SMALL MAMMALS IN MANAGED, NATURALLY YOUNG, AND OLD-GROWTH FORESTS[1]

ANDREW B. CAREY
Pacific Northwest Research Station, USDA Forest Service,
Olympia, Washington 98502 USA

MURRAY L. JOHNSON
Burke Memorial Museum, University of Washington,
Seattle, Washington 98185 USA

Abstract. Forest managers in the Pacific Northwest are faced with new challenges of providing for all wildlife in managed forests. Our objective was to elucidate the factors governing the composition and biomass of forest floor mammal communities that are amenable to management. We sampled small mammal communities in forests of various management histories on the Olympic Peninsula and contrasted our results with those of other large studies in the Pacific Northwest.

Forest floor mammal communities in forests >35 yr old in the Western Hemlock Zone of Washington and Oregon are composed of 5-8 characteristic species. These include *Sorex trowbridgii* (numerically the most dominant); one species each of *Clethrionomys*, the *Sorex vagrans* complex, and *Peromyscus*; and *Neurotrichus gibbsii*. Species composition changes from south to north, and the communities on the Olympic Peninsula contain two or three additional species compared to communities to the south. Communities in naturally regenerated and clearcutting regenerated (managed) young forests are similar in composition to those in old growth; old growth, however, supports 1.5 times more individuals and biomass than managed forest. Community diversity seems related to the south-north moisture-temperature gradient that is reflected in increased diversity of canopy conifers, development of forest floor litter layers, accumulation of coarse woody debris, and abundance of herbs, deciduous shrubs, and shade-tolerant seedlings (as opposed to understories dominated by evergreen shrubs). Previous work found few habitat variables that were good predictors of species abundance in natural young and old-growth stands. Naturally regenerated young stands had higher levels of coarse woody debris than old growth. Managed stands had much lower abundance of coarse woody debris and tall shrubs than old growth. Understory vegetation (herbs and shrubs) and coarse woody debris accounted for a major part of the variation in abundance of six of eight species in managed stands, but only two species in old growth. Management of Western Hemlock Zone forest for conservation of biodiversity and restoration of old-growth conditions should concentrate on providing multispecies canopies, coarse woody debris, and well-developed understories.

Key words: biodiversity; Clethrionomys; *forest ecology; habitat; mammal communities; micro-habitat;* Microtus; Neurotrichus; *old growth; Olympic Peninsula; Oregon;* Peromyscus; *silviculture;* Sorex; *Washington.*

INTRODUCTION

Small mammals (Muridae, Soricidae, and Talpidae) contribute to biodiversity of North American temperate forests, both to the diversity of species and life forms present and to the functional diversity of the forest ecosystem. Small mammals are prey for reptilian, avian, and mammalian predators. Also, small mammals prey on invertebrates, including some insects that have potential to significantly alter forest ecosystems. Small mammals consume plants (including seeds and fruits), lichen, and fungi and are important disseminators of the symbiotic ectomycorrhizal fungi that assist woody plants in obtaining nutrients and water.

For more than a decade, ecologists have speculated about the impacts of harvesting old-growth forests on biodiversity in the Pacific Northwest (Thomas et al.

1990). Old-growth forests in the Pacific Northwest are virgin forests >200 yr old characterized by a diversity of vegetation structure and composition: large dominant trees, smaller shade-tolerant trees, multilayered canopies, large snags, and an abundance of coarse woody debris (Franklin et al. 1981, Old-Growth Definition Task Group 1986). A major research effort to compare the ecological communities in old-growth forests to earlier stages of forest development (but still >35 yr old) was designed and implemented during 1982-1986 in the Pacific North-west (Carey and Spies 1991). Studies of small mammals were conducted in the southern Oregon Coast Ranges and the Cascade Range in Oregon and southern Washington. These small-mammal investigations showed few differences between young (35-79 yr old) and old-growth forest small-mammal communities. Species more abundant in old growth than in young stands were: *Phenacomys longicaudus* in the Oregon Cascades and Coast Ranges, *Peromyscus maniculatus* and *Peromyscus oreas* in the southern

Washington Cascades, and *Neurotrichus gibbsii* overall, but not in any individual area (Carey 1989, Aubry et al. 1991, Corn and Bury 1991 *a*, Gilbert and Allwine 1991, West 1991). Few "ecologically interpretable patterns" in small-mammal communities across age classes of forest stands were found (Aubry et al. 1991). However, these reports suggested that old-growth elements (especially coarse woody debris) that were retained through the natural catastrophic events (such as wildfire) may have obscured patterns that would have been evident had the stands originated after clearcutting. Timber management (e.g., clearcutting, site preparation, and thinning) can substantially reduce the amounts of coarse woody debris (Spies and Cline 1988:20-23). Complete utilization of standing trees, coupled with mechanical disruption of the existing coarse woody debris, reduces coarse woody debris in the short term. Removal of live trees to promote growth of retained trees forestalls mortality, reduces recruitment of coarse woody debris, and further reduces coarse woody debris over time.

Ecologists from Elton (1966) to Harmon et al. (1986) have emphasized the importance of coarse woody debris in ecosystem processes and in providing habitat for a myriad of organisms. Fallen trees are especially important to small mammals inhabiting the forest floor. These trees provide moist microclimates, protective cover, travel ways, sites for nests and burrows, and food in the form of fungi, plants, and invertebrates (Maser and Trappe 1984:19-36, Harmon et al. 1986:224-231). Maser and Trappe (1984) illustrate how fallen trees could be important to *Clethrionomys californicus*, *Sorex trowbridgii*, and *Neurotrichus gibbsii*. But the dependence of small mammals on fallen trees has not been documented to the same extent as the dependence of cavity-using birds on snags (Harmon et al. 1986).

