees were snags. We observed emergence of radiotagged bats from 17 different roosts on 31 nights. Fifteen emergence points were from beneath, exfoliating bark and 2 were from broken tops of snags. Radiotagged bats emerged 31 ± 2 min after sunset ($n = 33$), and on average 31 ± 5 bats (range = 1-88 bats, $n = 25$) exited roosts. Radiotagged bats remained at the same day roost 1.7 ± 0.2 consecutive days (range = 1-5 days, $n = 29$). Day roosts were $424 \pm$

57 m (range 29-980 m, $n = 23$) from capture sites and the distance between consecutive roosts was 254 ± 61 m (range 7-641 m, $n = 19$).

Roost Site Characteristics

Number of snags 22-30 cm dbh, percentage canopy cover, and distance to nearest stream channel were among the variables with the largest differences between roost and random sites (Table 1). The best model for discriminating between roost and random sites included number of snags ≥ 30 cm dbh (parameter estimate (β) = 0.520, SE = 0.191) and percentage canopy cover (β = -0.112, SE = 0.083; Table 2). The univariate model that included only number of snags ≥ 30 cm dbh was the most parsimonious (Burnham and Anderson 1998) and was a competing model. This model had the lowest univariate AIC_c value, its parameter estimate remained stable regardless of which additional parameter it was combined with, and it was included in all of the models that made up the 99.99% confidence set of models based on Akaike weights (Table 2). However, the model that also included canopy cover had a lower AIC_c value and was twice as likely, based on Akaike weights, to be the best model (Table 2). Using this model, each additional snag ≥ 30 cm dbh increased the odds that fringed myotis would roost at the site by 1.68 times (95% CI = 1.16-2.45). For example, the odds that a site with the mean number of snags present at a roost site ($\bar{x} = 8.3$) was used were about 16.6

times the odds that a site with the mean number of snags present in a random site was used ($\bar{x} = 2.9$; $8.3-2.9 = 5.4$ and $1.68^{5.4} = 16.6$). After the number of snags ≥ 30 cm dbh was accounted for, the odds that a site was used decreased 0.89 times (95% CI = 0.76-1.05) for every 1% increase in canopy cover. Despite a large parameter estimate-to-standard error ratio, distance to nearest stream channel was added to the best approximating model to form a second competing model (Table 2).

Roost Snag Characteristics

Twenty roosts were in Douglas-fir snags, 1 was in a ponderosa pine snag, and 2 were in sugar pine (*P. lambertiana*) snags. Douglas-fir accounted for 67% of snags ≥ 30 cm dbh at random sites, compared to 3.8% for ponderosa pine and 0.8% for sugar pine. Only decay class 2 and 3 snags were used as roosts which was different from the distributions of snags ≥ 30 cm dbh at random sites ($G = 29.0$, $P < 0.001$; Fig. 1) and roost sites ($G = 254.0$, $P < 0.001$; Fig. 1).

Fringed myotis roosted in large dbh snags (Table 3; range = 58.5-167.0 cm). Snags ≥ 30 cm dbh accounted for 40% of 749 snags we measured at 23 roost sites and 46 random sites combined. Roost snags were also tall (Table 3; range = 15.8-57.5 m). Among snags ≥ 30 cm dbh, 72.5% of snags at random sites and 42.5% of snags at roost sites were shorter than the shortest roost snag. Nineteen of 23 (83%) roosts were either

Table 1. Mean values for site-level habitat variables in 0.1 ha plots at fringed myotis roost sites ($n = 23$) and paired random sites ($n = 46$) in the Pilot Creek watershed, Humboldt County, California, 1997-1998. Parameter estimates, P -values for the Wald chi-squared statistic, and bias-corrected Akaike Information Criteria (AIC_c) are presented from a 1:2 paired logistic regression model.

