CHARACTERISTICS OF PONDEROSA PINE SNAG ROOSTS USED BY REPRODUCTIVE BATS IN NORTHERN ARIZONA

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Abstract: Little information exists on the roost habitat characteristics of reproductive forest bats; hence, we used radiotelemetry to locate 121 roosts of 8 species of bats in 2 study areas on the Coconino National Forest (CNF), northern Arizona, during 1993–95. Only pregnant or lactating bats were examined in the study. Ninety-seven (80%) roosts were in ponderosa pine (*Pinus ponderosa*) snags. Snags used by bats were larger in diameter at breast height (dbh) and were more likely to have exfoliating bark (bark peeling away from the snag, thus creating space between the bark and the snag) than random snags in both areas. In both study areas, roost snags were surrounded by forest with higher tree densities, greater tree species diversity, and trees had larger basal areas than forest surrounding random snags. Forests immediately surrounding roost snags also had higher densities of snags and logs than random snag areas. In the southern study area, roost snags were located closer to water than random snags and were more likely near the tops of slopes. Roost snags in the northern study area were on steeper slopes and were less likely within a recently harvested area. Radiomarked bats frequently used multiple roosts: 37 of 76 (49%) bats used ≥2 snags during the study. We recommend preserving all large snags with exfoliating bark and suggest steps to ensure that sufficient numbers of such snags are maintained for roosting bats in the future.

Key words: Arizona, bats, Coconino National Forest, habitat, ponderosa pine, radiotelemetry, reproductive, roosts, snags.

Although land managers are aware of the importance of maintaining nesting habitat for forest birds, little is known of the roost habitat requirements for forest bats. Most bat species in North America give birth to only 1 young/year and form groups of pregnant females in communal maternity roosts to raise their young, which makes bats particularly sensitive to environmental change and roost habitat destruction (Kunz 1982). Maternity roosts are important to bats because the small size of bats places tight thermal constraints on the young, but bats do not build nests of insulating materials. Bats in temperate environments must choose maternity roosts that minimize thermal gradients between themselves and the roost (Trune and Slobodchikoff 1976, Racey 1982). Roost thermal characteristics are particularly important in the development of newborn bats (Racey and Swift 1981, Racey 1982). In addition to these thermal constraints, bats are vulnerable to predation while roosting during the day and presumably must choose roosts that minimize predator access (Fenton et al. 1994).

The purpose of this study was to determine habitat characteristics of roosts used by reproducing female bats in ponderosa pine forests of northern Arizona and to develop models that land managers could use to identify potential bat roost habitat. We concentrated on snag roosts of 5 bat species previously (before 1996) listed as Category 2 species by the U.S. Fish and Wildlife Service (USFWS): Allen's lappet-browed bat (*Idionycteris phyllotis*), long-eared myotis (*Myotis evotis*), Arizona occult bat (*Myotis occultus*), fringed myotis (*Myotis thysanodes*), and long-legged myotis (*Myotis volans*). We also located roosts of big brown bats (*Eptesicus fuscus*), pallid bats (*Antrozous pallidus*), and southwestern myotis (*Myotis auriculus*).

STUDY AREAS

The study was conducted during June and July of 1993–95 in 2 separate 145-km^2 areas of the CNF in northern Arizona. One area (hereafter, Peaks) was centered (35°15′N, 111°45′W) 14 km