Recently, attention has begun to focus on the impacts of managing second-growth forests. For example, Thomas et al. (1990:365-372) and Lujan et al. (1992:226) stressed the need to examine alternative silvicultural approaches for managing second-growth forests for biodiversity, to restore old-growth ecosystems, and to provide habitat for the Northern Spotted *Owl* (*Strix occidentalis caurina*) and its mammalian prey. Understanding the responses of small-mammal populations to habitat conditions in young, managed stands is integral to formulating silvicultural prescriptions for providing habitat for small mammals. Abundance of fallen trees and understory vegetation (which also provides cover and food, in the form of associated ectomycorrhizal fungi, insects, foliage, seeds, and fruits) are the habitat factors of primary relevance to forest floor small mammals. Abundance and diversity of understory vegetation are determined by the interaction of canopy closure, site conditions, and stand history (Spies 1991) and not simply a result of stand age. Silvicultural manipulations of overstory vegetation can strongly influence understory vegetation and enhance tree growth as well.

Our goal in this paper is to elucidate those factors governing the composition and biomass of forest floor mammal communities that are amenable to manipulation. Governing processes are complex and may include regional stage-setting variables, including the influence of climate on forest structure and composition. Thus, consideration of regional variation in community structure aids considerably in understanding local variation. Specifically, we will (1) compare small-mammal community composition in forests on the Olympic Peninsula with the communities in forests in the southern Washington Cascades, Oregon Cascades, and Oregon Coast Ranges, (2) determine if small-mammal communities in old-growth forests differ from communities in managed forest on the Olympic Peninsula, (3) determine if the response of small-mammals species populations to coarse woody debris and understory vegetation differ between old-growth and managed forests, and (4) discuss the implications of our results to management of second-growth forests for biodiversity, including management to benefit Spotted Owls.

METHODS

Study area

The Olympic Peninsula is made up of a central core of rugged mountains surrounded by almost level lowlands (Franklin and Dyrness 1973). The core is in the Olympic National Park. Forested lands at middle elevations (100-600 m) are in the Park, the Olympic National Forest, and state and private timberlands; lowlands are in the Park, on tribal reservations, and in state and private timberlands. The Peninsula is characterized by sharp gradients in precipitation, elevation, and temperature that result in seven vegetation zones, ranging from the Sitka Spruce (*Picea sitchensis*) Zone in the western lowlands (near sea level) to the Western Hem*lock* (*Tsuga heterophylla*) Zone at low elevations (< 1200 m) to the Non-forest Zone at the highest elevations (2420 m). We confined our studies to the Western Hemlock Zone. Annual precipitation in this zone averages -300 cm on the west and south and 150 cm to the east. Fires are infrequent in the wet areas and windstorms are the primary natural source of catastrophic disturbance (Henderson et al. 1989). Major windstorms occur at 15-20 year intervals; in 1921, a violent windstorm along the entire coast of Washington created large areas of mixed-age forest. The eastern, dry areas have a high fire frequency; fire return rates are 138-234 yr. Most of the Western Hemlock Zone forests burned 280-350 yr ago. Human-generated catastrophic disturbances include fires on a large scale and clearcutting in varying scales, but cumulatively very extensive. Logging began in the late 19th century; logging was a major force shaping the forested landscape by the 1920s (Henderson et al. 1989).

TABLE 1. Study areas on the west (W), south (S), and east (E) sides of the Olympic Peninsula, Washington, and their elevations (Elev.), aspects, slopes, percentages of area influenced by streams and seeps (Water), and vegetation, 1987–1989.

Area	Age (yr)	Loc.	Elev. (m)	Aspect	Slope (deg)	Water (%)	Vegetation*
OG901	>300	W	610	SW	34	8	TSHE/ABAM/GASH/TSHE
OG902	>300	W	305	NW	16	22	TSHE/VAAL/TSHE
OG903	400	S	122	SW	2	0	PISI/TSHE/VAAL/TSHE
OG915	>250	W	214	W	21	22	TSHE/ABAM/VAAL/TSHE
OG917	350	S	305	SE	33	11	TSHE/ABAM/VAAL/TSHE
MA942	100/250	E	610	N	9	7	PSME/ALRU/TSHE/POMU
MA944	66/300	W	244	SW	17	22	TSHE/moss
MG960	64	E	335	N	13	13	PSME/ALRU/TSHE/POMU
MG961	67	W	335	S	7	7	PSME/GASH
MG962	62	S	116	W	7	7	PSME/GASH
MG963	60	S	134	NW	8	52	TSHE/OXOR
MG964	57	S	98	SE	4	0	TSHE/PSME/GASH/BENE
MG965	64	S	85	NW	11	17	TSHE/PSME/GASH/POMU
MG966	44	W	305	NW	1	0	PSME/TSHE/moss

 * Dominant trees followed by dominant understory plants, including tree seedlings; acronyms are the first two letters of genus and species: *Tsuga heterophylla, Abies amabilis; Picea sitchensis, Pseudotsuga menziesii; Gaultheria shallon; Vaccinium alaskaense; Alnus rubra; Polystichum munitum; Oxalis oregoni; Berberis nervosa.*

Experimental design

We chose 12 stands (6 old growth and 6 young) in 3 areas on the Olympic Peninsula to study for 3 yr, beginning in 1987. We attempted to pair managed and old-growth stands. The areas were on the east side of the Peninsula near Quilcene, on the south near Quinault, and on the west near Forks. In 1988, we learned that one of the landowners had changed harvest plans and we added two stands in the south to replace the stands to be harvested. After describing the vegetation in the stands it was apparent that two stands were neither managed nor old growth; they were mixed-age stands resulting from fire (MA942) and windstorm (MA944; Table 1). Our old-growth stands were ≈ 300-400 yr old and had not been subjected to silvicultural manipulation. Our managed stands were 44-67 yr old. All were established after clearcutting with high utilization of standing trees; none had residual trees. MG960 had been planted and thinned; MG961 had been seeded and thinned. The remaining young stands were seeded artificially and naturally. MG962 and MG963 were dense stands that had not been thinned, but were scheduled for thinning. MG964 and MG965 had not been thinned, but the trees were not crowded; both were scheduled for imminent harvest. MG966 was a dense, unthinned stand. Understory development reflected spacing of trees (Table 1).