Variable	Roost site $\bar{x}$ (SE)	Random site $\bar{x}$ (SE)	Parameter estimate (SE)	P -value	AIC _c
Number of snags ≥ 30 cm diameter at breast height (dbh)	8.3 (0.8)	2.9 (0.3)	0.593 (0.194)	0.002	21.30
Canopy cover (%)	78.5 (2.6)	89.2 (1.1)	-0.127 (0.044)	0.004	36.32
Distance to nearest stream channel (m)	43.7 (8.4)	84.3 (9.1)	-0.021 (0.009)	0.012	41.82
Standard deviation of tree dbh (cm)	35.3 (1.4)	30.1 (1.3)	0.092 (0.040)	0.019	45.86
Douglas-fir trees (%)	47.7 (5.3)	62.6 (4.0)	-0.025 (0.012)	0.036	47.31
Basal area (m ² /ha)	110.4 (4.6)	95.9 (3.9)	0.023 (0.011)	0.035	47.65
Mean dbh of trees (cm)	42.9 (3.0)	37.7 (1.3)	0.053 (0.028)	0.057	48.49
Elevation (m)	1,058.4 (18.2)	1,072.4 (11.6)	-0.014 (0.009)	0.109	49.67
Distance to nearest perennial water (m)	117.4 (27.3)	149.7 (19.2)	-0.004 (0.003)	0.185	50.57
Slope (%)	29.7 (5.2)	35.7 (2.2)	-0.018 (0.014)	0.214	50.97
Number of trees	50.6 (3.6)	57.7 (3.9)	-0.016 (0.018)	0.232	50.99
Canopy height (m)	42.9 (1.8)	45.3 (1.3)	-0.044 (0.036)	0.219	51.00
White fir trees (%)	18.9 (4.3)	14.8 (3.0)	0.016 (0.017)	0.332	51.61
Number of snags	10.8 (0.9)	11.3 (2.2)	-0.004 (0.024)	0.858	52.56

Table 2. Habitat models used to explain differences between fringed myotis roost sites or snags ($n = 23$) and paired random sites or snags ($n = 46$) in the Pilot Creek watershed, Humboldt County, California, 1997-1998. The bias-corrected Akaike Information Criteria (AIC_c), the difference in AIC_c values between the i th model and the model with the lowest AIC_c value (Δ_i), and the Akaike weights (w_i) are presented for the set of models that represents 99:99% of the Akaike weights.

Comparison	Model statement	AIC_c	Δ_i	w_i
Roost site to random site	Number of snags ≥ 30 cm diameter at breast height (dbh) + canopy cover (%)	19.84	0.00	0.277
	Number of snags ≥ 30 cm dbh	21.30	1.46	0.134
	Number of snags ≥ 30 cm dbh + canopy cover (%) + distance to nearest stream channel (m)	21.76	1.92	0.106
	Number of snags ≥ 30 cm dbh + distance to nearest stream channel (m)	21.99	2.15	0.095
	Number of snags ≥ 30 cm dbh + canopy cover (%) + standard deviation of dbh of trees (cm)	22.00	2.16	0.094
	Number of snags ≥ 30 cm dbh + standard deviation of dbh of trees (cm)	22.16	2.32	0.087
	Number of snags ≥ 30 cm dbh + elevation (m)	23.11	3.27	0.054
	Number of snags ≥ 30 cm dbh + mean dbh of trees (cm)	23.20	3.36	0.052
	Number of snags ≥ 30 cm dbh + mean dbh of trees (cm)	23.21	3.37	0.051
	Number of snags ≥ 30 cm dbh + basal area (m^2/ha)	23.30	3.46	0.049
Roost snag to focal snag	Snag height relative to canopy height (m) + snag dbh (cm)	9.72	0.00	0.704
	Snag: height relative to canopy height (m)	12.03	2.31	0.222
	Snag height (m)	15.52	5.80	0.039
	Distance from nearest snag to nearest tree > snag height (m)	15.69	5.97	0.036
Roost snag to nearby snag	Snag height (m) + snag dbh (cm)	12.80	0.00	0.905
	Snag height (m)	17.32	4.52	0.095

the tallest ($n = 12$) or second tallest snag ($n = 7$) at the roost site. Seven roost snags were taller than any other tree or snag at the roost site.

Comparison to Focal Snags.—Univariate logistic regression models eliminated all but 4 variables from consideration in multivariate models. The 3 best univariate models all had covariates related to snag height (Table 3). Snag height relative to canopy height increased as the height of the roost (or focal) snag increased ($r = 0.88$, $P < 0.0001$), as did the distance from the snag to the nearest tree taller than the roost (or focal) snag ($r = 0.71$, $P < 0.0001$). We selected snag height relative to canopy height for use in multivariate models because it had the lowest univariate AIC_c value and, because it was a combination of snag height and surrounding canopy height, included more information about the biological system.