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northwest of Flagstaff on the southwestern slopes of the San Francisco Peaks. Elevations at capture sites ranged from 2,260 to 2,620 m. This area contained 2 habitat types: a pine–grassland dominated by ponderosa pine, Arizona fescue (*Festuca arizonica*), and mountain muhly (*Muhlenbergia montana*) with occasional patches of aspen (*Populus tremuloides*), and a higher elevation mixed-conifer association of limber pine (*Pinus flexilis*), Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), ponderosa pine, and aspen (Merriam 1885, Warner 1981). The other area (hereafter, Bar M) was 30 km south of Flagstaff and centered in and around Bar M Canyon (34°53′N, 111°33′W). Bar M was a ponderosa pine–Gambel oak (*Quercus gambellii*) community that included occasional junipers (*Juniperus osteosperma, J. deppeana*) with a sparse understory of buckbrush (*Ceanothus fendleri*), creeping mahonia (*Berberis repens*), and locust (*Robinia neomexicana*). Elevations at Bar M capture sites ranged from 2,015 to 2,260 m. Both areas receive approximately 64 cm of precipitation each year, with the bulk of moisture as snow in winter (National Oceanic and Atmospheric Administration 1990, Schubert 1974), and they are managed for timber production, grazing, and recreation.

METHODS

We captured bats at 31 sites (Peaks: $n = 18$; Bar M: $n = 13$) by setting mist nets over water sources such as springs, pools in ephemeral watercourses, and earthen water catchments (cattle tanks). All captured bats were identified, sexed, and weighed to the nearest 0.2 g with a spring balance. Reproductive status and age (adult or juvenile, determined by the degree of ossification of the joints in the phalanges) of each bat were recorded (Barbour and Davis 1969). We classified females as pregnant if a fetus could be detected by abdominal palpation, or as lactating if milk could be expressed from a nipple.

Radiotransmitters (Holohil Systems, Carp, Ontario, Canada, or AVM Instruments, Livermore, California, USA) were glued to the backs of pregnant or lactating bats with a nontoxic, latex-based adhesive. After a 5–15-min holding period to allow glue to dry, we released bats at the capture site. Transmitter mass was not >10% of the mass of the bat; in most cases, it was ≤5% (Aldridge and Brigham 1988).

We used radiotelemetry to locate day-roosting bats. To confirm that roost locations were being used, we counted bats as they exited in the evening. Each known roost was periodically checked during the study to ensure the transmitter was present. If a radiomarked bat moved from a roost, we located the new roost. Roost switching, when it occurred, allowed us to locate multiple roosts via a single radiomarked individual. We repeated this process until the bat shed the transmitter or the battery failed.

To determine which habitat characteristics were important to forest-dwelling bats, we compared habitat characteristics of ponderosa roost-snag sites with randomly selected ponderosa snag sites. We selected random snags by locating the closest snag to a random point generated by a Geographic Information System. We defined random snags as dead ponderosa pines ≥30.5 cm dbh and ≥3 m in height. We chose these snag criteria because none of the roost snags were smaller than these dimensions.

At both roost snag and random snag sites, we measured 24 habitat variables at 2 spatial scales: (1) individual snag, and (2) forest immediately surrounding the snag. Snag variables included snag tree species, dbh, snag height, presence or absence of loose bark, percent slope, slope aspect, position of snag on slope, distance (m) to open water, distance (m) to the nearest forest opening ≥0.5 ha, and elevation. We recorded snag position on the slope on a 5-category scale based on snag location on a topographic map (e.g., top 20% to bottom 20% of slope). Aerial photographs were used to identify forest openings ≥0.5 ha, and open-water locations were obtained from topographic maps and verified in the field.

To gather information about the forest surrounding each snag, we established 5 nonoverlapping 11.3-m-radius plots (0.04 ha each). One plot was centered on the roost snag, and the other plots were at random distances (23–50 m) from the snag in each of 4 cardinal directions. Within each plot, we measured basal area, percent canopy closure, number of trees in each of 5 dbh classes (≤12.4, 12.5–30.2, 30.3–45.5, 45.6–61.0, >61.0 cm; Reynolds et al. 1992:82), number of shrub species, number of individual shrub plants, number of snags, number of logs, recent grazing, timber harvest activity, and presence or absence of dwarf mistletoe (*Arceuthobium vaginatum*), which is a parasite that can weaken pines and contribute to snag creation. Basal area was estimated with a prism at the center of each of the 5 plots and averaged to a