Sampling procedures

We established 16-ha, 10 X 10 grids with 40-m spacing in each stand as part of a study of arboreal rodents (Carey et al. 1992). Each grid point was described with 55 variables, including species and diameter of the nearest dominant or codominant tree, aspect, slope, and type of water (none, stream, seep, pond) within 10.6 m. Vegetation was described using nested 5.6-m radius and 10.6-m radius plots. Within the 10.6-m radius plots we recorded the number of snags by size and decay classes, the number of trees by size and type (conifer or deciduous), and ocular estimates of overstory cover. Within 5.6 m, we described the forest floor cover of fine litter (needles, leaves, twigs, cones), coarse litter (bark, branches, chunks of wood), coarse woody debris (fallen trees, by decay class), moss, total herbaceous vegetation, dominant and codominant species of vegetation, total woody vegetation <2 m tall, dominant and codominant species of woody vegetation <2 m tall, total woody vegetation >2 m tall, but below the canopy, and dominant and codominant species of woody vegetation >2 m tall, but below the canopy.

Two adjacent, parallel grid lines in each stand were chosen each year for snap-trapping of small mammals. Different pairs of lines were chosen for each year the stand was studied to avoid depleting local populations. Two Museum Special snap-traps, baited with peanut butter and oats, were placed at each of 25 stations located 15 m apart along the grid lines, for a total of 50 stations and 100 traps. Traps were set for 4 nights to ensure we sampled a closed population. Trapping was conducted in July and August to avoid periods of high immigration. All old-growth, mixed-age, and western and eastern managed stands were trapped in 3 yr (19871989); managed stands in the southern area were trapped in 2 yr each (MG964 and MG965 in 1987 and 1988; MG962 and MG963 in 1988 and 1989). Captured animals were provisionally identified, numbered, labeled, frozen, and deposited in the Burke Memorial Museum at the University of Washington in Seattle. Museum mammalogists provided final identifications of species, sex, age (young or adult), reproductive status

(including counts of placental scars or fetuses), and body weight; study skins and skeletons were prepared.

Taxonomy and nomenclature

Taxonomy and nomenclature in this paper follow Jones et al. (1992), who adopted Carraway's (1990) revision of the *Sorex vagrans* species complex. The taxonomy of the *Sorex pacificus-monticolus-vagrans* complex has been debated for >50 yr (Carraway 1990). Hall (1981) lists *S. pacificus*, *S. monticolus*, and *S. vagrans* as intergrading subspecies of *Sorex* vagrans; Carraway (1990) elevated two subspecies to specific status. Glaciation and geographic separation led to the speciation of *Sorex* (Carraway 1990). These species of *Sorex* (Jones et al. 1992) are very similar morphologyically and sometimes cannot be distinguished on the basis of morphology, especially in old individuals. Carraway's (1990) revision clarifies the situation but presents uncertainties about studies conducted in Oregon. The shrews classified as *Sorex pacificus* in the Coast Ranges by Corn and Bury (1991a) and the southern Cascades by Gilbert and Allwine (1991) were either S. *sonomae* or *S. pacificus*, but most were S. *sonomae* (P. S. Corn, *personal communication)*. The degree of ecological separation of the two species is unknown. In our analyses, these shrews had a rank of 3 (relative abundance of 4-12% of the catch) in both areas; insofar as one species dominated or exclusively occupied a given stand, our analyses would be unaffected. Shrews in the central Cascades were particularly difficult to assign to specific status as Gilbert and Allwine (1991) reported; up to 3 species in the complex could have been present. Again ranks were low (1-3) and comparisons with Washington should not have been affected. Shrews in the northern Cascades of Oregon (above latitude 44) classified as *S. monticolus* were *S. bairdii*, although some at their northernmost sites near the Columbia River might have been *S. monticolus.* Carraway's (1990) revision appeared after the preparation (in 1989) of the papers by Corn and Bury (1991 a), Gilbert and Allwine (1991), West (1991), and Aubry et al. (1991). In analyzing data and preparing tables for this paper, we used the taxonomy reported by these authors. The revised taxonomy is used in the text and table footnotes. However, mammalian taxonomy is constantly being refined and we expect continued change to the arrangement used here (Wilson and Reeder 1993).

Statistical procedures

Habitat variables (stand means) were used for three purposes: (1) to describe the study stands in terms of age, site, and forest type (Table 1), (2) to contrast the structure (mean dbh of dominant trees, cover of fallen trees, abundance of snags, and layering of vegetation) of the old-growth stands with that of the young stands, and (3) to examine relationships between species abundances and features directly influencing the forest floor;

abundance of fallen trees and the prevalence (percent of grid points) with significant (>16%) cover of moss, litter, and herbaceous vegetation and cover of shrubby vegetation >24%. Variables were examined for correlations; highly correlated ($r > 0.80$) variables were eliminated or, when categories were related, were combined. Cover variables were transformed with an arcsin-square root transformation.