The model that best discriminated between roost and focal snags included snag height relative to canopy height ($\beta = 0.477$, $SE = 0.377$) and snag dbh ($\beta = 0.053$, $SE = 0.049$; Table 2). This model was 3 times as likely, based on the Akaike weights, as the model that included only snag height relative to canopy height. Using this model, the odds that a

snag was used for a roost increased 1.61 times (95% CI = 0.78-3.32) for every meter increase in height relative to canopy height. Once snag height relative to canopy height was accounted for, the odds that a snag was used increased 1.06 times (95% CI = 0.96-1.16) for each cm increase in dbh.

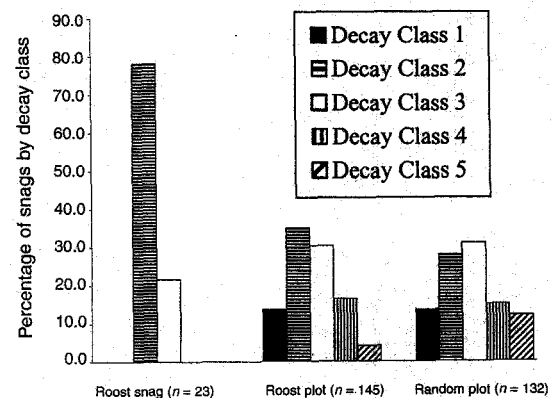


Fig. 1. Decay classes (Cline 1980) of fringed myotis day roost snags (>30 cm diameter at breast height and >3 m tall) located in 0.1-ha plots around the roost and in random plots in the Pilot Creek watershed, Humboldt County, California, 1997-1998.

Table 3. Mean values for snags used as roosts by fringed myotis ($n = 23$) and random focal snags (≥ 30 cm diameter at breast height [dbh] and ≥ 3 m tall, $n = 46$) in the Pilot Creek watershed; Humboldt County, California, 1997-1998. Parameter estimates, P -values for the Wald chi-squared statistic, and bias-corrected Akaike Information Criteria (AIC_c) values are presented from a 1:2 paired univariate logistic regression model.

Variable	Roost snag $\bar{x}$ (SE)	Focal snag $\bar{x}$ (SE)	Parameter estimate (SE)	P -value	AIC_c
Snag height relative to canopy height (m)	-2.3 (2.6)	-32.1 (1.6)	0.248 (0.145)	0.086	12.03
Snag height (m)	40.5 (2.9)	13.2 (1.3)	0.160 (0.057)	0.005	15.52
Distance from snag to nearest tree $\geq$ snag height (m)	16.5 (3.6)	3.7 (0.4)	0.599 (0.235)	0.011	15.69
Snag dbh (cm)	120.8 (5.3)	78.5 (6.8)	0.028 (0.009)	0.002	37.17
Bark remaining on snag (%)	74.1 (5.4)	63.3 (6.0)	0.008 (0.007)	0.288	51.40
Distance from snag to nearest tree ≥ 30 cm dbh (m)	4.3 (0.4)	3.7 (0.4)	0.084 (0.099)	0.397	51.87
Distance from snag to nearest tree (m)	2.7 (0.4)	2.4 (0.2)	0.117 (0.145)	0.422	52.00

Comparison to Nearby Snags.--Roost snags were twice as tall as nearby snags (Table 4). The model that included snag height ($\beta = 0.281$, SE = 0.131) and snag dbh ($\beta = 0.083$, SE = 0.047) was the best model for discriminating between roost and nearby snags. This model was nearly 10 times as likely as the univariate model for snag height, and together these 2 models contained 99.99% of the Akaike weights. Using the best model, the odds that a snag was used as a roost increased 1.33 times (95% CI = 1.03-1.71) for every meter increase in height. After snag height was accounted for, the odds that a snag was used as a day roost increased 1.09 times (95% CI = 0.99-1.19) for every centimeter increase in dbh:

between day roosts for fringed myotis were comparable to values for other *Myotis* spp. that roost in snags in forests of the Pacific Northwest (Ormsbee 1996, Vonhof and Barclay 1996, Brigham et al. 1997, Waldien et al. 2000). As with California myotis (*M. californicus*, Brigham et al. 1997), fringed myotis did not appear to form stable colonies in our study area. The lack of roost fidelity in forest habitat contrasts with earlier suggestions that these bats exhibit strong fidelity (O'Farrell and Studier 1980, U.S. Department of Agriculture and U.S. Department of the Interior 1993). This difference in roosting behavior may occur because fringed myotis in our study area roosted in snags, which are more abundant but less permanent than buildings or caves (Kunz 1982, Brigham 1991, Lewis 1995).

