WASHINGTON

Pacific
Ocean

Southern
Washington
Cascade
Range

OREGON

Oregon
Coast
Range

Oregon
Cascade
Range

Location of study sites within the three physiographic provinces.

Regional Patterns of Small Mammal Abundance and Community Composition in Oregon and Washington

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Authors

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Abstract

Pitfall traps were used by a team of investigators to study forest-floor small mammal communities in 144 different-aged Douglas-fir forest stands in three physiographic provinces in the Pacific Northwest: the Oregon Coast Range, Oregon Cascade Range, and Southern Washington Cascade Range. All three small mammal assemblages were numerically dominated by a few species. The Trowbridge's shrew was the most abundant species in all three provinces and accounted for 47 percent of 8661 small mammals captured. Most remaining captures were of only one or two other species: in the Coast Range, the western red-backed vole and Pacific shrew; in the Oregon Cascades, the western red-backed vole; and in the southern Washington Cascades, the southern red-backed vole and montane shrew. Other species each accounted for less than 6 percent of total captures in all three provinces. Ordination analysis of small mammal communities, both among and within provinces, revealed few ecologically interpretable patterns or differences among forest age-classes. Most variation was attributable to differences in species composition resulting from zoogeographic barriers. The shrew-mole and red tree vole were closely associated with old-growth forests in all provinces where they occurred. These species should be given high priority in the development of management strategies for small mammals in Pacific Northwest forests.

Introduction

The fate of old-growth Douglas-fir forests in the Pacific Northwest has become one of the most controversial resource management issues of this century (see Norse 1990, Norse and others 1986, Wilcove 1988). Research on the composition, structure, and function of these forests, however, has only recently been undertaken (see Franklin and others 1981, Gutierrez and Carey 1985, Meehan and others 1984, Raphael 1984, Raphael and Barrett 1984, Spies and others 1988).

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Before these studies, lists of small mammal species believed to be associated with old-growth forests were based primarily on natural history observations and speculation (for example, Franklin and others 1981, Lumen and Neitro 1980, Meslow and others 1981). The comprehensive program of research described in this volume was undertaken to provide quantitative information on wildlife habitat relationships in Douglas-fir forests, and to provide a scientific basis for the management of old-growth forests (Carey and Spies, this volume; Ruggiero and Carey 1984).

The primary objectives of the small mammal studies conducted in the Oregon Coast Range (Corn and Bury, this volume a), Oregon Cascade Range (Gilbert and Allwine, this volume a), and southern Washington Cascade Range (West, this volume) were to identify small mammal species that are associated with old-growth Douglas-fir forests within each province, and to investigate potential correlations between small mammal abundances and vegetative or structural features of unmanaged Douglas-fir forests. The purpose of this paper is to combine these three data sets and compare and contrast observed habitat association patterns among physiographic provinces to evaluate the extent to which observed patterns vary on a regional scale. Data from studies conducted in the Northern California province were not included because the ecological characteristics of stands occurring there *were* considered to be too different from those in Oregon and Washington for the data to be combined into a single data set (T. Spies and J. Franklin, pers. comm.).

By combining the data in a single analysis, results from each province can be compared quantitatively with those from other provinces. In addition, larger sample sizes resulting from the pooling of data increase the power of statistical analyses, especially for relatively rare species. Knowledge of regional variation in the habitat relationships of small mammal species associated with old-growth forests will enable wildlife managers to set priorities for management activities within different areas of the Pacific Northwest, and will provide additional insights into the habitat relationships of small mammals in unmanaged Douglas-fir forests. The specific objectives of this paper are to:

- Describe the forest-floor small mammal communities occurring in unmanaged Douglas-fir forests in three physiographic provinces in Oregon and Washington; and

- Compare patterns of community composition, species abundances, and habitat associations among provinces.

Methods

Study Areas

Forest-floor small mammals were studied in 144 stands in Oregon and Washington in 1984 and 1985 by a team of investigators. Study sites were located in three physiographic provinces (Franklin and Dymess 1973): 45 in the Oregon Coast Range, 54 in the Oregon Cascade Range, and 45 in the southern Washington Cascade Range. Data were collected in all stands in both years, with the exception of the Oregon Cascades province in which only 15 stands in the central Cascade Range were sampled in 1985.

Homogeneous forest stands of at least 20 ha with Douglas-fir as the dominant tree species were selected for study. None of the sites had been logged; all had resulted from natural regeneration after catastrophic wildfires. All stands are within the Western Hemlock Zone and lower elevations of the Pacific Silver Fir Zone (Franklin and Dyrness 1973).

Stands were classified into three broad age-classes: young (35-79 yrs), mature (80-195 yrs), and old-growth (200-730 yrs). Ages were based on growth-ring counts, either by increment coring or examination of cut stumps in nearby stands (Spies and others 1988). Old-growth stands typically contained high proportions of Douglas-fir and western hemlock and, in wet sites, western redcedar. Mature and *young* stands were dominated by Douglas-fir. In all age-classes, other species such as red alder, vine maple, bigleaf maple, Pacific silver fir, and western hemlock occurred in lesser amounts. See Spies and Franklin (this volume) and Spies (this volume) for more detailed descriptions of the vegetative and structural characteristics of the study stands.

Within each province, stands of comparable moisture condition were placed into an age gradient as a means of assessing variation in small mammal abundances resulting primarily from differences in stand age-class. The age gradient consisted of 127 stands, including 43 from the Coast Range, 48 from the Oregon Cascades, and 36 from the southern Washington Cascades. Although the range of ages sampled was similar among provinces, old-growth stands in the southern Washington Cascades contained nine stands that were 25 to 205 years older than the oldest stands sampled in either the Coast Range or the Oregon Cascades, Ranges for the age-classes in each province are: Oregon Coast Range, young, 40 to 75; mature, 80 to 120; and old-growth, 200 to 525 years old; Oregon Cascades, young, 35 to 79; mature, 84 to 180; and old-growth, 200 to 500 years old; and southern Washington Cascades, young, 55 to 75; mature, 80 to 195; and old-growth, 210 to 730 years old.

Small Mammal Sampling

Within each province, forest-floor small mammals were sampled with pitfall traps, snap-traps, and tracking stations (see Carey and Spies, this volume). Only pitfall trapping, however, was used in all three provinces in both years. Other techniques were used either in only one or two provinces, or were not equally applied in both years. To compare results among physiographic provinces, we therefore used only data derived from pitfall trapping.

Thirty-six pitfall traps were installed in each stand in a 6 x 6 square array with traps spaced 15 m apart. New pitfall grids were established in each stand in the southern Washington Cascades during the second year of the study; in the Coast Range and Oregon Cascades, grids were retrapped in the second year. Comparisons of results between new grids and a subset of grids retrapped the second year showed no differences in small mammal species composition or abundances (Gilbert and Allwine, this volume a). All stands were sampled for about 30 days each fall, and checked about once per week. All specimens were collected for identification and all salvageable specimens were preserved.

Pitfall traps were opened after the onset of fall rains in 1984 and again in 1985 in the southern Washington Cascades and in the Coast Range; traps were opened a month earlier in the Oregon Cascades. Trapping dates for each province were: Coast Range, 1 October-7 November 1984 and 30 September-1 November 1985; Oregon Cascades, 28 August-6 October 1984 and 29 August-5 October 1985; and southern Washington Cascades, 30 September-5 November 1984 and 27 September-3 November 1985.

Data Analyses

For all analyses, we included only data for species that had >20 total captures or that occurred in >l0 percent of the stands sampled. Species not meeting these criteria were considered to be inadequately sampled with our techniques. Although we captured 77 Pacific jumping mice, 58 of these captures were from the Oregon Cascades where trapping probably occurred before the onset of hibernation for this species (Dalquest 1948). Because of potential bias resulting from regional differences in the influence of hibernation on our results, and the likelihood of jumping mice escaping from pitfall traps (Bury and Corn 1987), this species was excluded from all analyses. The extent to which differences in sampling dates may have influenced results for other species is unknown.

Three species, the red tree vole, Pacific shrew, and western red-backed vole, occur in both of the Oregon provinces, but not in Washington. Conversely, the southern red-backed vole and forest deer mouse occur only in the southern Washington Cascades. One species, the montane shrew, occurs throughout the southern Washington Cascades but is found only in the northernmost portion of the Oregon Cascades (Carey and Spies, this volume; Ingles 1965). Stand sample sizes were adjusted for these species.