single value. Similarly, we determined percent canopy closure at each of the 5 plots with a spherical densiometer and used the mean of the values for analysis. We tallied numbers of shrub species and individual shrubs over all 5 plots. We recorded dwarf mistletoe as present if it occured in any of the 5 plots. The number of snags ≥30 cm dbh and 3 m tall, and down logs ≥25.5 cm diameter at midpoint and 3.6 m in length, were summed over all 5 plots and expressed as number per hectare. We used relative frequencies of tree species within all 5 plots to calculate a Shannon-Wiener (H′) diversity index (Lloyd et al. 1968). Mylar overlays of active cattle grazing areas (grazed within 2 yr) and recent timber harvest boundaries (cut within 5 yr) allowed us to classify the roost and random snags as within or outside these boundaries.

To ensure that random snags did not contain active bat roosts, we scratched the snag and listened for squeaking bats, searched the base for guano, and struck the snag base. We surveyed 54 random snags in the Peaks area and 58 at Bar M.

Statistical Analysis

Because the purpose of our study was to provide general guidelines for the management of reproductive bat roosts, and all bat species used ponderosa pine snags as roosts, we combined all bat species by study area for analyses. For variables measured at ordinal or higher level, we used univariate Mann-Whitney U-tests to test for differences between roost snags and random snags (Conover 1980). To compare categorical variables, we used maximum likelihood G-tests for independence (Sokal and Rohlf 1995). For the circular variable (slope aspect) we grouped measurements into 8 45° categories and used a Rayleigh test to determine if slope aspect was nonrandom. If roost snags exhibited a nonrandom direction, we used a chi-square test (Batschelet 1981:109–111) to compare roost snag to random snag aspect for both study areas.

We used stepwise logistic regression (SAS Institute 1994) to determine which habitat variables best discriminated roost snags from random snags in each study area (Press and Wilson 1978, Freeman 1987). All variables (except slope aspect) were initially entered into the stepwise regression, but we confirmed that variables included in final regression models made biological sense and were not highly correlated with other variables in the model (Hosmer and Lemeshow 1989). We used Wald's chi-square

statistics to assess the contribution of individual variables to the multivariate model. Overall model significance was based on log-likelihood chi-square statistics, classification accuracy (based on a logistic cut point of 0.5 to classify snags as roost or random), and the Hosmer-Lemeshow lack-of-fit test. Positive parameter coefficients in the logistic regression equations indicated that an increase in the value of a variable increased the probability of a snag being a bat roost. Conversely, a negative coefficient indicated that as value of the variable increased, probability of the snag being a roost decreased. We considered $P \leq 0.05$ as the indicator of significance for all our statistical tests.

RESULTS

We attached transmitters to 76 bats belonging to 8 species in both study areas and located a total of 121 roosts of which 97 (80%) were in ponderosa pine snags and 2 (1.7%) were in Douglas-fir snags. Long-eared myotis were observed roosting in 5 different roost types: 24 in ponderosa snag roosts, 14 in cracks in rocks on the ground, 2 in down logs, 2 in Gambel oak tree cavities, and 2 in Gambel oak snags. Roosts of 21 Arizona occult bats and 15 fringed myotis were in ponderosa snags. Two individuals of these 2 species also used the same Douglas-fir snag in different years. Ponderosa pine snags were exclusively used as roosts by Allen's lappet-browed bat ($n = 16$), long-legged myotis ($n = 13$), big brown bat ($n = 6$), and pallid bat ($n = 3$). A single southwestern myotis used 2 Gambel oak tree cavities. We also found 1 Arizona occult bat roost in the attic of a cabin. We did not confirm that a colony located with a particular bat species contained only that species. Roost exit counts ranged from 1 to 984 bats (10.5% of the roosts contained single bats).

Thirty-seven of the 76 (49%) bats that roosted in ponderosa pine snags used >1 roost during the study. In roosts containing ≥1 bat and where the radiomarked individual(s) moved to a second roost, exit counts of the 2 roosts often indicated the first roost was abandoned, and the colony had moved as a unit. Statistical comparisons (Mann-Whitney U-test and G-test) between primary roosts (roosts where bats did not move during the time we observed them) and secondary roosts (roosts where bats moved during the study) did not reveal any differences between the roost types. Mean (± SE) distances

Table 1. Snag and surrounding forest habitat characteristics for ponderosa pine bat snag roosts and random ponderosa snags in the Peaks area, northern Arizona, during June–August, 1993–95.