Predator avoidance and locating roosts with greater structural stability may have been the most important reasons for roost-switching in this area (Lewis 1995, Weller 2000). Although bats may have been seeking snags with more suitable

DISCUSSION

Roost Fidelity

Fringed myotis switched roosts often, and group size in roosts was variable (Weller 2000). The frequency of roost switching and distance

Table 4. Mean values for snags used as roosts by fringed myotis bats ($n = 23$) and nearby (< 30 m from roost snags) random snags (≥ 30 cm diameter at breast height [dbh] and ≥ 3 m tall, $n = 46$) in the Pilot Creek watershed, Humboldt County, California, 1997-1998. Parameter estimates, P -values for the Wald chi-squared statistic, and bias-corrected Akaike Information Criteria (AIC_c) values are presented from a 1:2 paired, univariate logistic regression model.

Variable	Roost snag $\bar{x}$ (SE)	Focal snag $\bar{x}$ (SE)	Parameter estimate (SE)	P -value	AIC_c
Snag height (m)	40.5 (2.9)	19.5 (1.9)	0.207 (0.074)	0.005	17.32
Distance to nearest tree $\geq$ snag height (m)	16.5 (3.6)	6.4 (0.8)	0.220 (0.079)	0.005	33.15
Snag dbh (cm)	120.8 (5.3)	91.3 (4.9)	0.056 (0.018)	0.002	33.59
Distance from snag to nearest tree ≥ 30 cm dbh (m)	4.3 (0.4)	4.1 (0.4)	0.040 (0.117)	0.730	52.46
Distance from snag to nearest tree (m)	2.7 (0.4)	2.7 (0.3)	0.012 (0.157)	0.937	52.59

microclimates, they often did so in the absence of obvious shifts in ambient temperature or humidity. Roosts beneath exfoliating bark provide ephemeral shelters for bats because bark peels and sloughs off the bole of the tree (Kurta et al. 1993). Further, snags themselves can be unreliable roost structures because they fall and break (Rendell and Robertson 1989). By the end of our study, 3 of 23 roost snags had broken, leaving them at less than half of their height at the time they were used. If microsites beneath sloughing bark and snags themselves are ephemeral resources, it would be beneficial for bats to be familiar with several suitable roosts. This may explain why tree-roosting bats show fidelity to small areas rather than specific roost trees and provides evidence that the distribution and abundance of snags is important in habitat selection by bats (O'Donnell and Sedgely 1999).

Roost Site Comparisons

The number of snags ≥ 30 cm dbh (not the total number of snags) was the most important covariate that discriminated between roost and random sites. Several studies did not find that roost sites had more snags than random sites (Vonhof and Barclay 1996, Brigham et al. 1997, Ormsbee and McComb 1998); however, those that compared densities of snags ≥ 30 cm dbh (Campbell et al. 1996, Rabe et al. 1998) or within specific decay classes (Waldien et al. 2000) found differences. Having several large snags in the same area may provide alternative roosting structures that could be located with limited energy expenditure (O'Donnell and Sedgely 1999). In addition, the presence of several large snags in a small area meant that canopy cover was reduced and solar exposure was increased for snags that occurred there (Waldien et al. 2000).

Inclusion of canopy cover with number of snags ≥ 30 cm dbh provided the best model and corroborated our observations from the field. Our results are consistent with other studies that found bats roosting in areas with less canopy cover than was available at random sites (Campbell et al. 1996, Vonhof and Barclay 1996, Brigham et al. 1997). Lower canopy cover around roosts facilitates greater solar exposure that probably increases the diurnal temperature of roosts (Kurta et al. 1993, Betts 1998). An open canopy around roost entrances may also benefit bats by giving them easier access to and from the roost (Campbell et al. 1996, Vonhof and Barclay 1996, Crampton and Barclay 1998, but see Kalcounis and Brigham 1998).