Community analyses-Although yearly variations in population numbers may influence results in studies of wildlife habitat relationships, 2 years of data is not sufficient to adequately evaluate temporal variation in small mammal abundances. Furthermore, without corresponding demographic information, causative factors for observed variation cannot be determined (Van Home 1983). For these reasons, we pooled data from both years, and calculated abundance indices for each stand as mean captures for both years per 100 trap-nights. We examined community patterns of small mammal abundance with detrended correspondence analysis (DCA) using DECORANA (Hill 1979a). We interpreted ordination axes by correlating ordination scores for the small mammal communities with major physiographic and vegetative gradients by using Spearman rank correlations (Norusis 1988a). The vegetative gradients we included as variables represented multivariate gradients derived by Spies and Franklin (this volume) in their analyses of the vegetative characteristics of the study stands. These variables represented gradients of stand development (primarily stand age and abundance of western hemlocks), coarse woody debris, stand temperature, and stand moisture.

We conducted ordination analyses at two scales: region-wide analyses that included stands of all age- and moisture-classes from all three provinces (144 stands), and province-specific ordinations conducted separately for each province (Coast Range, 45; Oregon Cascades, 54; and southern Washington Cascades, 45 stands). We conducted region-wide ordinations both on the 15 species that were considered to be adequately sampled with our techniques, and on data from only the subset of nine species that occur in all areas studied. The first approach identifies regional community patterns that include variation resulting from differences in species composition, and the second approach examines differences in community composition and structure independent of the confounding effects of differences in species' distributions. We also conducted province-specific ordinations to examine community-scale variation among age-classes within each province. This approach enabled us to evaluate the effects of stand age on small mammal community patterns for each province, and provided a means of comparing these patterns among provinces that is not affected by differences in potential community composition or by deleting a substantial portion of the community.

Species analyses-To investigate the extent to which patterns of association due to differences in stand age vary regionally, we conducted all species analyses using data only from stands within each age gradient (127 stands). We used two-way ANOVA (Norusis 1988a) on abundance data for species with >100 captures, and log-linear analysis (Kennedy 1983) of presence-or-absence data for species with <100 captures.

Because of the limited number of sites that could be studied with available resources, study areas were preferentially selected to sample the full range of variation occurring in each stratum (Carey and Spies, this volume). Because study sites were not selected randomly, rigorous statistical inference based on hypothesis testing is not possible with our data sets. We used statistical tests only as a means of examining patterns of variation in the data. However, because we intentionally sampled the full range of variation within each stratum, the variances in our data would be expected to exceed those resulting from random sampling. Consequently, observed differences are less likely to result from chance than if our sites had been selected randomly (Ruggiero and others, this volume).

To identify regional patterns in the habitat relationships of small mammals occurring along environmental gradients, we examined the relationships between individual species' abundances and major physiographic and vegetative gradients using Spearman rank correlations (Norusis 1988a). We used only abundance data for species with >l00 captures in these analyses.

Results

Altogether, 8661 small mammals of 29 species were captured, including 6 shrews, 3 moles, 4 squirrels, 1 gopher, 14 mice and voles, and 1 weasel. Only 15 species had >20 total captures or occurred in >10 percent of stands studied: the marsh, montane, Pacific, Trowbridge's, and vagrant shrews; the shrew-mole and coast mole; the deer mouse and forest deer mouse; the red tree, southern and western red-backed, and creeping voles; the northern flying squirrel; and the ermine (table 1).

The structure and composition of the small mammal communities sampled varied somewhat among provinces (fig. 1). The Trowbridge's shrew was captured in every stand sampled, and it was the most abundant small mammal in all three provinces. This species accounted for 47 percent of total captures for all provinces combined. In all three provinces, the Trowbridge's shrew and one or two other species accounted for most captures. In the Coast Range, the Trowbridge's shrew represented 56 percent of total captures; the western red-backed vole, 21 percent; and the Pacific shrew, 11 percent. All other species contributed less than 4 percent each to total captures. In the Oregon Cascades, 69 percent of total captures were of the Trowbridge's shrew. The western red-backed vole accounted for 13 percent, and all other species each represented less than 5 percent of total captures. In the southern Washington Cascades, Trowbridge's shrews were relatively less important, representing only 36 percent of total captures. Two other species, the montane shrew and southern red-backed vole, were captured in relatively high numbers, with each representing about 23 percent of total captures. No other species accounted for more than 6 percent of captures.

Community relationships-Ordination analysis of the combined abundance data from all provinces for 15 small mammal species revealed community patterns that reflect differences in the species composition and diversity of small mammals occurring in each province (fig. 2). The Coast Range cluster forms a subset of the Oregon Cascades cluster, indicating less variability in the composition and structure of small mammal communities in the Coast Range stands compared to the Oregon Cascades stands. The Coast Range and the Oregon Cascades are most similar in small mammal species composition (fig. l), and their ordination clusters separated out almost completely from the southern Washington Cascades cluster.

The first ordination axis (X axis) was significantly correlated to gradients of increasing moisture ($P = 0.000$), elevation ($P = 0.000$), and stand age ($P = 0.010$), and decreasing temperature ($P = 0.000$). The second axis (Y axis) was more difficult to interpret, as would be expected based on the lack of separation of clusters in this direction. This axis was correlated primarily with decreasing moisture $(P = 0.009)$ and increasing temperature $(P = 0.034)$.

Ordination results using only the nine species that occur in all three provinces (table 1) revealed a high degree of overlap in the structure and composition of the communities occurring within each province (fig. 3). Community patterns observed in figure 2, however, are still evident. The Coast Range cluster is again much smaller than the Oregon Cascades cluster and constitutes a subset of that cluster, and the southern Washington Cascades cluster still contains points unique to that cluster. Environmental gradients represented by the ordination axes are virtually identical to those reported for figure 2.

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Table 1—Mean, standard error, and percentage occurrence of small mammal species with >20 total captures in pitfall traps by province and age-class (number of stands sampled is in parentheses)

Species		Oregon Coast Range			Oregon Cascade Range			Southern Washington Cascade Range		
		Old growth (25)	Mature (10)	Young (8)	Old growth (22)	Mature (17)	Young (9)	Old Growth (18)	Mature (9)	Young (9)
Marsh shrew	$\bar{x}$[a]	0.016	0.022	0.006	0.012	0.020	0.006	0.018	0.016	0.041
	SE[b]	0.004	0.012	0.006	0.009	0.009	0.006	0.008	0.008	0.009
	%[c]	36	30	13	14	24	11	28	33	78
Montane shrew	$\bar{x}$	—[d]	—	—	0.093[e]	0.463	0.556	0.912	1.079	0.965
	SE	—	—	—	0.093	0.161	0.334	0.115	0.141	0.233
	%	—	—	—	33	100	100	100	100	100
Pacific shrew	$\bar{x}$	0.256	0.599	0.256	0.131[e]	0.094	0.077	—	—	—
	SE	0.033	0.158	0.070	0.046	0.027	0.043	—	—	—
	%	96	100	100	53	57	50	—	—	—
Trowbridge's shrew	$\bar{x}$	1.677	1.905	1.360	1.322	1.101	1.422	1.374	1.559	1.439
	SE	0.111	0.221	0.086	0.134	0.168	0.324	0.112	0.217	0.257
	%	100	100	100	100	100	100	100	100	100
Vagrant shrew	$\bar{x}$	0.009	0.052	0.005	0.010	0.020	0.030	0.046	0.061	0.082
	SE	0.004	0.029	0.005	0.006	0.009	0.015	0.026	0.035	0.065
	%	20	40	13	14	29	33	33	44	44
Shrew-mole	$\bar{x}$	0.101	0.080	0.051	0.068	0.013	0.025	0.151	0.112	0.072
	SE	0.025	0.030	0.019	0.020	0.007	0.013	0.038	0.045	0.035
	%	68	70	63	45	18	33	72	56	56
Coast mole	$\bar{x}$	0.061	0.039	0.044	0.022	0.056	0.019	0.013	0.020	0.021
	SE	0.013	0.012	0.022	0.008	0.015	0.013	0.006	0.011	0.016
	%	64	60	38	32	53	22	22	33	22
Northern flying squirrel	$\bar{x}$	0.032	0.018	0.017	0.017	0.011	0.021	0.036	0.026	0.015
	SE	0.013	0.010	0.012	0.010	0.011	0.014	0.013	0.014	0.011
	%	32	30	25	14	6	22	39	33	22
Deer mouse	$\bar{x}$	0.144	0.054	0.135	0.029	0.009	0.049	0.235	0.112	0.077
	SE	0.020	0.017	0.085	0.012	0.007	0.039	0.037	0.036	0.041
	%	96	60	75	27	12	22	83	78	33
Forest deer mouse	$\bar{x}$	—	—	—	—	—	—	0.308	0.251	0.082
	SE	—	—	—	—	—	—	0.056	0.059	0.040
	%	—	—	—	—	—	—	94	100	56
Red tree vole	$\bar{x}$	0.020	0.000	0.006	0.014	0.003	0.000	—	—	—
	SE	0.007	0.000	0.006	0.007	0.003	0.000	—	—	—
	%	32	0	13	18	6	0	—	—	—
Western red-backed vole	$\bar{x}$	0.607	0.830	0.562	0.313	0.221	0.285	—	—	—
	SE	0.072	0.150	0.118	0.069	0.055	0.123	—	—	—
	%	100	100	88	82	71	78	—	—	—
Southern red-backed vole	$\bar{x}$	—	—	—	—	—	—	1.166	0.845	0.529
	SE	—	—	—	—	—	—	0.205	0.162	0.114
	%	—	—	—	—	—	—	100	100	100
Creeping vole	$\bar{x}$	0.005	0.018	0.000	0.004	0.008	0.000	0.015	0.031	0.062
	SE	0.003	0.010	0.000	0.004	0.006	0.000	0.005	0.022	0.051
	%	12	30	0	5	12	0	33	22	33
Ermine	$\bar{x}$	0.007	0.000	0.011	0.000	0.012	0.000	0.020	0.021	0.005
	SE	0.003	0.000	0.011	0.000	0.008	0.000	0.008	0.011	0.005
	%	16	0	13	0	12	0	33	33	11