Variable	Bat roost snags (n = 54)			Random snags (n = 54)			P^a
	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	
Snag variables							
Dbh (cm)	69.2	2.0	31.2–101.6	58.6	2.1	30.5–102.9	<0.001
Snag height (m)	17.8	1.1	2.8–36.5	15.9	1.2	4.3–38.7	0.232
Percent slope	13^b	1	2–40	7	1	1–28	<0.001
Distance to open water (m)	759	48	80–1,710	855	76	100–2,815	0.888
Distance to forest opening (m)	468	65	30–2,615	541	56	0–1,910	0.179
Elevation (m)	2,366	16	2,243–2,694	2,341	14	2,186–2,640	0.279
Forest structure variables							
Basal area (m²/ha)	30.7	1.3	9.7–58.8	24.6	1.54	0.9–49.6	0.002
Percent canopy closure	52	2	27–86	57	2	30–108	0.613
Total tree density (stems/ha)	1,046.7	100.9	0–3,800	666.4	439.6	235–2,685	<0.001
Trees ≤12.4 cm dbh (stems/ha)	701.2	90.3	0–3,115	275.0	59.8	5–1,500	<0.001
Trees 12.5–30.2 cm (stems/ha)	252.8	20.5	0–675	301.9	29.1	0–1,080	0.330
Trees 30.3–45.5 cm (stems/ha)	61.6	6.0	0–205	71.2	6.7	0–190	0.545
Trees 45.6–61.0 cm (stems/ha)	19.1	2.4	0–75	13.1	2.0	0–70	0.052
Trees >61.0 cm (stems/ha)	12.0	1.5	0–40	6.3	1.4	0–45	<0.001
No. shrub species	4.5	0.5	0–17	3.0	0.5	0–13	0.003
No. individual shrubs	107.1	36.8	0–1,488	130.0	48.2	0–2,295	0.198
Snag density (snags/ha)	10.6	1.4	0–40	2.0	0.6	0–20	<0.001
Log density (logs/ha)	26.1	3.3	0–120	6.3	1.0	0–25	<0.001
Shannon index	0.28	0.06	0–1.32	0.09	0.03	0–1.11	0.017

[a] Mann-Whitney U-test.
[b] n = 53.

Table 2. Frequencies of categorical variable types for bat roost snags and random snags in the Peaks and Bar M areas of the Coconino National Forest, northern Arizona, 1993–95.

	Peaks				Bar M			
Variable	Roost (n = 54)	Random (n = 54)	χ^{2a}	P	Roost (n = 43)	Random (n = 58)	χ^{2a}	P
Grazed by cattle	9	28			43	58		
Not grazed[b]	45	24	16.70	<0.001	0	0		
Loose bark present	43	16			29	19		
Loose bark absent	11	37	27.69	<0.001	14	39	12.14	0.001
Harvest (within 5 yrs)	1	14			1	2		
Not harvested	53	39	15.58	<0.001	41	53	0.13	0.720
Dwarf mistletoe present	36	28			9	20		
Dwarf mistletoe absent	18	26	2.25	0.116	34	38	2.28	0.132
Slope position 1[c]	4	4			7	19		
Slope position 2	1	9			5	15		
Slope position 3	11	9			6	9		
Slope position 4	18	12			10	8		
Slope position 5	20	20	8.77	0.067	15	7	12.55	0.014

[a] Maximum-likelihood G-test.
[b] All Bar M sites were grazed by cattle within 2 years.
[c] Slope position 1 = bottom 20% of slope; slope position 5 = top 20% of slope.

between old and new roosts were 1,170 ± 445 m at Peaks and 688 ± 123 at Bar M.