Community structures of managed and old stands on the Olympic Peninsula were examined by comparing relative evenness (Spearman rank correlation of species abundances), richness (number of species), and ranked abundance (Carey et al. 1991). Individual species abundances were calculated as catch per unit effort (CPU, numbers/] 00 trap nights) with corrections for sprung traps and captures of other species (Nelson and Clarke 1973). Species abundances were transformed by In (CPU + 1) for contrasts between young and old stands and for regression against habitat variables. Analysis of variance of abundance by stand type (old, young) over years (with type-year interaction) was performed. We calculated relative biomass as the product of CPU and mean body mass (weighted means were used when analysis of variance showed differences in body mass with year or sex). We classified females with thickened uteri, embryos, placental scars, or lactating mammaries as reproductive and calculated reproductive-female CPUs. We defined fecundity as the mean number of placental scars or embryos per pregnant or postpartum female and calculated relative productivity by multiplying mean reproductive-female CPU by mean fecundity. Simple linear regressions and multiple (2-variable) regressions were used to relate species abundance to selected habitat variables (mean cover of fallen trees, prevalence of woody vegetation, prevalence of herbaceous vegetation) hypothesized to be of importance for forest floor mammals. Selection of species for analysis was based simply on their abundance and constancy of occurrence in the stands; rare species were not examined. Regressions were performed separately for managed stands and old stands and with managed and old stands (but not mixed-age stands) combined. If managed and old forests are markedly different environments, as hypothesized, then factors limiting species would be expected to be different in the two types. Regressions were accepted only if $P <$ 0. 10, regression coefficients were significantly different from 0 $(P < 0.10)$, and normal probability plots suggested residuals were normally distributed.

A different ranking scheme was used to contrast community structures of young and old-growth stands among physiographic provinces. Combined snap-trap and pitfall data presented by West (1991) and overall snap-trap captures provided by S. D. West (*personal communication*) for the southern Washington Cascades, snap-trap and pitfall data presented by Gilbert and All-wine (1991) for the Oregon Cascades, and pitfall data presented by Corn and Bury (1991*a*) for the Oregon

TABLE 2. Mean habitat values of young, managed stands and old-growth stands on the Olympic Peninsula, Washington, 1987–1989.

Habitat element*	Old-growth stands			Young, managed stands		
	$\bar{X}$ ± SE		Range	$\bar{X}$ ± SE		Range
Slope (degrees)	21	6	2–34	7	2	1–13
Water (%)	13	4	0–22	13	7	0–52
Dbh of trees (cm)	71	7	60–97	42	4	33–56
CWD cover (%)	13	4	6–24	8	1	5–16
CWD (%)	69	11	46–99	53	10	29–95
Large snags/ha	24	3	15–35	3	1	<1–10
Moss (%)	78	7	55–99	83	8	39–99
Litter (%)	57	16	0–86	56	10	25–97
Forb-fern (%)	46	16	21–95	46	12	1–73
Low shrub (%)	42	8	15–64	42	12	0–95
Tall shrub (%)	33	6	18–52	14	5	1–34
Canopy (%)	57	7	46–74	86	5	63–97

*Variables with % are prevalences, percentages of 100 sampling points having values >0% (water), >6% (forest floor coarse woody debris, CWD), >16% moss, litter, forb-fern); >24% (low shrub, tall shrub); and >64% (canopy).

Coast Ranges were used for the comparisons. Because of differences in methodology and in the years sampled, direct comparison of CPU was not possible. In addition, any trapping technique catches species outside the taxa being targeted, transient individuals of species not normally associated with the sampled habitat, and some individuals of species not effectively sampled by the technique (West 1985, Bury and Corn 1987, McComb et al. 1991). Therefore, we limited our analyses to those species that were captured consistently in either old-growth or young stands and made up >1.5% of total captures. *Scapanus orarius, Sorex bendirii, Sorex palustris, Tamias townsendii,* and *Zapus trinotatus* and other rare or transient species were not included in the analyses. We list all the species we caught on the Olympic Peninsula; complete species lists were reported by the authors we cite. The screening procedures identified five to eight species that made up >92% of the total captures in each physiographic province. Relative abundances were calculated as percentages of total CPU. Relative abundances were then ranked (1-6) on a log scale (2, 4, 8, 16, 32, 64%; Preston 1981). Ranked relative abundances were used to represent community structure and to compare community structures among physiographic provinces.

RESULTS

Characteristics of Olympic stand types

Old-growth stands differed compositionally from managed stands in having more *Tsuga heterophylla, Abies amabilis, Picea sitchensis,* and *Vaccinium alaskaense* and less *Pseudotsuga menziesii* and *Gaultheria shallon,* as would be expected for forests approaching climax (Table 1). Old growth tended to be on steeper slopes than managed forest (Table 2) and had larger

trees, greater numbers of snags ≥50 cm dbh, more coarse woody debris on the forest floor, and greater development of an understory of tall shrubs and young trees (Tables 1 and 2). Managed stands had greater canopy closure and more small snags. Mixed-age stands had intermediate values for stand descriptors. Measures of forest floor coarse woody debris were positively correlated ($r \geq 0.89$, $P = 0.01$) and only the mean total percent cover of fallen trees was retained for analysis with mammal captures. Abundances of herbaceous plants, low (≤2m) shrubs, litter, and moss were highly variable and not directly related to type of stand. Because cover values of herbaceous and woody plants appeared to be distributed nonnormally (i.e., a little or a lot), we used prevalences (percent of stations with cover≥16% for herbs and >24% for shrubs). Prevalence of low shrubs was highly correlated with prevalence of tall shrubs within managed stands ($r = 0.84$, $P < 0.01$) and old growth ($r = 0.97$, $P < 0.01$); therefore, we created a new variable, prevalence of total shrubs that was highly correlated with both ($r > 0.91$, $P < 0.05$). Litter and herbaceous cover were negatively correlated ($r = -0.90$, $P < 0.01$) and only herbaceous prevalence was retained for analysis.

Mammal communities

We caught 2638 animals of 13 species; all 13 species were caught in both old-growth and managed stands. Three rarely caught species were not caught in the small sample of mixed-age stands. Eight species were captured >50 times each and made up 97% of the total captures (Table 3). Five of these eight species were caught in all stands sampled; *Microtus oregoni* and *Sorex vagrans* were caught in four of five old-growth stands, both mixed-age stands, and five of seven managed

TABLE 3. Captures of small mammals in managed, mixed-age, and old-growth stands, Olympic Peninsula, Washington, 1987–1989.