[a] Mean number per 100 trap-nights.
[b] Standard error of mean.
[c] Percentage of stands sampled in which species was found.
[d] Does not occur in this geographic area.
[e] Does not occur in all subprovinces in the Oregon Cascades. Number of stands sampled within the geographic range of montane shrews is 3 in old-growth, 3 in mature, and 3 in young stands; and for Pacific shrews is 19 in old-growth, 14 in mature, and 6 in young stands.

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Figure 2—Ordination analysis of mean abundances of small mammals among provinces using data from all 15 species. All ordination points for each province are contained within the lines drawn; for clarity, individual points were omitted.
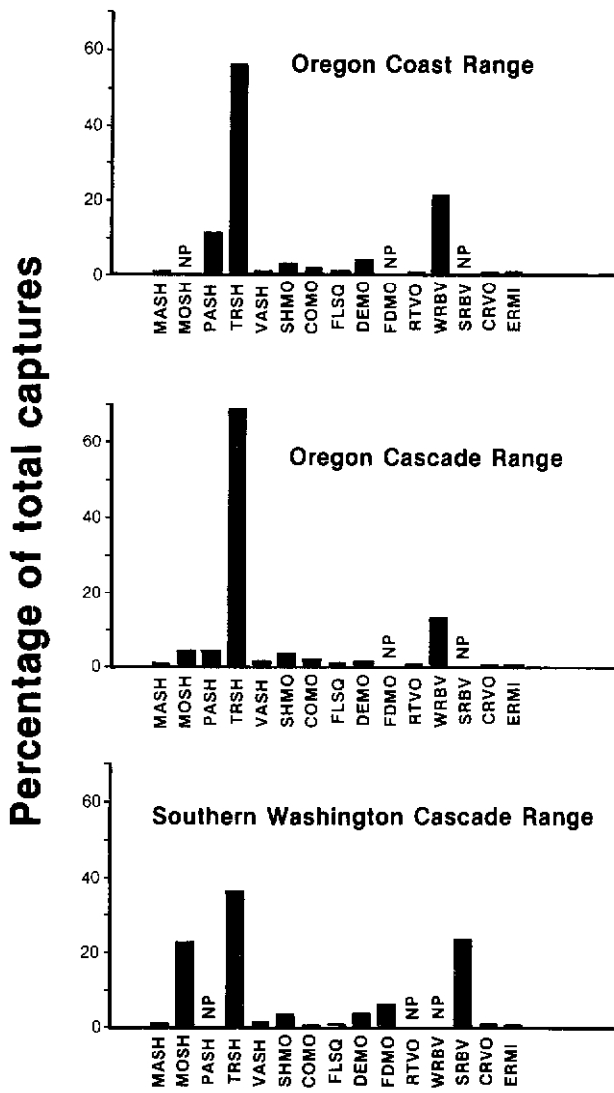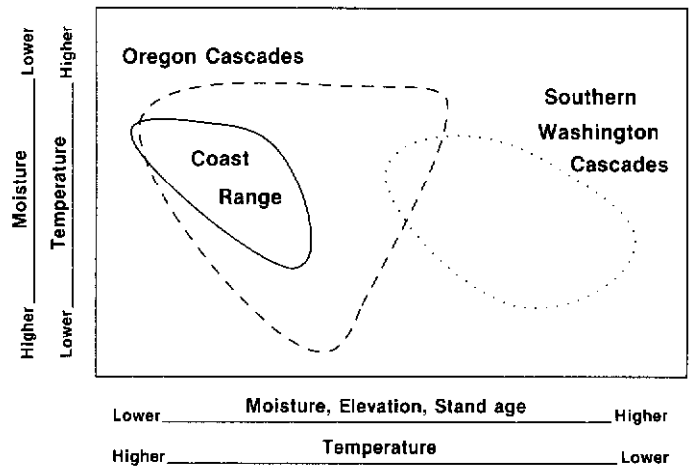
Figure 1—Histograms showing the percentage contribution of each species to total captures within each province. MASH, marsh shrew; MOSH, montane shrew; PASH, Pacific shrew; TRSH, Trowbridge's shrew; VASH, vagrant shrew; SHMO, shrew-mole; COMO, coast mole; FLSQ, northern flying squirrel; DEMO, deer mouse; FDMO, forest deer mouse; RTVO, red tree vole; WRBV, western red-backed vole; SRBV, southern red-backed vole; CRVO, creeping vole; ERMI, ermine; and NP, the species is not present in that province.
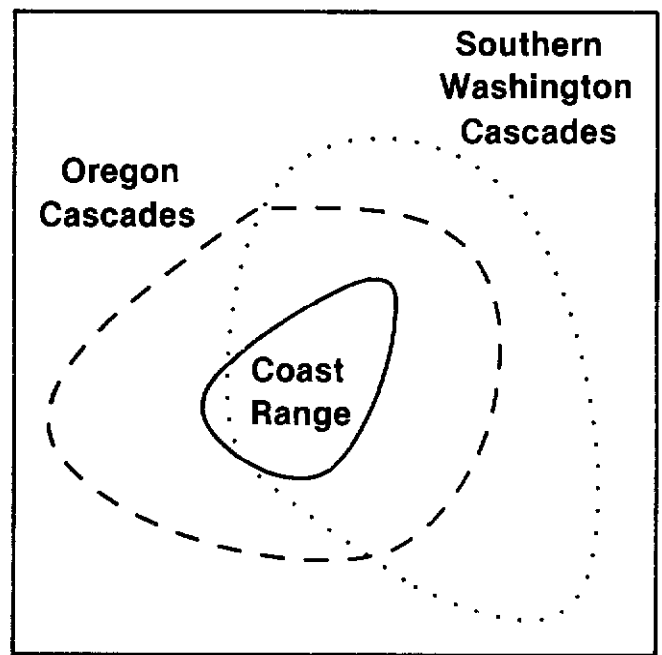

Figure 3—Ordination analysis of mean abundances of small mammals among provinces using only data from the nine species that occur in all three provinces. All ordination points for each province are contained within the lines drawn; for clarity, individual points were omitted. Environmental gradients associated with the X and Y axes are the same as for figure 2.

Coast Range

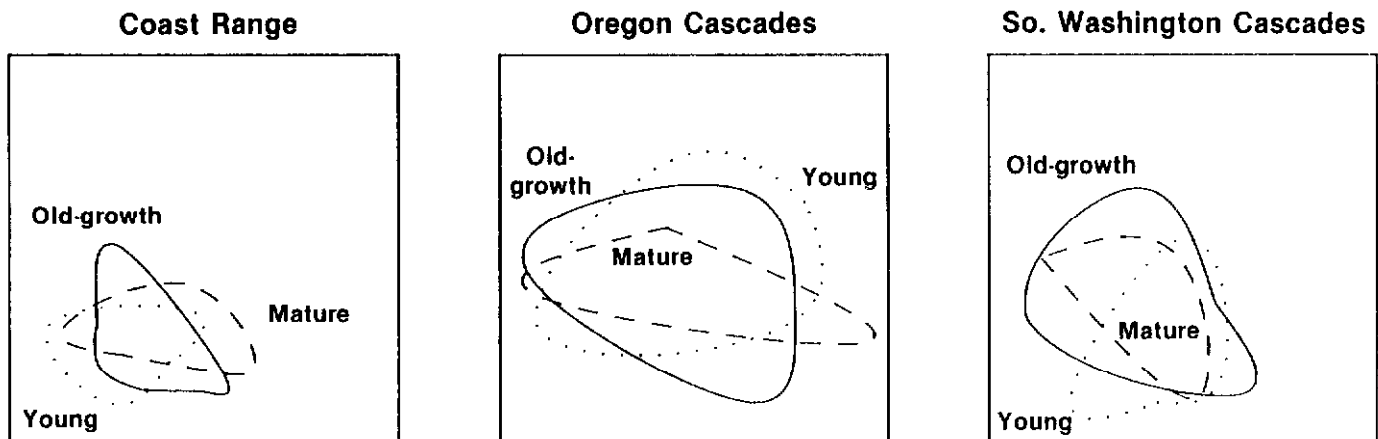## Oregon Cascades

So. Washington Cascades

Figure 4—Ordination analysis of mean abundances for each province clustered by age-class. Scales used for both ordination axes are the same for each province. The number of species included in each analysis is as follows: Oregon Coast Range, 12; Oregon Cascades, 13; and southern Washington Cascades, 12. All ordination points for each age-class are contained within the lines drawn; for clarity, individual points were omitted.