Peaks Area

Roost snags at Peaks were of larger diameter and on steeper slopes than were random snags (Table 1). Roost snags were surrounded by forest with trees of greater basal areas and higher overall tree densities than random snags. Snag densities, log densities, and densities of trees in the ≤2.4 and >61.0 cm dbh classes were greater around roost snags than around random snags. Forests surrounding roost snags had more shrub species and greater tree diversity than forests around random snags. Roost snags were more likely to have loose bark and less likely to be found within active cattle grazing areas or recent timber harvests than were random snags (Table 2). There was a significant slope aspect direction for both roost snags (Raleigh test: mean angle = 212°, r = 0.46, P < 0.001) and random snags (mean angle = 211°, r = 0.85, P < 0.001), but these mean angles were not different (χ^2_3 = 0.24, P = 0.971).

The final logistic model for the Peaks area contained 6 variables (Table 3). Large-diameter snags with loose, exfoliating bark (bark peeling away from the snag, thus creating space between the bark and the snag), high surrounding basal areas, high surrounding snag and log densities, and snag heights shorter than random were most likely used as roosts by bats. This model accurately classified 86.8% of the random snags and 90.8% of the roosts. A Hosmer-

Lemeshow lack-of-fit test (χ^2_8 = 6.18, P = 0.627) indicated a good fit of the data to the logistic model.

Bar M Area

Roost snags at Bar M were larger in diameter, closer to water, and located at lower elevations than were random snags (Table 4). Like the Peaks roost snags, Bar M roost snags were surrounded by forests with greater basal areas and higher overall tree, snag, and log densities. Tree densities in the 12.5–30.2 and 30.3–45.5 cm dbh classes were higher around roost snags. Higher Shannon-Wiener (H′) indices indicated there was greater tree species diversity around roost snags than around random snags. Roost snags were located higher on slopes and were more likely to have loose bark (Table 2) than were random snags. Rayleigh tests indicated there were no significant mean directions in the slope aspect of either roosts (r = 0.87, P = 0.782, n = 43) or random (r = 0.21, P = 0.112, n = 57) snags.

Seven variables contributed to the Bar M logistic regression model (Table 3). Compared to random snags, snag roosts were closer to water and were large dbh snags with loose bark located in areas with higher snag and down log densities and greater tree diversity. Roost snags were found higher (slope position) and on steeper slopes (percent slope) than random snags. The model correctly classified 91.2% of the random snags and 83.7% of the roosts. The Hosmer-Le-

Table 3. Parameter coefficients and standard errors, Wald χ^2 scores, and P-values for the variables passing the enter ($P < 0.25$) and remove ($P > 0.05$) criteria in stepwise logistic regression models for the Peaks and Bar M study areas of the Coconino National Forest in northern Arizona, 1993–95. Variables common to both models are listed first.

Peaks model[a]					Bar M model[b]				
Variable	Coefficient	SE	Wald χ^2	P	Variable	Coefficient	SE	Wald χ^2	P
Constant	-10.264	2.551	16.233	<0.001	Constant	-11.428	2.834	16.326	<0.001
Dbh (cm)	0.086	0.027	10.176	0.006	Dbh (cm)	0.079	0.028	8.030	0.005
Loose bark[c]	3.343	0.915	13.364	<0.001	Loose bark[c]	2.576	0.786	10.750	0.001
Snags/ha	0.028	0.010	8.540	0.004	Snags/ha	0.068	0.023	8.625	0.003
Basal area (m²/ha)	0.022	0.074	8.999	0.003	Slope position	0.641	0.273	5.509	0.019
Logs/ha	0.028	0.010	8.783	0.004	Percent slope	0.184	0.086	4.630	0.031
Tree ht.	-0.130	0.524	6.144	0.013	Dist to water (km)	-4.123	1.390	8.800	0.003
					Shannon-Wiener (H')	5.852	1.654	12.549	0.001

[a] No. bat roosts (1s) = 53; no. random snags (0s) = 54. Overall log likelihood χ^2_6 = 88.44, $P < 0.001$. Hosmer-Lemeshow lack-of-fit χ^2_8 = 6.18, $P = 0.627$.