	Old growth	Mixed age	Man-aged	Total
Trap nights	6000	2400	6800	15 200
Number of stands	5	2	7	14
Sorex trowbridgii	396	110	291	797
Peromyscus oreas	319	86	132	537
Sorex monticolus	257	71	144	472
Clethrionomys gapperi	134	44	140	318
Neurotrichus gibbsii	66	57	47	170
Microtus oregoni	42	15	68	125
Sorex vagrans	29	14	29	72
Peromyscus maniculatus	29	5	25	59
Zapus trinotatus	10	3	8	21
Tamias townsendii	6	0	15	21
Scapanus orarius	3	0	2	5
Sorex palustris	1	1	1	3
Sorex bendirii	1	0	1	2
Sorex spp.	29	0	7	36
Total no. of captures	1322	406	910	2638
Catch/100 trap nights	22	17	13	···

TABLE 4. Ranked relative abundances of small mammals consistently captured in pitfalls and snap traps in young and old stands in Oregon and Washington, 1985–1989.

Species*	Trap: Age:†	Coast Range Pit O	Y	Oregon Cascades Pit O	Y	Snap O	Y	Washington Cascades Both O	Y	Snap A	Olympic Peninsula Snap O	Y
Sorex trowbridgii		6	6	6	6	6	5	5	5	4	5	5
Clethrionomys californicus		4	4	4	4	4	5					
Clethrionomys gapperi								5	4	4	3	4
Sorex pacificus		3	3	3	1	3	3					
Sorex monticolus				1	3	1	2	4	5	4	4	4
Peromyscus maniculatus		2	2	1	1	2	2	2	1	2	2	2
Peromyscus oreas								4	3	4	4	4
Neurotrichus gibbsii		2	1	1	1	1	1	2	1	2	3	3
Microtus oregoni											3	3
Sorex vagrans											2	2

* Sorex pacificus includes S. sonomae in the southern Coast Range and the Cascade Range in Oregon; S. monticolus includes S. bairdii in the northern Cascade Range of Oregon.
† O = old, Y = young, A = old and young combined.

stands. Peromyscus maniculatus were caught in all stands except two managed stands. There were no significant differences in evenness, richness, or rank order of numerical abundance between managed, mixed-age, and old stands; indeed the ranked abundances of the eight species with ≥25 captures were positively correlated between managed and old-growth stands (Spearman rank correlation = 0.93, P = 0.009). Total numerical abundance of small mammals was inversely related to stand age (Table 3).

The forest floor small-mammal communities in Oregon seem to be more dominated by Sorex trowbridgii than communities in Washington (Table 4). Clethrionomys gapperi replaces C. californicus in Washington and appears to have lesser importance in Olympic Peninsula old growth than elsewhere. Sorex monticolus replaces S. pacificus (now including S. sonomae in southern Oregon and S. bairdii in northern Oregon) and assumes greater importance in the communities in Washington. Peromyscus oreas is added to the Washington communities while P. maniculatus maintains its low relative numerical abundance. Neurotrichus gibbsii assumes more importance in the Washington communities, especially

on the Olympic Peninsula, than it does in Oregon. These differences result in more diverse communities (in terms of evenness) in Washington than in Oregon. In addition, the Olympic Peninsula communities include Microtus oregoni as a major component, and Sorex vagrans as a minor component, of the forest floor small-mammal community.

Species responses to Olympic stand types

Old growth on the Olympic Peninsula supported 1.6 times more small mammals than managed stands. Sorex trowbridgii, Peromyscus oreas, Sorex monticolus, and Neurotrichus gibbsii were significantly more abundant (P < 0.10) in old growth than in managed stands (Table 5). Neurotrichus gibbsii attained its highest abundance in mixed-age stands, but the other three species were intermediate in abundance in mixed-age stands (Table 3). Abundance of Clethrionomys gapperi was especially variable (Table 5), ranging from 0.1 (OG902) to 8.4 captures/100 trap nights (OG901) in old growth; the range in young stands was 0.3–7.1 captures/100 trap nights. Relative numerical abundances of reproductive females

TABLE 5. Transformed (ln + 1) abundances (captures/100 trap nights, CPU, corrected for sprung traps and captures) of small mammals consistently caught in young-managed and old-growth stands on the Olympic Peninsula, 1987–1989, and analysis of variance of log-transformed CPU.

	Old growth CPU	(SE)	Young managed CPU	(SE)	ANOVA results F	df	P
Sorex trowbridgii	2.12	(.11)	1.65	(.15)	9.3	1, 26	0.005
Peromyscus oreas	1.71	(.19)	1.10	(.16)	10.6	1, 26	0.003
Sorex monticolus	1.58	(.19)	1.00	(.14)	7.5	1, 26	0.011
Clethrionomys gapperi	0.93	(.34)	0.98	(.25)	0.0	1, 26	0.904
Neurotrichus gibbsii	0.74	(.12)	0.56	(.14)	3.1	1, 26	0.089
Microtus oregoni	0.45	(.23)	0.55	(.19)	0.2	1, 26	0.679
Peromyscus maniculatus	0.40	(.14)	0.33	(.13)	0.7	1, 26	0.418
Sorex vagrans	0.30	(.14)	0.30	(.11)	0.0	1, 26	0.987

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TABLE 6.   Mean (SE) captures/100 trap nights (TCPU), body mass, relative biomass (abundance times body mass), abundance of reproductive females (RFCPU), fecundity (number of placental scars and embryos), and relative productivity (RFCPU × fecundity) and the correlations (r) between RFCPU and TCPU for small mammal species inhabiting old growth and managed conifer stands on the Olympic Peninsula, Washington, 1987–1989.