Results of province-specific ordinations showed little variation among age-classes for any province (fig. 4). No distinct clusters resulted from these analyses, which indicates that the structure and composition of the forest-floor small mammal communities we studied is largely independent of stand age. As would be expected from these results, none of the ordination axes were correlated with stand age. Attempts to correlate ordination axes with major environmental gradients revealed no interpretable patterns in community structure or composition within provinces.

Species relationships—Two-way ANOVA (table 2) and log-linear analysis (table 3) revealed strong stand age-effects for only two species: the shrew-mole ($P = 0.070$) and red tree vole ($P = 0.067$). Both species reached highest abundances or occurred most frequently in old-growth stands (table 1). The shrew-mole showed a strong province-effect ($P = 0.005$), but the effect appeared to be largely due to varying abundance values for young and mature stands (table 1). For the red tree vole, no province-effect was found ($P = 0.191$), indicating that patterns of occurrence were consistent between provinces. Although a very strong age-effect was also found for the deer mouse ($P = 0.001$), a strong interaction-effect between stand age and province ($P = 0.058$) complicates the interpretation of these results. Furthermore, the deer mouse occupies virtually all available habitats in the Pacific Northwest (Dalquest 1948; Ingles 1965; West, this volume; and others); it is not primarily a forest-dwelling species. As such, it should not be considered a species of concern to forest managers. The strong province-effects found for most species indicate that patterns of abundance are extremely variable among the provinces studied.

Table 2—Results of two-way ANOVA on abundance data for stand age vs. province (analyses were conducted only on data from stands within the age gradient for species that occurred in more than one province and had >100 total captures)

| Species | Source of variation | | |
	Stand age	Province	Interaction
Montane shrew	0.268[a]	0.001	0.468
Trowbridge's shrew	0.835	0.022	0.301
Pacific shrew	0.143	0.000	0.130
Shrew-mole	0.070	0.005	0.830
Deer mouse	0.001	0.000	0.058
Western red-backed vole	0.756	0.000	0.288

[a] P value.

Table 3—Results of log-linear analysis on presence-or-absence data for stand age vs. province (analyses were conducted only on data from stands within the age gradient for species that occurred in more than one province and had <100 total captures)

| Species | Source of variation | | |
	Stand age[a]	Province	Interaction
Marsh shrew	0.691	0.047	0.117
Vagrant shrew	0.238	0.230	0.811
Coast mole	0.213	0.013	0.798
Northern flying squirrel	0.849	0.052	0.777
Red tree vole	0.067	0.191	0.652
Creeping vole	0.595	0.018	0.575
Ermine	0.691	0.015	0.367

[a] P values for stand age-effect are component chi-squares after province-effects have been removed from the analysis.

Table 4-Significant Spearman rank correlations *(P ≤ 0.1)* between small mammal abundances and major physiographic and vegetative gradients (only species that occurred in more than one province and had >100 captures were included)

Species	Stand age	Elevation	Aspect	Slope	Vegetative gradients[a]			
					STDV	CWDB	TEMP	MOE
Montane shrew				+ 0.094[b]			- 0.000	
Trowbridge's shrew		- 0.017						
Pacific shrew		- 0.000					+ 0.000	
Shrew-mole	+ 0.002			*- 0.067*	*+ 0.007*	+ 0.015		+ 0.001
Deer mouse	*+ 0.030*	- 0.001			+ 0.000			
Western red-backed vole		- 0.021						- 0.002

[a] STDV represents a stand-development gradient; CWDB, a coarse woody debris gradient; TEMP, a temperature gradient; and MOIS, a moisture gradient.
[b] *P* value.

Correlation analyses for the six most abundant species are shown in table 4. These analyses support the results of ANOVA for the shrew-mole and deer mouse; abundances for both species were significantly correlated with increasing stand age. The shrew-mole was also associated with old, moist, relatively flat stands with large amounts of coarse woody debris.

Discussion

The small mammal assemblages described here represent only subsets of the total small mammal communities in each stand. **As with any one technique for sampling an entire** vertebrate community, pitfall trapping is more effective at sampling certain species than others (Bury and Corn 1987, Williams and Braun 1983). Consequently, our results apply only to **the** subset of species that are well-sampled with pitfall traps; extrapolation of our results for species not included here is unwarranted.

Community relationships-Variation in the structure and composition of small mammal communities in unmanaged, closed-canopy, Douglas-fir forests is influenced more by geography and climate than by stand age. Ecologically interpretable patterns were detected only in the region-wide analyses (see figs. 2-4). Although differences between the Southern Washington Cascades province and the Oregon provinces largely disappeared when only the nine species common to all three provinces were included (figs. 2,3), several important patterns remain. In both analyses, small mammal communities were more variable in the Oregon Cascades than in the Coast Range; the Coast Range communities represent a subset of those occurring in the Oregon Cascades. Also, a subset of the stands in the Southern Washington Cascades province separate out 'from both of the Oregon provinces along the first ordination axis.

The first ordination axis is correlated to many of the environmental and physiographic features that distinguish the Southern Washington Cascades province from the Oregon provinces: older stands, higher elevations, and cooler, wetter forest environments (Franklin and Dymess 1973; Spies and Franklin, this volume). The second axis, which separates the Coast Range stands from a portion of the Oregon Cascades stands, represents a gradient of increasingly warmer and drier conditions. Thus, although the Oregon Cascades and Coast Range provinces have very similar small mammal species composition (fig. l), only the warmest and driest stands in the Oregon Cascades contain mammal communities comparable to those occurring in the Coast Range. In terms of both environmental conditions (T. Spies, unpubl. data; Spies and Franklin, this volume) and the composition of small mammal communities, the Coast Range stands are most similar to the southernmost stands in the Oregon Cascades. Additionally, the oldest and wettest stands in the southern Washington Cascades contain small mammal communities **unlike any in the Oregon provinces.**

In contrast, we could detect little interpretable variation in community composition and structure among age-classes within each province (fig. 4). This finding agrees with the province-specific ordinations of understory floristics conducted by Spies and Franklin (this volume) and with the province-specific small mammal studies reported elsewhere in this volume by Corn and Bury, Gilbert and Allwine, and West. Within these physiographic provinces, unmanaged, closed-canopy Douglas-fir forests apparently support small mammal communities of similar composition and structure, regardless of stand age. Our results agree with the conclusion of Corn and Bury (this volume a) that different age-classes of unmanaged, closed-canopy forest appear to represent a single habitat type for most species. Although the communities as a whole are very similar among age-classes, several individual mammal species do exhibit a significant association with stand age in unmanaged Douglas-fir forests.

Species relationships-Only two forest-dwelling species, the shrew-mole and the red tree vole, were closely associated with older forests (tables 3,4). Abundance values for the shrew-mole and frequencies of occurrence for the red tree vole were highest in old growth in each of the provinces in which they occur (table 1).

The results of several other studies using similar sampling designs provide support for these results. Raphael (1984) reported a significant positive association with stand age for the shrew-mole in Douglas-fir forests in northern California, although results were based on only 1 year of data. A later report, based on 3 years of data (Raphael 1988c), showed that shrew-moles reached highest abundances in stands older than 50 years and were very low in abundance in clearcuts or in brush/sapling stands (0-20 yrs). In the Oregon Coast Range, Corn and Bury (this volume a) found shrew-moles to be 2.0 and 1.3 times more abundant in old-growth than in young and mature stands, respectively.