While distance to water has been suggested as a factor that may influence roost-site selection, by bats in other areas (Tidemann and Flavel 1987, Rabe et al. 1998), this has not held true for *Myotis* spp. in the Pack Northwest (Ormsbee and McComb 1998, Waldien et al. 2000). At our study site, no roost or random site was >570 m from the nearest perennial water source. Thus, all areas within the watershed were probably close enough to water for bats to use for roost sites. However, although distance to nearest perennial water source was not an important covariate for identifying roosts in our study, distance to nearest stream channel entered a competing model and was the third-best univariate habitat model. In the Pilot Creek watershed, Seidman and Zabel (2001) used bat detectors to determine that there were high levels of bat activity along stream channels even when water was not present. Because bats use stream channels for foraging and as travel corridors, proximity of roosts to intermittent stream channels may be an important characteristic of roost sites.

Roost Snag Comparisons

Decay classes of snags used by fringed myotis were similar to those reported for other forest-dwelling bat species (Vonhof and Barclay 1996, Brigham et al. 1997, Waldien et al. 2000). Fringed myotis often roosted beneath loose bark on snags, and this behavior may explain their selection of snags only in decay classes 2 and 3. Decay class 1 snags have intact bark, and decay class 4 and 5 snags may not retain enough bark to be suitable roost snags for fringed myotis.

Similar to our findings, other studies identified height as an important factor for selection of roost snags by bats (Vonhof and Barclay 1996, Crampton and Barclay 1998). Snag height relative to canopy height (Campbell et al. 1996, Betts 1998, Ormsbee and McComb 1998) and distance to nearest tree height of roost snag (Vonhof and Barclay 1996, Brigham et al. 1997, Betts 1998) were important for roost selection by other forest-dwelling bat species and were correlated with snag height in our study.

Bats may roost in the tallest available snags because such snags receive greater solar radiation, than shorter snags (Kurta et al. 1993, Betts 1998). Use of roosts with higher temperatures may provide energetic benefits to bats, especially juveniles and reproductive females (Lewis 1993, Hamilton and Barclay 1994). Snags that are at or above the height of the surrounding canopy may also be

easier for bats to find (Campbell et al. 1996, Vonhof and Barclay 1996, Betts 1998). Roosting in tall trees (Betts 1998) and switching roosts regularly (Lewis 1995) may be predator avoidance strategies.

Snag diameter has been identified as an important variable in describing day roosts of other bat species in coniferous forests (Campbell et al. 1996, Vonhof and Barclay 1996, Brigham et al. 1997, Rabe et al. 1998). Large-diameter snags remain on the landscape longer than smaller-diameter snags (Morrison and Raphael 1993, Bull et al. 1997) and thus may provide more permanent roost structures. Larger and taller snags are also more likely to have the appropriate decay classes at the preferred height than are smaller trees (Bull et al. 1997).

MANAGEMENT IMPLICATIONS

Habitat use and selection by bats is influenced by the availability of suitable roosts (Humphrey 1975, Kunz 1982, O'Donnell and Sedgely 1999). Our results are comparable to studies of other forest-dwelling bat species: they use tall snags in early stages of decay for day roosting and multiple day roosts within a stand. Therefore, forest management plans that recommend removal of the tallest dead and dying trees are unlikely to be compatible with maintenance of bat roosting habitat. Both roost and random sites (and snags) were located within a watershed that was mature and old-growth forest, yet we found large differences in habitat characteristics between roost and random sites (and snags). That is, old-growth forests are rare, and fringed myotis used some of the least common structural elements within 1 of these forests. Fringed myotis are rare in the Pacific Northwest and their distribution in relation to forest age is unknown. If fringed myotis populations occur in younger seral stage forests, these bats may use and/or select different roosts than reported here (Waldien et al. 2000).