Species	Habitat type	TCPU		Mass (g)		Rel. biom.	RFCPU		Fecundity		Rel. prod.	Species r
		$\bar{X}$	(SE)	$\bar{X}$	(SE)		$\bar{X}$	(SE)	$\bar{X}$	(SE)		
Peromyscus oreas	OLD	5.4	(1.2)	20.5	(0.2)	110.7	0.9	(0.1)	4.6	(0.1)	4.1	0.87
	MGD	2.4	(0.6)	20.8	(0.8)	49.9	0.4	(0.1)	5.1	(0.3)	2.0	
Clethrionomys gapperi	OLD	2.8	(1.5)	22.5	(0.8)	63.0	0.5	(0.3)	2.2	(0.2)	1.1	0.91
	MGD	2.6	(0.9)	22.1	(0.8)	57.5	0.8	(0.2)	2.6	(0.2)	2.1	
Microtus oregoni	OLD	2.8	(1.5)	19.1	(0.9)	53.5	0.2	(0.1)	3.1	(0.7)	0.6	0.83
	MGD	2.6	(0.9)	18.3	(0.3)	47.6	0.2	(0.9)	2.0	(0.3)	0.4	
Sorex trowbridgii	OLD	8.0	(1.0)	5.3	(0.0)	42.4	1.3	(0.3)	3.3	(0.3)	4.3	0.76
	MGD	5.2	(0.9)	5.2	(0.0)	27.0	0.9	(0.3)	4.0	···	3.6	
Sorex monticolus	OLD	5.2	(1.0)	6.9	(0.3)	35.9	0.8	(0.2)	4.5	(1.5)	3.6	0.90
	MGD	2.3	(0.6)	6.2	(0.2)	14.3	0.4	(0.1)	3.6	(0.8)	1.4	
Neurotrichus gibbsii	OLD	1.3	(0.4)	9.1	(0.1)	11.8	0.2	(0.0)	2.0	···	0.4	0.71
	MGD	0.9	(0.3)	9.1	(0.2)	8.2	0.1	(0.1)	···	···	0.2	
Peromyscus maniculatus	OLD	0.6	(0.2)	19.0	(0.5)	11.4	0.2	(0.1)	5.2	(1.7)	0.8	0.77
	MGD	0.5	(0.2)	17.2	(1.2)	8.6	0.04	(0.0)	2.0	···	0.1	
Sorex vagrans	OLD	0.5	(0.3)	4.1	(0.0)	2.0	···	···	···	···	···	···
	MGD	0.5	(0.2)	4.5	(0.4)	2.4	···	···	···	···	···	

(females with thickened uteri, embryos, placental scars, or evidence of lactation) were positively correlated with species total numerical abundance (Table 6), but reproductive female *Peromyscus maniculatus* were much more abundant in old growth than in managed stands.

Body masses of males and females of the abundant species were normally distributed excepting *Sorexmonticolus*, whose distributions were bimodal with means of 5.5 g and 7.5 g for both males and females. Body lengths and tail lengths were normally distributed. The bimodal weight distributions suggest that two age classes of *S. monticolus* were present. Distributions for other species suggest few young animals were caught; *Peromyscus* spp. in juvenile pelage were caught, could not be assigned to a species, and were not considered in analyses. Analysis of variance (incorporating year of capture, stand age class, and sex) showed no significant differences in mass except for *Peromyscus oreas*. Female *P. oreas* were larger (22.0 ± 0.26 g in old growth and 22.3 ± 0.80 g in managed stands) than males (19.7 ± 0.23 g and 20.0 ± 0.43 g, respectively); thus, we used weighted averages to calculate biomass of *P. oreas*. Biomass followed the same pattern as numerical abundance, as would be expected given no statistically significant differences in average mass of species between stand age classes (Table 6). Old growth supported 1.5 times more biomass than managed stands. Because species differ markedly in mass, a different rank order of abundance emerged. *Peromyscus oreas, Clethrionomys gapperi,* and *Microtus oregoni* be-came dominant and *Sorex trowbridgii* and *Sorex monticolus* became subordinate. We caught enough pregnant females to calculate variances for old vs. managed comparisons of fecundity for *Peromyscus oreas, Clethrionomys gapperi,* and *Microtus oregoni;* no differences were apparent. Relative productivity followed the same patterns as numerical abundance and biomass; production in old growth was

1.5 times that in managed stands. *Peromyscus maniculatus* seemed to produce more young in old growth than in managed stands, but only two pregnant *P. maniculatus* were caught in managed stands; the two embryos and two placental scars found in these mice may or may not be representative of the population mean. Too few female *Sorex vagrans* were caught to evaluate productivity; 69% of *S. vagrans* were male and the reproductive status of the majority of females could not be ascertained.

Predictors of species abundances

Most relationships between species and habitat variables (forest floor coarse woody debris and prevalence of shrub cover) were nonlinear across age classes. Some linear relationships were apparent within age classes. Four species (*S. trowbridgii, N. gibbsii, P. maniculatus,* and *C. gapperi)* increased with coarse woody debris in managed stands. *Sorex trowbridgii* increased in abundance with forest floor coarse woody debris in managed stands (71 % of variance explained), but not old stands. In old stands, coarse woody debris and prevalence of shrub cover explained 96% of the variance in the abundance of *S. trowbridgii* (Table 7). Coarse woody debris was a good predictor of the abundance of *Neurotrichus gibbsii,* particularly in old stands (84% of variance explained); *N. gibbsii* increased in abundance with coarse woody debris in both managed and old stands and overall. Coarse woody debris and prevalence of shrub cover accounted for 83% of the variance in the abundance of *Peromyscus maniculatus* and 77% of *Clethrionomys gapperi* in managed stands, but no significant regression was found in old stands. *Peromyscus oreas* increased with shrub abundance in managed stands (67% of variance explained) and overall (but with only 26% of variance explained). *Microtus oregoni* were best predicted by prevalence of herbaceous cover

TABLE 7. Linear regressions of abundances of common mammal species (ln of captures/100 trap nights + 1) on mean abundance of forest floor coarse woody debris (CWD) and prevalence of shrub cover >24% in old growth and young, managed stands on the Olympic Peninsula, 1987–1989.