Other studies in Oregon and Washington reported here and elsewhere, however, have revealed no clear pattern of association between shrew-mole abundances and stand age. The shrew-mole was reported to be weakly associated with old-growth forests in the Oregon Cascades (Gilbert and Allwine, this volume a), or to show no age-effect at all (Corn and others 1988). Several studies in the southern Washington Cascades have found little evidence that shrew-moles are associated with stand age (Corn and others 1988; West, this volume). Results reported by Corn and others (1988), however, are based on only 1 year of data collected in 12 stands, and West (this volume) reported the combined results of pitfall trapping and snap-trapping as a means of evaluating responses of the broadest possible assemblage of small mammals. As mentioned previously, however, these techniques are not equally effective at sampling insectivores. Meaningful patterns in the data for this species may have been obscured by the addition of snap-trap results. Based only on pitfall data, results from the southern Washington Cascades also showed a trend of increasing abundance of shrew-moles with stand age (table 1). Consequently, increased sample sizes resulting from the pooling of data revealed a strong pattern of association that was not clearly evident at the province scale.

Shrew-mole abundances were also highly correlated with increasing stand age, stand development, stand moisture, amounts of coarse woody debris, and flatter slopes (table 4). As with any series of statistical tests, these results should be viewed with some caution. With 48 separate correlation analyses, we would expect five (10 percent) to be significant by chance alone at $P \leq 0.1$. Fifteen (31 percent) of the tests were significant, however, and all but two were significant at $P \leq 0.05$, indicating that most of these correlations reflect actual patterns of association.

Terry (1974, 1981) described preferred shrew-mole habitat in west-central Washington to consist of closed forests containing few herbs or shrubs to interfere with its burrowing activities, and a high organic matter content in the soil. She also reported that shrew-moles were significantly correlated with the cover of dead wood.

Tevis (1956) described shrew-moles as primarily inhabitants of unmanaged forests; he rarely found them in cutover areas. Results from other studies provide support for this assertion. In west-central Oregon, Hooven and Black (1976) found shrew-moles to be most abundant in unmanaged forest. Shrew-moles were less abundant in an area that had been cut and not burned, leaving coarse slash on the site, and were not present at all in an area that had been cut and broadcast-burned, leaving only fine litter. Dalquest and Orcutt (1942) reported shrew-moles to be very scarce in logged areas in western Washington. Corn and Bury (this volume a) sampled three clearcuts and adjacent old-growth stands in the Coast Range, but captured shrew-moles only in the old-growth stands. West (this volume) captured only two shrew-moles in eight clearcuts sampled in southern Washington.

These results indicate that shrew-moles are closely associated with moist old-growth forests containing relatively deep soils and many logs. However, shrew-moles appear to be responding primarily to microhabitats that occur most frequently in old-growth forests, since they are found in relatively high numbers in younger forests with appropriate forest-floor conditions (table 1). Catastrophic wildfires or clearcut logging practices that include removing most of the small and large woody debris, however, would be expected to eliminate shrew-moles from that site until canopy closure is reestablished and forest-floor conditions again become suitable.

Corn and Bury (this volume a) reported the red tree vole to be present significantly more often in old-growth forests than in either mature or young forests. Although they collected relatively few data, Gilbert and Allwine (this volume a) reported capturing red tree voles only in mature and old-growth forests in the Oregon Cascades. Similar studies conducted by other workers in the Oregon Cascades (Corn and Bury 1986, Corn and others 1988) indicated that red tree voles were associated with old-growth forests, but their data were insufficient to generate statistically significant results.

Our results (table 3) indicate that red tree voles are closely associated with old-growth forests in both the Coast and Cascade Ranges in Oregon. This species showed a significant age-effect, with nonsignificant province- or interaction-effects, indicating that patterns of variation were the same in both provinces. Although this species has been reported to nest in second-growth stands in the Coast Range (Maser 1966), recent work based on nest surveys in the Coast Range (Gillesberg and Carey, this volume) and in northern California (Meiselman and Doyle, in press) provide support for a close association with old-growth forests. Both studies also indicated a strong preference for very large (>l00 cm in d.b.h.) Douglas-fir trees for nesting and foraging. Bailey (1936) speculated that because red tree voles move about the forest largely within the canopy, they would be expected to occur only in areas of extensive, or recently isolated, forest.

Although the data are minimal, existing information indicates that red tree voles are largely restricted to old-growth forests; younger forests apparently do not provide suitable habitat for this species.

Management Implications

The similarity of species composition and structure of the small mammal communities in the Coast Range and Oregon Cascades provinces (figs. l-3) suggest that management strategies intended to provide for the habitat needs of small mammals in these provinces need not be designed specifically for either province. If management activities are conducted on a province, rather than a regional scale, stands in the southern Oregon Cascades should be considered to be more closely allied with stands in the Coast Range, rather than those in the central and northern Oregon Cascades. Very old (>500 yr) and wet stands in the southern Washington Cascades contain distinct small mammal communities that may require unique management approaches.

Shrew-moles are closely associated with moist, relatively flat, old-growth stands, Silvicultural prescriptions that remove the forest canopy, disturb the upper soil layers, and remove large amounts of coarse woody debris would be expected to eliminate this species from the site. Extensive clearcutting that creates large expanses of unsuitable habitat could result in local population extinctions. Shrew-moles could probably be maintained in managed landscapes, however, if old-growth areas are preserved as survival refugia to enable the species to recolonize younger forests when suitable microhabitats are reestablished.

Although relatively little is known about their specific habitat requirements, red tree voles apparently require old-growth stands containing large Douglas-fir trees for nesting and foraging. For this reason, and because they use the forest canopy as travel routes (but see Corn and Bury 1986), extensive loss or fragmentation of old-growth forests could eliminate this species from forested landscapes.

Forest Age Associations of Bats in the Southern Washington Cascade and Oregon Coast Ranges[1]

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Abstract

We studied the use by bats of old-growth, mature, and young Douglas-fir stands in the southern Washington Cascade and Oregon Coast Ranges. Bat activity was measured with ultrasonic detectors. In Washington, the *Myotis* species were detected 2.7 to 5.7 times more frequently in old-growth than in younger stands. In Oregon, the *Myotis* species and the silver-haired bat were detected 2.5 to 9.8 times more frequently in old growth. Feeding rates were extremely low in the forest stands, and most bat activity was confined to a brief peak during the first 15 minutes of the evening, which suggests that bats used old-growth stands for roosting. Vegetation features, such as the abundance of damaged or diseased trees and snags, appeared to be important to bat populations, but correlations of bat activity with these features were weak. No reproductive females were captured at sites >300 m in elevation on the western slope of the Washington Cascades, but they were common to the east and south. Old-growth forests appear to be important habitats for bats in the Cascade and Coast Ranges, but management priority should be given to the latter region.

Introduction

The area west of the crest of the Cascade Range and extending from mid-Washington to southern Oregon supports 12 species of insectivorous bats (Barbour and Davis 1969, Thomas 1988). If biological importance is measured by taxonomic diversity, then the Chiroptera rank second only to the Rodentia in this region. Yet little is known about how bat species use the range of age and composition of forest patches in the Pacific Northwest. Because timber harvest and stand-management practices are rapidly restructuring the landscape, such knowledge is of increasing importance. Without it, no predictions can be made of the effect of vegetation changes on bat populations, and no management decisions can be reached to alleviate any negative effects.

In this paper, we describe how bat activity varied across a range of age- and moisture-classes of Douglas-fir forests in the southern Washington Cascade Range and Oregon Coast Range, bat use of forest stands in relation to the availability of food or roost resources, and specific vegetation characteristics that may influence the use of stands by bats.

Methods

Study Sites

In summer 1984, our field work was concentrated on the western slope of the southern Washington Cascades; in summer 1985, the study area was expanded to the Oregon Coast Range. In each region, 45 stands were selected; nine Douglas-fir stands in each of five stand types represented important age and soil-moisture conditions [old-growth (OG) wet, OG mesic, OG dry, mature mesic, and young mesic]. Descriptions of stand characteristics and selection criteria are presented elsewhere in this volume.

Capture and Sampling Methods

To provide an index of what bat species were common at the Washington and Oregon study sites, as well as to record their echolocation calls, we captured bats in 10-m mist nets set over streams and ponds during June, July, and August. No capture sites were inside any of the study plots, but most were within 20-km distance and 100-m elevation of the stands. We identified bats to sex, age, and species and recorded females as parous (pregnant, lactating, or postlactating) or nonparous (no evidence of reproduction in the current year). Bats were then released and their echolocation calls were recorded with a "divide-by-lo" ultrasonic detector (Miller and Andersen 1984) coupled with a Panasonic RQ-355 tape recorder to store the calls. See Fenton (1988) and Thomas and West (1989) for further details on the recording and analysis of bat echolocation calls. We also netted bats on the eastern slope of the Washington Cascades (near Goldendale) on 5 and 6 August 1985 to provide a contrast with captures on the western slope.