[b] Number of bat roosts (1s) = 43; no. of random snags (0s) = 57; Overall log likelihood χ^2_7 = 78.93, $P < 0.001$. Hosmer-Lemeshow lack-of-fit χ^2_8 = 4.68, $P = 0.792$.

[c] Presence (1) or absence (0) of loose bark on snag.

meshow statistic of 4.68 (df = 8, $P = 0.792$) indicated a good fit to the logistic model.

DISCUSSION

Most (74%) bats roosted under loose, exfoliating bark of large diameter ponderosa pine snags. Bats that did not roost under bark used vertical cracks like those typically caused by lightning strikes. Roosts often consisted of large sheets of bark that encompassed the entire circumference of the snag. Differential shading of these bark sheets by surrounding snags and trees could result in a variety of temperatures under the bark, but bats may seek optimum temperatures by moving around under these bark sheets during the day. Bats may choose large snags because they have thicker exfoliating bark than smaller snags (Meyers 1963), and the thicker bark provides more insulation. As an insulator, bark may serve an important thermoregulatory function for roosting bats, especially lactating females with young (Racey 1973, Kurta 1985).

Larger snags used by bats in this study may have been found in areas of higher snag density due to the local conditions that favored snag creation (i.e., beetle kill, disease, lightning, wildfire). Historically, timber harvest activities on the CNF left pockets of large trees, many of which died and formed snags that are typically much larger than the living trees that surround them. Mannan et al. (1980:789) referred to these as "remnant snags." Management activities on the CNF have removed most large-diameter trees (Cooper 1960, Covington and Moore 1994); hence, without management intervention, future snags will be much smaller than current snags.

Higher log densities around roost snags may result from tops breaking off large snags as they age (either the roost snag itself or surrounding snags), and from fire suppression policies that preserve downed wood from wildfire (Cline et al. 1980). Greater basal areas, higher tree densities, and increased tree diversity around roost snags appeared due to ponderosa pine regeneration (Peaks and Bar M) and Gambel oak growth (Bar M) around older snags. At Bar M, Gambel oaks were widespread as suppressed clonal shrubs under ponderosa pine tree canopies. When large trees die, they create large canopy openings, and Gambel oaks grow into thick stands around snags. These openings also encourage establishment of pine seedlings and recruitment of other trees and shrubs. These secondary growth dynamics are more pronounced around larger snags than

Table 4. Habitat characteristics of Bar M area ponderosa pine bat roost snags and random snags for both the snag itself and the forest characteristics surrounding the snag in northern Arizona during June–August 1994–95.

Variable	Bat roost snags (n = 43)			Random snags (n = 58)			P^a
	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	
Snag variables							
Dbh (cm)	66.0	1.8	45.7–91.4	57.4[b]	2.2	30.5–101.6	0.002
Snag height (m)	18.8	1.0	9.1–35.0	17.7	1.1	3.8–35.1	0.706
Percent slope	8	1	0–35	6	1	1–19	0.591
Distance to open water (m)	458	48	40–1,207	701	46	60–1,609	<0.001
Distance to forest opening (m)	223	22	0–604	335	41	0–1,408	0.222
Elevation (m)	2,099	12	2,011–2,335	2,142	13	1,951–2,365	0.023
Forest structure variables							
Basal area (m²/ha)	24.0	1.1	6.4–38.6	20.6	1.0	1.8–44.1	0.011
Percent canopy closure	48	2	25–68	53	3	20–155	0.169
Total tree density (stems/ha)	1,114.2[c]	112.3	315–3,855	819.5	64.0	40–2,410	0.026
Trees ≤12.4 cm dbh (stems/ha)	746.3[c]	109.4	130–3,555	509.6	55.1	15–2,020	0.090
Trees 12.5–30.2 cm (stems/ha)	270.9	14.6	110–525	226.3	15.6	0–495	0.039
Trees 30.3–45.5 cm (stems/ha)	81.0	5.4	25–145	63.9	5.2	5–190	0.016
Trees 45.6–61.0 cm (stems/ha)	11.2	1.5	0–35	12.4	1.6	0–50	0.906
Trees >61.0 cm (stems/ha)	7.7	1.3	0–45	7.2	1.3	0–50	0.436
No. shrub species	5.6	0.8	0–30	6.3	0.4	0–13	0.068
No. individual shrubs	478.1	74.5	0–1,812	437.1	45.4	0–1,639	0.698
Snag density (snags/ha)	6.5	1.0	0–20	1.0	0.4	0–15	<0.001
Log density (logs/ha)	11.3	1.8	0–45	4.0	0.9	0–40	<0.001
Shannon index	0.60	0.04	0–1.04	0.43	0.03	0–1.00	0.002