		Coefficients			
	Intercept	CWD	Shrubs	P	R^2
Sorex trowbridgii					
Old growth	1.650	−0.014	0.856	0.04	96
Young	0.870	0.0	*	0.02	71
Clethrionomys gapperi					
Old growth	*	*	*	>0.10	*
Young	−0.240	0.096	0.686	0.06	77
Neurotrichus gibbsii					
Old growth	0.331	0.032	*	<0.01	84
Young	−0.083	0.077	*	0.04	59
Peromyscus oreas					
Old growth	*	*	*	>0.10	*
Young	0.680	*	0.668	0.02	67
Peromyscus maniculatus					
Old growth	*	*	*	>0.10	*
Young	−0.375	0.060	0.318	0.03	83

* No significant relationships found.

(57% of variance explained). None of the three habitat variables (coarse woody debris, shrubs, herbs) was a good predictor of the abundance of *Sorex monticolus* or *Sorex vagrans*. The abundance of *S. vagrans*, however, was positively correlated with that of *Microtus oregoni*. No significant correlations were found between the other species of small mammals.

<center>DISCUSSION</center>

<center>*Experimental design*</center>

Our study of small mammals on the Olympic Peninsula was a retrospective survey, not a controlled experiment; thus, our analyses are exploratory and cannot show cause and effect relationships. Our sample sizes of managed and old-growth stands were small relative to complexity and variability that exists at middle elevations on the peninsula, thus some of our statistical tests had low power. Under such conditions, failure to demonstrate differences may simply reflect low sample size. Small sample sizes (seven managed stands and five old-growth stands) do not allow exploration of possible interactive effects and cannot cover well the full potential range of forest development. Few stands, however, exist in the intervening age classes between our managed stands and old growth, and those are often mixed-age stands. Still, we did find considerable overlap in the ranges of the variables in which we were most interested between the old-growth and managed stands (Table 2). We performed multiple comparisons (8 species and numerous attributes) on the 12 samples; thus, nominal P-values are overestimates of significance. Some of our reported differences could have

been due to chance. We studied the mammals in only one season of the year. It is possible that sampling in other seasons could discover additional important relationships between the mammals and their environments. Contrasting our results with those of other researchers in the Pacific Northwest was complicated because of differences in methodology and timing of sampling. Thus, in all our analyses, we endeavored to employ robust analytical methodologies. And the consistency and strength of patterns we observed lead us to have confidence in our results. We believe our results have important implications for forest management as well as providing hypotheses that can be tested in controlled, experimental studies.

<center>*Structure and composition of mammal communities*</center>

The structure of the forest floor mammal communities was similar in all physiographic provinces, regardless of sampling method (Table 4). Communities were dominated numerically by *Sorex trowbridgii*, a 5-g insectivore considered to be the most adaptable of the Pacific Northwest shrews, occupying a wide array of habitat types, consuming 47 types of invertebrates (Whitaker and Maser 1976) and large quantities of conifer seed (Terry 1974). Numerically next are a species of *Clethrionomys*, 22- to 23-g mycophagous microtines, and a species of *Peromyscus*, 18- to 21-g insectivorous and granivorous cricetines, which, together, constitute a majority of the biomass. A 5- to 7-g member of the *Sorex-pacificus-monticolus-vagrans* complex is intermediate in numerical dominance between *Clethrionomys* and *Peromyscus*. Finally, *Neurotricus gibbsii*, a 9-g talpid that consumes large and small invertebrates (annelids, centipedes, isopods) and seeds and berries (Dalquest and Orcutt 1942, Terry 1974, Whitaker et al. 1979), constitutes a small but consistent portion of the community.

Community composition differed south to north: *Sorex sonomae*, abundant in the southern Coast Ranges and Cascades, was gradually replaced by *S. bairdii* beginning in the central Oregon Cascades and markedly in the northern Oregon Cascades (Carraway 1990, Gilbert and Allwine 1991), and by *S. monticolus* in the southern Washington Cascades (Table 4). In the Oregon Cascades, *S. vagrans* constituted <1% of the community in all the areas studied, but was >4 times more abundant in the northernmost Cascades than in the central and southern Cascades (Gilbert and Allwine 1991). *Sorex monticolus* maintained its position in the mammal community on the Olympic Peninsula but *S. vagrans* also became a significant member of the community. *Peromyscus maniculatus* maintained its place in the community from south to north, but *P. oreas* was added as an even more important community member in Washington. *Microtus oregoni*, a 19-g herbivore that occurred in low numbers in Oregon, emerged as a significant member of the forest floor small-mammal community on the Olympic Peninsula.

As community composition changed, so did com-

munity structure. Complexity of structure increased as more species attained consistent membership and as individuals were more evenly distributed among species. This was particularly true on the Olympic Peninsula where the relative importances of *Neurotrichus gibbsii*, *Microtus oregoni*, and *Sorex vagrans* increased, even though all three occur throughout the forests of western Oregon and Washington. Additonal dimensions were added to the community by *Peromyscus oreas*, which is more arboreal (climbing to 15 m) than *P. maniculatus* (Dalquest 1948, Sheppe 1961), and the substitution of *Clethrionomys gapperi* for *C. californicus*. *Clethrionomys gapperi* occupies a wider array of habitats, including forest openings and high elevation meadows (Dalquest 1948, Dragavon 1978, Schmidt 1987), and has a more catholic diet that includes invertebrates, herbaceous material, conifer seed, lichens, and fungi (Ure and Maser 1982, Gunther et al. 1983) than the strictly mycophagous, forest dwelling, fallen tree-associated *C. californicus* (Tevis 1956, Ingles 1965, Ure and Maser 1982, Hayes and Cross 1987).