In 1984 and 1985, we used ultrasonic bat detectors to detect and identify bats flying in the study stands. The methods used to sample bat activity in the forest stands differed somewhat between the two years, however. In 1984, we sampled bat activity in 41 of the 45 stands by using hand-held, divide-by-10 detectors coupled with sound-activated Panasonic RQ-355 tape recorders to store echolocation calls. Each stand was visited three times between mid-July and early September. In each stand, we sampled bat activity by recording echolocation calls for 15 minutes at each of five stations spaced at 100-m intervals along a transect through the stand. We began sampling when the green of the vegetation could no longer be discerned (about 30 minutes after sunset, depending on canopy coverage). This light intensity corresponds roughly with the onset of bat activity.

In 1985, we used automated detector systems (Thomas and West 1989) to detect and record bat echolocation calls in Washington and Oregon. In each study stand, we set out two detector systems, one to sample the subcanopy (ground) stratum and the other to sample the mid- to upper-canopy stratum about 30 m above the ground. Both detectors were

left in place to sample bat activity continuously over two consecutive nights. The automated detectors began sampling about 30 minutes after sunset and continued for 9 hours each night. The detectors entered time markers at intervals of 32 ± 1 minute after start-up. We sampled all 45 stands in each of the two regions in June and again in July and about half the stands in August. Many samples, however, were either lost because of equipment malfunctions or cut short when insect or other noise interference caused the tapes to run out.

We analyzed the tapes containing the echolocation calls in the laboratory by using a period meter to display the echolocation frequency and time characteristics on a calibrated Telequipment D32 oscilloscope (Fenton 1988, Simmons and others 1979, Thomas and West 1989). Recordings from known species, together with previously published information (Thomas and others 1987), provided the reference data base on frequency, time, and shape characteristics of echolocation calls. These call characteristics were used to identify the bats detected and recorded in the stands. For each stand, bat activity was measured as the number of bat passes recorded in a given sample period; a bat pass is defined as a sequence of two or more echolocation calls recorded as a bat flies by the detector microphone. For the 1985 data, we standardized bat activity as passes per 100 minutes of sampling. We recognized feeding efforts by the high repetition rate (about 100 pulses per second) "feeding buzz" associated with each prey capture attempt. We measured feeding rates as the percentage of passes that contained a feeding buzz. To provide a comparison with feeding activity within the stands, we also measured the feeding activity over three stream or pond sites in Washington (5 sample-hours) and over two pond sites in Oregon (3 hours).

Species Recognition and Groupings

Ultrasonic bat detectors permit species to be assigned to categories according to their echolocation characteristics. Some categories contain single species, but others contain assemblages of species with similar call structures (see Thomas and West 1989). In the Pacific Northwest, we were able to identify the following seven groups: *Myotis* A (the little brown and Yuma myotis, or both); *Myotis* B (the California, Keen's, long-eared, and western small-footed myotis, or combinations): the long-legged myotis; the silver-haired bat; the hoary bat; Townsend's big-eared bat; and the big brown bat or fringed myotis. Because the fringed myotis appeared to be uncommon in our study area, we will refer to the last group as the big brown bat only.

Prey Abundance

In August 1984, we used Bioquip ultraviolet light traps to provide an index of the relative abundance of nocturnal, phototactic, flying insects in the stands and over water. At each site, we set one trap 1.5 m above the ground and

activated it for 90 minutes, starting at dusk. Any insects on or inside the trap at the end of this period were killed with a spray insecticide and sorted into three size-classes based on total body length (small: <5 mm, medium: 5-10 mm, large: >l0 mm). The sorted samples were dried to constant mass at 60 $^{\circ}$C. We obtained samples from 44 stands (9 OG dry, 8 OG wet, 9 OG mesic, 9 mature, and 10 young) and three stream sites.

Vegetation Sampling

Vegetation in the study stands was sampled in a parallel study (see Spies and Franklin, this volume) that characterized the stands by age- and moisture-class and provided data on 35 variables (appendix table 5) that might affect bat abundance.

Statistical Analyses

Bat detection rates did not meet the assumptions required for parametric statistical tests. For all species, detection rates were highly leptokurtic (Kolmogorov-Smirnov test for normality; $P < 0.001$), and the variances were unequal (F_{max} test; $P < 0.001$). Because no simple transformation rectified these problems, only Mann-Whitney and Kruskal-Wallis tests (Seigel 1956) were used to compare detection rates among stand types. Significance levels in all tests were a = 0.05.

To test for significant correlations between bat detection rates and vegetation characteristics, we replaced the classical discriminant function analysis, which is highly sensitive to departures from normality (Press and Wilson 1978), with the nonparametric stepwise logistic regression (SAS computer package; LOGIST, Frank E. Harrell, Jr., Duke University Medical Center, Durham, NC). The logistic regression model requires that the dependent variable (here, bat detection rates for each species) be categorical. Depending on the species, we regrouped detection rates into two or three equal categories. The number of independent variables that the logistic regression can test is approximated by n/10, where n is the sample size of the smallest category. In our data sets, categories contained 50 to 70 entries, which limited the number of variables that could be tested to five to seven. To circumvent this limitation, we ran logistic regressions seven times for each species, using five or six new variables each time (total of 35 variables) to identify potentially significant effects. We then combined the significant variables from the preliminary runs and reran the tests. Those variables that had significant correlation coefficients (rij.k) in the final grouping were considered to have a significant influence on bat detection rates.

Results

Sex and Age of Netted Bats

Important differences in the sex and age structure of the three bat communities were shown by netting over streams and ponds in the western and eastern Washington Cascades and in the Oregon Coast Range (table 1). In the western Washington Cascades, the netting effort yielded 191 individuals of 12 species; males constituted 88.8 percent of the 161 adults. None of the 18 adult females showed any signs of reproduction in the current year. Juveniles constituted 16 percent of the captures, but they were never captured before 21 August. In the Oregon Coast Range, males comprised 72 percent of the adults (N = 49). Unlike the western Washington Cascades, 91 percent of the adult females were pregnant, lactating, or postlactating-indicating that they would produce or had produced young in the current year. Juveniles constituted 20 percent of the catch and made their first appearance in late July. In the eastern Washington Cascades, only 56 percent of the adults caught were male (N = 61). The majority of adult females (82 percent) were either lactating or postlactating. Juveniles comprised 34 percent of the catch on 5 and 6 August. These data suggest that the females present in the western Washington Cascades were not reproductively active, but those present in the Oregon Coast Range and the eastern Washington Cascades were.

Bat Activity in 1984

In 1984, 153.8 hours of sampling yielded only 277 detections, of which only 151 were sufficiently clear to be identified to species group. The low number of identified detections rendered a rigorous analysis of stand use by the different bat groups impossible. We thus regrouped the bats into two categories based on their probable roosting locations: cavity-roosting bats *(Myotis* A, *Myotis* B, the long-legged myotis, and the big brown bat) and foliage-roosting bats (the silver-haired and hoary bats). We also grouped the three moisture-classes of old-growth stands. Detections of both cavity- and foliage-roosting bats were significantly different across the three stand age-classes (cavity: $X^2 = 7.9$, 2 df, $P < 0.05$; foliage: $X^2 = 6.1$, 2 df, $P < 0.05$). Young and mature stands did not differ significantly (cavity: $X = 0.4$, 1 df, $P > 0.05$; foliage: $X^2 = 1.2$, 1 df, $P > 0.05$), indicating a disproportionately high use of old-growth stands by both cavity- and foliage-roosting bats.

Table 1—Sex and age composition of bats netted in the Washington Cascades and the Oregon Coast Range in 1984 and 1985

Bat species	Males		Females		
	Adult	Juvenile	Nonparous	Parous	Juveniles
Western Washington Cascades:					
Big brown bat	3	0	0	0	0
California myotis	26	1	10	0	1
Western small-footed myotis	4	0	0	0	0
Long-eared myotis	5	0	0	0	0
Little brown myotis	92	27	7	0	1
Keen's myotis	2	0	0	0	0
Fringed myotis	1	0	0	0	0
Long-legged myotis	6	0	0	0	0
Yuma myotis	2	0	0	0	0
Silver-haired bat	0	0	1	0	0
Hoary bat	1	0	0	0	0
Townsend's big-eared bat	1	0	0	0	0
Eastern Washington Cascades:					
Big brown bat	2	3	0	2	3
Western small-footed myotis	5	4	1	7	1
Long-eared myotis	0	1	0	0	0
Little brown myotis	10	5	2	7	3
Hoary bat	5	0	0	0	0
Oregon Coast Range:					
Big brown bat	8	0	0	2	0
California myotis	4	0	1	6	2
Western small-footed myotis	1	0	0	0	0
Long-eared myotis	0	0	0	2	0
Fringed myotis	1	0	0	0	0
Long-legged myotis	3	0	0	0	0
Yuma myotis	8	5	0	0	3
Silver-haired bat	3	0	0	0	0

Bat Activity in 1985

In Washington, the total sample effort of 1599 hours yielded 3029 detections of all recognizable species (table 2). The genus *Myotis* (*Myotis* A, *Myotis* B, the long-legged myotis, and unidentified *Myotis* species) accounted for 94 percent of these detections and the silver-haired bat for 5 percent. Detections of the big brown, hoary, and Townsend's big-eared bats were too rare to be subjected to statistical analysis. In Oregon, the total sample effort of 1500 hours yielded 6211 bat passes for all species (table 2). The genus *Myotis* accounted for 79 percent of all detections, and the silver-haired and big brown bat accounted for 6 and 4 percent of all detections, respectively. Detections of the hoary bat and Townsend's big-eared bat (2 and 1 percent of detections, respectively) were too rare for statistical analysis.