Roost sites were closer to stream channels than paired random sites, but roosts did not occur only in riparian areas. Several of the roosts were in snags outside of the riparian buffer widths mandated by the Northwest Forest Plan (U.S. Department of Agriculture and U.S. Department of the Interior 1994) and would need to be protected under snag-retention guidelines. Roost-habitat requirements of bats were so poorly understood when the Northwest Forest Plan was written that snag-retention guidelines were based on the needs of cavity-nesting birds (U.S. Department of Agriculture and U.S. Department of the Interior 1994). Most

birds that nest or roost in snags in Douglas-fir forests use cavities (Mannan et al. 1980), but fringed myotis and other bat species often roost beneath bark. Recent recommendations for cavity-nesting bird habitat management included retaining large-diameter, heavily decayed snags in clumps on the landscape (Saab and Dudley 1998). Except for decay class, these recommendations would provide roosting habitat important for fringed myotis and other bats in coniferous forests (Waldien et al. 2000). Retaining snags and the oldest live trees within green-tree retention zones could provide future bat roost habitat (U.S. Department of Agriculture and U.S. Department of the Interior 1994, Waldien et al. 2000).

Because our transmitters were limited by battery life, we did not determine the number of day roosts used by individual bats over the course of a summer; this issue needs additional research. Furthermore, night roost areas, winter hibernacula, and foraging habitat also require consideration when managing habitat for fringed myotis or other forest dwelling bats. All of these habitat requirements are poorly understood for forest-dwelling bats and thus require further research.

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LITERATURE CITED

- ANTHONY, E. L. P. 1988. Age determination in bats. Pages 47-58 in T. H. Kunz, editor. *Ecological and behavioral methods for the study of bats*. Smithsonian Institution Press, Washington, D.C., USA.
- BARBOUR, R. W., AND W. H. DAVIS. 1969. *Bats of America*. University Press of Kentucky, Lexington, USA.
- BETTS, B. J. 1998. Roosts used by maternity colonies of silver-haired bats in northeastern Oregon. *Journal of Mammalogy* 79:643-650.
- BRIGHAM, R. M. 1991. Flexibility in foraging and roosting behavior by the big brown bat (*Eptesicus fuscus*). *Canadian Journal of Zoology* 69:117-121.
- _____, M. J. VONHOF, R. M. R. BARCLAY AND J. C. GWILLIAM. 1997. Roosting behavior and roost site preferences of forest-dwelling California bats (*Myotis californicus*). *Journal of Mammalogy* 78:1231-1239.
- BULL, E. L., C. G. PARKS, AND T. R. TORGENSEN. 1997. Trees and logs important to wildlife in the interior Columbia River Basin. U.S. Forest Service General