[a] Mann-Whitney U-test.
[b] n = 57.
[c] n = 42.

around smaller snags. Hence, although large roost snags (often surrounded by other large snags) were surrounded by thick, diverse stands of small trees and shrubs, these factors may be the result of forest management history, structure, and the dynamics of large snag creation rather than bat roost-selection criteria.

The relatively high occurrence of lactating female bats changing roosts was unexpected given the high energetic costs of moving young (Brigham and Fenton 1986, Lewis 1995). Bats may switch roosts to reduce parasite load (Fleming 1988), avoid disturbance or predation (Kunz 1982), acquaint young with possible future roost sites (O'Shea and Vaughn 1977), or respond to changing roost conditions (Lewis 1995). Brigham (1991) found that big brown bats roosting in tree cavities changed roosts more often than bats roosting in human-made structures and rock crevices. He hypothesized that because tree roosts were more common and less stable than rock crevices and buildings, bats were forced to use multiple tree roosts. He also suggested that tree-roosting bats may switch roosts in response to shifts in prey availability, thus minimizing commuting distance to new foraging areas and improving reproductive success. Vonhof and Barclay (1996) also found that tree-roosting bats in southern British Columbia switched roosts frequently.

By including multiple roosts in the sample (located when individual bats switch roosts), we risked introducing bias because individuals may select similar habitats for subsequent roosts. We chose to include the multiple roosts, however, because comparisons between roost snags from bats that moved with roost snags of bats that did not move were statistically indistinguishable, indicating that the bias was not serious. The increased sample size that resulted from including all roosts also allowed for more powerful statistical analyses.

We observed many of the snag roosts lose a considerable proportion of their bark, and suspect this ephemeral nature of loose bark on snags may force bats to move with changing conditions under the bark. As bark loosens from a snag, roost space that was warm and dry may let in rain and become drafty and cold. In 1 instance, a roost lost the section of bark that had sheltered a colony of Allen's lappet-browed females with young, forcing them to move to a nearby snag. Other studies on snag-roosting forest bats (Brigham 1991, Vonhof and Barclay

1996) also suggest that because bark roosts are transitory roost spaces, bats may require >1 snag during a reproductive cycle.

Due to interactions with other variables, 2 variables (snag height at the Peaks and percent slope at Bar M) not significant in univariate analyses were significant in multivariate models. Mean height of roost snags at Peaks was larger than mean random height of snags, yet the negative parameter coefficient indicated bats chose shorter snags. In a logistic model containing only a constant and the snag height, snag height coefficient for the Peaks was positive, suggesting that bats chose taller snags. However, the sign changed when dbh was included in the model, indicating an interaction between snag height and dbh. This result may reflect the fact that tops often break off older snags, and thus snag height is not a linear function of dbh. Percent slope in the Bar M model likewise interacted with slope position and only became significant when combined with slope position in a multivariate model.