The detection rates for the first and second nights of each 2-night sample in a given stand were significantly correlated in both Washington and Oregon (Spearman rank correlation, $P < 0.05$ for all species). These two consecutive nights clearly did not represent independent samples of bat activity, so the two nights were pooled and the mean detection rate (passes per 100 sample-minute) was calculated for each stand visit.

Sampling height (ground vs. canopy) had no clear effect on detection rates for either Washington or Oregon. In Washington, detections of only the silver-haired bat differed significantly between ground and canopy layers (Mann-Whitney U test; $P < 0.001$, canopy>ground). All other species were

Table 3—Detection of bats in old-growth, young, and mature stands in the southern Washington Cascades and the Oregon Coast Range

Species or group[a]	Old growth	Younger	Old growth/ younger[b]	P[c]
Washington				
Myotis A	1.23±0.27[d]	0.33±0.09	3.73	<0.005
Myotis B	2.41±1.75	0.91±0.25	2.65	<0.001
Long-legged myotis	0.34±0.08	0.06±0.02	5.67	<0.01
Silver-haired bat	0.27±0.11	0.15±0.64	—	Ns
Oregon				
Myotis A	6.29±1.98	2.48±1.13	2.54	<0.001
Myotis B	6.54±1.81	1.48±0.50	4.42	<0.001
Long-legged myotis	1.46±0.50	0.53±0.30	2.75	<0.01
Silver-haired bat	2.73±1.15	0.28±0.22	9.75	<0.005
Big brown bat	0.53±0.26	0.16±0.08	3.31	<0.05

[a] *Myotis* A includes the little brown and Yuma moytis. *Myotis* B includes the California, Keen's, long-eared, and western small-footed moytis.
[b] Detection rates are expressed as a ratio of old-growth to younger stands.
[c] Differences between detection rates in old-growth and younger stands were tested by a Mann-Whitney test and P is the resulting probability.
[d] Detection rate as bats per 100 sample minutes ($x \pm$ SE).

both Washington and Oregon. Feeding rates ranged from 1 percent for the silver-haired bat to 4 percent for *Myotis* A in Washington. In the Oregon Coast Range, feeding rates ranged from 1 percent (silver-haired bat) to 4 percent (*Myotis* A). Feeding rates were dramatically higher over water in the same areas, ranging from 27 percent (long-legged myotis) to 39 percent (*Myotis* A) in the Cascades and from 20 percent (long-legged myotis) to 38.5 percent (*Myotis* B) in the Coast Range. For all *Myotis* species, feeding rates averaged 10.3 (Cascades) and 10.1 times (Coast Range) higher over water than in the forest stands. Forest stands do not appear to be primary feeding sites for the *Myotis* species.

Some evidence was found of higher feeding activity in old-growth stands than young and mature stands. *Myotis* B in the southern Washington Cascades and *Myotis* A and *Myotis* B in the Oregon Coast Range all had higher feeding rates in old-growth stands (2 × 2 contingency tests, P < 0.05). Sample sizes were too small to permit testing for other species.

Detection Rates in Washington and Oregon

Detection rates in old-growth stands were significantly higher in Oregon than in Washington for all species except the long-legged myotis (table 3). The Oregon Coast Range had detection rates 2.2 times higher than the Washington Cascades when all detections were pooled. *Myotis* A, *Myotis* B, and

the silver-haired bat were detected at rates 5.1, 2.7, and 10.1 times higher, respectively, in Oregon old-growth stands than in comparable stands in Washington.

Patterns of Prey Abundance

Insect biomass did not differ significantly among stand types for any insect size-class. Stream samples had significantly more small and medium-sized insects than did forest samples (small: F = 1539.8, P < 0.001; medium: F = 108.7, P < 0.001), but the mass of large insects did not differ between the two (F = 3.1, P > 0.05). The approximately 166-fold increase in small and 10-fold increase in medium-sized insects over water as compared with forest stands resulted in a major shift in the biomass and size distribution of insects. In forests, large insects accounted for 65 percent of the total insect biomass, and small insects represented only 5 percent. The pattern was reversed over water: large-bodied insects accounted for only 11 percent of the insect mass, and small-bodied insects accounted for 64 percent.

Vegetative Variables

The logistic regression models showed a confusing pattern of significant relations (table 4). In both Washington and Oregon, seven variables were significantly correlated with the detection rates for one or more bat species; however, they explained only a small proportion of the total variance in bat activity among stands. In Washington, only 6 to 8 percent and in Oregon only 4 to 17 percent of the variance was explained by variables used in the regression models. Also, these variables did not explain the significant association of various bat species with the old-growth age-class. Detection rates for the long-legged myotis were significantly higher in old-growth stands in Washington, but they were not correlated with any variables in the regression models. Stand age was not a significant variable for any bat species in Washington and was only significant for *Myotis* B in Oregon. Clearly, the significant regression variables do not adequately explain the old-growth associations observed for bats, nor do they have a strong predictive value for use in further studies.

Discussion

Detection rates cannot be directly converted into density estimates because individual bats may be detected more than once as they fly near the microphone and because resident and transient individuals cannot be differentiated. Both factors negate any simple one-to-one correlation between detection rates and quantitative measures of bat population density (Thomas and LaVal 1988). Because any biases are likely to be constant across sample sites, however, detection rates can provide a relative index of bat abundance in different habitats or stand types. With the exception of the silver-haired bat in Washington, all the common bat species in the southern Washington Cascades and the Oregon Coast

Table 4—Vegetative variables that were significantly associated with bat activity in the southern Washington Cascades and the Oregon Coast Range

Variable	Myotis A[a]	Myotis B[a]	Long-legged myotis	Silver-haired bat
Washington				
Broken tops	0.15**[b]	Ns	Ns	Ns
Frost scars	−0.16**	Ns	Ns	Ns
Conks	0.13*	Ns	Ns	Ns
Snag 3	Ns	−0.26***	Ns	Ns
Snag 4	Ns	0.10**	Ns	Ns
Snag DC1	Ns	0.14**	Ns	Ns
Snag Vol1	0.09*	Ns	Ns	Ns
Overall R^2	0.06	Ns	0.08	Ns
Oregon				
Snag D.B.H.	0.20***	Ns	0.15*	Ns
Snag DC3	Ns	0.15*	Ns	Ns
Snag Vol	Ns	0.20***	Ns	Ns
Snag Vol4	Ns	−0.09*	Ns	Ns
Age	Ns	0.24***	Ns	Ns
Elevation	0.27***	Ns	0.20**	Ns
Dens 50	Ns	Ns	Ns	−0.21**
Overall R^2	0.12	0.09	0.17	0.04

[a]*Myotis* A includes the little brown and Yuma myotis. *Myotis* B includes the California, Keen's, long-eared, and western small-footed myotis.
[b]Values are the partial regression coefficients (r_{ijk}) and *, **, and *** indicate significance levels of 0.05, 0.01, and 0.001, respectively. Ns indicates not significant.

Ranges have dramatically higher detection rates in old-growth than in mature or young stands. Thus, this study indicates that bats are 2.5 to 9.8 times more abundant in old-growth than in young or mature stands in both study regions. Clearly, old-growth stands provide important habitats for bats in the Pacific Northwest.