- Technical Report PNW 391.
- BURNHAM, K. P., AND D. R. ANDERSON. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, USA.
- 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.
- CHRISTY, R. E., AND S. D. WEST. 1993. Biology of bats in Douglas-fir forests. U.S. Forest Service General Technical Report PNW 308.
- CHUNG-MACCOUBREY, A. L. 1996. Bat species composition and roost use in pinyon juniper woodlands of New Mexico. Pages 118-123 in R. M. R. Barclay and R. M. Brigham, editors. Bats and forests symposium. British Columbia Ministry of Forests, Victoria, Canada.
- CLINE, S. P., A. B. BERG, AND H. M. WRIGHT. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *Journal of Wildlife Management* 44:773-786.
- CRAMPTON, L. H., AND R. M. R. BARCLAY. 1998. Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. *Conservation Biology* 12:1347-1358.
- CRYAN, P. M. 1997. Distribution and roosting habits of bats in the southern Black Hills, South Dakota. Thesis, University of New Mexico, Albuquerque, USA.
- HAMILTON, I. M., AND R. M. R. BARCLAY. 1994. Patterns of daily torpor and day-roost selection by male and female big brown bats (*Eptesicus fuscus*). *Canadian Journal of Zoology* 72:744-749.
- HOSMER, D. W., AND S. LEMESHOW. 1989. Applied logistic regression. John Wiley & Sons, New York, USA.
- HUMPHREY, S. R. 1975. Nursery roosts and community diversity of nearctic bats. *Journal of Mammalogy* 56:321-346.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- KALCOUNIS, M. C., AND R. M. BRIGHAM. 1998. Secondary use of aspen cavities by tree-roosting big brown bats. *Journal of Wildlife Management* 62:603-611.
- KUNZ, T. H. 1982. Roosting ecology of bats. Pages 1-55 in T. H. Kunz, editor. *Ecology of bats*. Plenum Press, New York, USA.
- KURTA, A., D. KING, J. A. TERAMINO, J. M. STRIBLEY, AND K. J. WILLIAMS. 1993. Summer roosts of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. *American Midland Naturalist* 129:132-138.
- LEWIS, S. E. 1993. Effect of climatic variation on reproduction by pallid bats (*Antrozous pallidus*). *Canadian Journal of Zoology* 71:1429-1433.
- _____. 1995. Roost fidelity of bats: a review. *Journal of Mammalogy* 76:481-496.
- MANNAN, R. W., E. C. MESLOW, AND H. M. WIGHT. 1980. Use of snags by birds in Douglas-fir forests, western Oregon. *Journal of Wildlife Management* 44:787-797.
- MORRISON, M. L., AND M. G. RAPHAEL. 1993. Modeling the dynamics of snags. *Ecological Applications* 3:322-330.
- NAGORSSEN, D. W., AND R. M. BRIGHAM. 1993. The bats of British Columbia. University of British Columbia Press, Vancouver, Canada.
- O'DONNELL, C. F. J., AND J. A. SEDGELEY. 1999. Use of roosts by the long-tailed bat, *Chalinolobus tuberculatus*, in temperate rainforest in New Zealand. *Journal of Mammalogy* 80:913-923.
- O'FARRELL, M. J., AND E. H. STUDIER. 1980. *Myotis thysanodes*. *Mammalian Species* 137:1-5.
- ORMSBEE, P. 1996. Selection of day roosts by female long-legged myotis (*Myotis volans*) in forests of the central Oregon Cascades. Thesis, Oregon State University, Corvallis, USA.
- ORMSBEE, P. C., AND W. C. MCCOMB. 1998. Selection of day roosts by female long-legged myotis in the central Oregon Cascade range. *Journal of Wildlife Management* 62:596-603.
- RABE, M. J., T. E. MORRELL, H. GREEN, J. C. DEVOS, JR., AND C. R. MILLER. 1998. Characteristics of ponderosa pine snag roosts used by reproductive bats in northern Arizona. *Journal of Wildlife Management* 62:612-621.
- RACEY, P. A. 1988. Reproductive assessment in bats. Pages 31-45 in T. H. Kunz, editor. *Ecological and behavioral methods for the study of bats*. Smithsonian Institution Press, Washington, D.C., USA.
- RENDELL, W. B., AND R. J. ROBERTSON. 1989. Nest-site characteristics, reproductive success and cavity availability for tree swallows breeding in natural cavities. *Condor* 91:875-885.
- SAAB, V. A., AND J. G. DUDLEY. 1998. Responses of cavity nesting birds to stand replacement fire and salvage logging in ponderosa pine/Douglas-fir forests of southwestern Idaho. U.S. Forest Service Research Paper RMRS-11.
- SAS INSTITUTE. 1990. SAS procedures guide. Version 6. Third edition. SAS Institute, Cary, North Carolina, USA.
- _____. 1997. The PHREG procedure. Pages 873-948 in SAS/STAT® software: changes and enhancements through release 6.12. SAS Institute, Cary, North Carolina, USA.
- SEIDMAN, V. M., AND C. J. ZABEL. 2001. Bat activity along intermittent streams in northwestern California. *Journal of Mammalogy* 82: in press.
- TIDEMANN, C. R., AND S. C. FLAVEL. 1987. Factors affecting choice of diurnal roost site by tree-hole bats (Microchiroptera) in south-eastern Australia. *Australian Journal of Wildlife Research* 14:459-473.
- U.S. DEPARTMENT OF AGRICULTURE AND U.S. DEPARTMENT OF THE INTERIOR. 1993. Forest ecosystem management: an ecological, economic and social assessment. U.S. Forest Service, Portland, Oregon, USA.
- _____, AND _____. 1994. Record of decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the northern spotted owl. U.S. Forest Service, Portland, Oregon, USA.
- VONHOF, M. A., 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., 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. 2000. Snag use and roost fidelity of fringed myotis in an old-growth Douglas-fir forest in northern California. Thesis, Humboldt State University, Arcata, California, USA.
- ZAR, J. H. 1984. Biostatistical analysis. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

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