We had expected slope aspect to be an important selection criterion for bats because of thermal characteristics associated with aspect. However, in neither area was mean slope aspect significantly different between roost snags and random snags. The slopes on which Peaks roosts and random snags were found had similar aspects because the study area was located on the southwest side of a mountain, and most slopes faced southwest. In contrast, the Bar M area was more broken, with numerous small canyons and gullies. Lack of a different mean slope aspect at Bar M indicates either that slope aspect was unimportant to bats or that there were other important variables that we did not measure. We did not measure aspect of the roost on the snag because many roosts had multiple entrances and exits, and we could not tell precisely where bats were roosting within the snags.

Mean snag densities around bat roosts at Peaks (10.6/ha) and Bar M (6.5/ha; see Tables 1, 4) were consistent with local recommendations of 5.2–6.5 snags/ha to maintain diverse populations of cavity-nesting birds in northern Arizona (Balda 1975, Cunningham et al. 1980). However, use of multiple snags by maternity colonies of bats and the ephemeral nature of bark on roost snags suggest bats may require higher snag densities than birds, particularly snags in early decompositional stages and with loose bark. Cavities excavated in snags by birds

may be available for many years, but bat roosts under loose bark may be a relatively short-lived resource. More research is needed to determine how long ponderosa pine snags in the Southwest remain in this exfoliating bark stage.

Within the same national forest and with the same species of bats, we developed 2 different logistic models containing characteristics of both snag and surrounding forest structure. In both study areas, roost snags were large diameter with exfoliating bark and were surrounded by higher snag densities than random snags. The 3 variables common to both models were apparently the most critical factors influencing snag use by reproducing forest bats on the CNF. Characteristics of the forests immediately surrounding the snags varied between the study sites, reflecting their different habitat types and management histories. Areas with different management histories than our study areas will likely have different distributions of required snag types; hence, applications of our models to other areas must account for these differences.

MANAGEMENT IMPLICATIONS

To manage snags for bat habitat, sufficient numbers of large trees should be retained and allowed to die in place, and all existing snags should be preserved. Snags can be lost through windthrow, wildfire, prescribed fire, or be felled because of safety concerns or for fuelwood. Of particular concern is fuelwood cutting of large snags. Although current regulations on the CNF prohibit cutting standing ponderosa pine snags >30.5 cm dbh, large snags with loose bark are still targeted by illegal fuelwood cutters because the wood is solid and dry.

Current CNF forest plan recommendations suggest 5 snags/ha (in ponderosa pine habitats), which may be insufficient to provide long-term availability of bat roost snags. The loose bark stage composes only a fraction of the snags available in the landscape and is a relatively brief stage in the lifespan of a snag (Thomas et al. 1979, Cline et al. 1980). Because large trees available for snag recruitment are now uncommon in most areas of the CNF, natural recruitment of suitable bat roost trees through time may be too slow to avoid periods when insufficient snags are available for reproducing bats. Competition among excessive numbers of smaller trees in some areas may slow tree growth and further delay recruitment of large snags. Thinning small trees may improve

growth rates of remaining trees and allow them to grow large enough to be recruited as snags sooner. In areas of the forest where few standing snags in the loose-bark phase exist, large trees could be killed to create snags, which would provide bat roost habitat in the near term and benefit cavity-nesting birds as well.

Exclusion of wildfire from the CNF has preserved some snags but also has removed an important mechanism of snag creation. Natural fire regimes removed smaller trees from the forest, promoted growth of larger trees, and created snags by killing trees (Cooper 1960, Covington and Moore 1994). Implementation of periodic prescribed fire to selected areas of the CNF could reinstate this process, but prescribed fire plans should include the preservation of existing snags in all stages.

The CNF should implement a long-term management plan to assure that sufficient numbers of large snags in the loose-bark stage are available to bats through time. This plan should include both research to determine how long ponderosa pine snags remain in the loose bark stage and distributional surveys of snag densities in the forest by snag stage. This information should be used to build recruitment models of snag stage that are forest specific. Additionally, research to determine how many existing snags shelter roosting bats would enable resource managers to model bat reproduction in the forest through time.

ACKNOWLEDGMENTS

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