Forest stands can provide bats two critical resources: food and day roosts. The short duration of activity in early evening and the low feeding rates during this time suggest that forest stands are not important feeding sites for bats. Early evening peaks in activity over ponds and streams and in adjacent riparian habitat have been described for several species, including the California, long-eared, little brown, Keen's, long-legged, and Yuma myotis and big brown and silver-haired bats (Anthony and Kunz 1977, Bell 1980, Cross 1976, Kunz 1973, O'Farrell and Bradley 1970). These early activity peaks over water generally last 45 to 180 minutes, much longer than the peaks observed in the forest stands (about 15 minutes). The length of activity peaks over water appears to be determined by the insect capture rate that bats achieve and the amount of food they require. Pregnant and lactating little brown myotis foraging over water capture only 19 percent and 28 percent of their first meal in 20 minutes despite capture rates as high as five to eight insects

per minute (Anthony and Kunz 1977; Gould 1955, 1959). Similarly, wild European pipistrelles and captive western small-footed myotis achieve high capture rates when feeding on insect swarms (10 insects per minute), but have feeding periods lasting ≥45 minutes (Griffin and others 1960, Racey and Swift 1985). Because feeding rates decline with decreasing insect abundance (Racey and Swift 1985), habitats with lower insect abundance than aquatic sites have should show prolonged activity peaks, which was clearly not true in forest stands. Although insects in the size range taken by *Myotis* species (<10 mm; Anthony and Kunz 1977, Belwood and Fenton 1976) were only 1 to 10 percent as abundant as over water, the activity peak in forests was brief, lasting only about 15 minutes. Thus, this peak is unlikely to correspond with any significant feeding activity, but rather originated from bats commuting from day roosts to feeding sites located outside the stands and over water. That feeding rates of the *Myotis* species were more than 10 times higher over ponds and streams in Washington and Oregon lends further support to this conclusion.

Our data suggested that the activity of the *Myotis* species and the big brown and silver-haired bats (Oregon) was skewed towards old-growth forests because they offer an increased variety or abundance of day roosts. Although the highest densities of snags occur in young and mature forests, these snags are typically dominated by small-diameter Douglas-fir with low longevity (Cline and others 1980). The greatest species diversity, largest diameters, the most advanced decay-classes, and the greatest snag longevity all occur in old-growth compared with younger forests. These features likely provide a greater abundance and diversity of bat roosts in old growth than in younger forests.

Although bat activity was greater in old-growth stands in both Washington and Oregon, important differences were found between the two regions. Detection rates were significantly lower in the southern Washington Cascades for all species except the long-legged myotis, and no evidence of reproduction was found in this region. In the western Washington Cascades, few bats were female (11 percent), none showed any evidence of reproductive activity, and juveniles were only captured after the dissolution of maternity colonies in late August (Humphrey and Cope 1976). This contrasted sharply with the Oregon Coast Range and the eastern Washington Cascades, where pregnant and lactating females were abundant and juveniles constituted a higher proportion of the captures during the late maternity period. These data suggest that reproductive females were absent from the 300- to 600-m elevation zone on the western slope of the Cascades, but that they were present at similar elevations to the east and south. Similar skews towards nonreproductive females and males at high elevations and towards reproductive females at lower elevations have been reported in the Cascades and the Rocky Mountains (Fenton and others 1980, Perkins 1983).

Table 4-Vegetative variables that were significantly associated with bat activity in the southern Washington Cascades and the Oregon Coast Range

Variable	*Myotis* A"	**Myotis** B[a]	Long-legged myotis	Silver-haired bat
Washington				
Broken tops	0.15**[b]	**Ns**	Ns	Ns
Frost scars	-0.16**	**Ns**	Ns	Ns
conks	0.13*	**Ns**	Ns	Ns
Snag 3	Ns	-0.26***	Ns	Ns
Snag 4	Ns	0.10**	Ns	Ns
Snag DC1	Ns	0.14**	Ns	Ns
Snag Voll	0.09*	**Ns**	Ns	Ns
Overall R^2	0.06	**Ns**	0.08	Ns
Oregon				
Snag D.B.H.	0.20***	Ns	0.15*	Ns
Snag DC3	Ns	0.15*	Ns	Ns
Snag Vol	Ns	0.20***	Ns	Ns
Snag Vo14	Ns	-0.09*	Ns	Ns
Age	Ns	0.24***	Ns	Ns
Elevation	0.27***	Ns	0.20**	Ns
Dens 50	Ns	Ns	Ns	-0.21**
overall R^2	0.12	0.09	0.17	0.04

[a]Myotis A includes the little brown and Yuma myotis. Myotis B includes the California, Keen's, long-eared, and western small-footed myotis.
'Values are the partial regression coefficients (rijk) and *, **, and *** indicate significance levels of 0.05, 0.01, and 0.001, respectively. Ns indicates not significant.

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Differences in the incidence of reproductive females may be related to climate. Forests in the western Washington Cascades receive higher rainfall, more days of rain, and are more frequently shrouded by low clouds during the pregnancy and lactation periods (April to July) than sites to the east, to the south, and at lower elevations (NOAA 1960-85). These factors may cause more frequent interruptions in foraging activities and make timing of food availability less predictable. Racey (1973) and Racey and Swift (1981) showed that pregnant females that could not forage daily were incapable of sustaining the energy demands of homeothermy. Torpor in females delayed parturition both in the laboratory and under natural conditions (Racey 1973, Racey and Swift 1981). Low clouds and frequent rain in the western Washington Cascades may make timing of insect availability too patchy for pregnant or lactating females to remain homeothermic. Females may not be able to complete the reproductive season and prehibernation fattening in the limited time available during summer. If nonreproductive females and males are able to resort to torpor without a reproductive penalty, they would be less sensitive to temporal patchiness in prey availability and so could make use of the more adverse, high-rainfall sites (Kurta and Kunz 1988).

Vegetative Relationships

The correlations of bat activity to vegetative features indicate that the abundance of damaged or diseased trees or snag size and decay states were associated with higher bat activity. These variables explained such a small proportion of the total variance in bat activity that they did not identify specific vegetation features that affect bat abundance. These weak correlations are probably a result of the study design; vegetative characteristics were measured to describe differences in stand types rather than to quantify roosting sites for bats. Until more precise data on the roosting requirements of bats in the Pacific Northwest become available, the only way to manage for bat populations will be to retain undisturbed stands of old-growth forest. The minimum size of these stands can only be determined by the size in which the full range of snag sizes and decay-classes are represented. If the abundance and diversity of snags and diseased or damaged trees influences bat abundance in stands, then several avenues for future research

are apparent. Managed and thinned stands where damaged trees and snags have been removed should be essentially devoid of bats and can provide a valuable contrast with fire-generated young and mature stands. Young stands produced from old-growth stands damaged by canopy fires should retain the snag characteristics of the original stand for about 41 years (Cline and others 1980), and they may have an increased diversity of roost sites because these stands have more standing dead trees. These stands should have bat activity equivalent to or higher than intact old-growth stands. In contrast, young stands produced by logging operations that remove the large snags should have low bat activity. Because most of the young stands studied here were not a product of logging, this contrast was not tested. Coupled with these possible contrasts based on ultrasonic detection, locating and characterizing suitable roosts would seem imperative.

This study shows that old-growth forests provide important habitats to bats in both the Cascade and Coast Ranges. We predict that forestry practices that remove old growth and thus reduce the overall age structure of forests without retaining snags and damaged trees will significantly affect bat populations. The evidence that reproductive females are less abundant on or absent from the western Washington Cascades suggests that protection of old growth in the Coast Ranges and mountains to the south should receive highest priority.

Appendix

Table 5-Vegetation, elevation, and topography variables used in logistic regressions

Variable	Description
Broken tops	Live trees with broken tops
Dead tops	Live trees with dead tops
AnScar	Trees with animal-induced scars
LiScar	Trees with lightning scars
Frost Scar	Trees with frost scars
ExCav	Trees or snags with excavated cavities
NatCav	Trees or snags with natural cavities
conks	Trees with conks of primary pathogens
Snag3[a]	Snags: height = 1.5-5.0 m; d.b.h. = l0-50 cm
Snag4	Snags: height >15 m; d.b.h. = l0-50 cm
Snag5	Snags: height = 5-15 m; d.b.h. >50 cm
Snag6	Snags: height >15 m; d.b.h. >50 cm
SnagDCl-5[b]	Snags: decay classes 1 to 5
SnagD.B.H.	Snags: mean d.b.h.
SnagMass	Snags: total biomass
SnagVol	Snags: total volume
SnagVol1-5	Snags: volumes in decay classes 1 to 5
Age	Chronological age in years
Topo	Topography: crest; upper, middle, lower slope, depression
Elevation	Mean stand elevation
Species	Total number of tree species
TotDens	Total tree density
D.B.H.	Mean tree d.b.h.
D.B.H.75	D.b.h. of the 75 percent quantile
Dens50	Density of trees with d.b.h. = 50-99 cm
Dens100	Density of trees with d.b.h. = 100-149 cm
Dens150	Density of trees with d.b.h. >149 cm

[a]Snag number designators conform with those used in vegetation studies (this volume).
[b]Snag decay-classes follow those in Clime and others (1980).

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