Factors underlying differences in mammal communities

Comparison of the structure and composition of forest floor mammal communities is complicated by zoogeography and systematics. The Columbia River is a zoogeographic barrier; *Peromyscus oreas* does not occur south of the Columbia River and *Sorex pacificus*, *S. sonomae,* and *S. bairdii* do not occur north of the Columbia River. *Sorex monticolus* only occurs north of the Columbia River except just south of a former natural bridge across the river. *Clethrionomys gapperi* replaces *C. californicus* north of the river. Systematic confusion (Hall 1981, Carraway 1990, Jones et al. 1992) is a hindrance in the use of the literature as an aid to understanding ecological relationships. Results reported here differ from previous published geographic distributions for some of the species. Furthermore, the geographic separation of *Clethrionomys, Microtus, Peromyscus,* and *Sorex* has lead to speciation, subspeciation, and ecological specialization that is coincident with the major, complex, north-south, moisture-temperature gradient that markedly influences forest structure and composition (Franklin and Dyrness 1973). Thus, the influence of forest structure and composition on small-mammal communities cannot be separated completely from zoogeographic and evolutionary influences.

The pervasive influence of the north-south moisture-temperature gradient is best reflected in the composition and structure of old-growth forests. Spies and Franklin (1991) compared the forest communities in the Oregon Coast Range, Oregon Cascades, and southern Washington Cascades. The warm, dry Coast Range and southern Oregon Cascades are the ecotone between the Western Hemlock Zone and the Mixed-Conifer Zone and are characterized by broadleaf species (including evergreen hardwoods), evergreen shrubs, and graminoids

noids. Northward, these plant life forms are replaced by shade-tolerant conifers and herbaceous plants in the understory. Fire return rates decrease and there is low to moderate large-scale disturbance during the life of the stands in the north. Concomitantly, coarse woody debris decays more slowly, lasts longer, and persists in larger pieces in the north; development of soil organic layers including humus and litter is greater in the north. *Pseudotsuga menziesii* loses importance in the canopy and *Tsuga heterophylla* and *Thuja plicata* increase (Spies and Franklin 1991). This transition in canopy species produces, in old growth, a more abundant, more consistent, less seasonal, and more diverse seed resource than is available in forests dominated by *P. menziesii* or in young forests (see Carey 1991:17). Trees and shrubs tend to become established on and in fallen trees in the north, as opposed to in mineral soil in the south. In cool, wet Western Hemlock Zone forests and the ecotone to the Sitka Spruce Zone, dicotyledonous herbs, ferns, and cryptogams become very abundant and varied, with the coverage of epiphytes (especially lichens) conspicuous (Franklin and Dyrness 1973:60-86). Hypogeous, ectomycorrhizal fungi, however, show a reverse trend with 8 species commonly encountered on the Olympic Peninsula, 47 species in the Oregon Cascades, and 97 species in southwestern Oregon (Carey 1991:11). Increasing soil organic matter, humus, and litter, coarse woody debris, and abundance and diversity of seed, combined with a transition from hard-leaved shrubs to deciduous shrubs, forbs, and ferns and reduced diversity of hypogeous fungi are reflected in changes in forest mammal communities, incuding the forest floor communities described here and the arboreal rodent communities described by Carey (1991, 1995) and Carey et al. (1992).

In Western Hemlock Zone forests in Washington, most small mammals consume (in order of relative frequency) invertebrates, conifer seed, lichens, and fungi. Even *Peromyscus* consume more invertebrates than seeds in forested habitats (Tevis 1956, Van Horne 1982, Gunther et. al. 1983). The forest floor small-mammal communities on the Olympic Peninsula have a greater diversity and evenness of insectivores, and an additional species of *Peromyscus* than the communities in Oregon. Increased emphasis on insectivory may be tied to the abundance and variety of decaying organic matter on the forest floor. Decaying wood and forest litter support vast numbers of invertebrates, including the kinds consumed by insectivores (Harmon et al. 1986).

Conifer seeds are the second most important food for forest floor small mammals. For example, both survivorship and reproduction in *Peromyscus maniculatus* may vary with seed abundance, particularly the seed of *Pseudotsuga menziesii* and *Tsuga heterophylla* (Gashwiler 1979). The seeds of *T. heterophylla* are smaller, more abundant, and more consistently available than the seed of *P. menziesii* and also may contribute to the greater diversity of shrews and *Peromyscus* in the Olympic Peninsula forests. All consume significant amounts of conifer seed. *Sorex,* however, do not respond as strongly

as *Peromyscus* to seed abundance (Sullivan and Sullivan 1982). The conifer-seed specialist, *Tamiasciurus douglasii*, also increases in abundance in old growth from southwestern Oregon through southwestern Washington (Carey 1989:157), on the Olympic Peninsula and in the North Cascades (Carey 1995).

Fungi are a third major food resource. However, the mycophagous and conifer-seed eating *Tamias townsendii* declines markedly in abundance from Oregon to the Olympic Peninsula, as does the mycophagous *Glaucomys sabrinus* (Carey 1991, 1995; Carey et al. 1992). These two species are reduced even further in abundance in the North Cascades (Carey 1995). *Tamias townsendii* seems to be food limited (Sullivan et al. 1983) and, in Oregon, depends upon two seasonally abundant types of food (conifer seed and hypogeous fungi). Thus, its lowered abundance in northern Washington might reflect the changes in fungal diversity and abundance. Whereas *Clethrionomys californicus* in Oregon is a mycophagist, *C. gapperi* has a broad diet (emphasizing lichens and seed in addition to fungi), but is still among the least insectivorous of the forest floor small-mammal community. Fungi are important food for small mammals in Washington, but strict mycophagy necessitates a consistent supply of fungi. The abundance of fungal sporocarps, particularly hypogeous sporocarps, is highly variable among years and seasons (Luoma 1988, 1991); low fungal species diversity could preclude strict mycophagy. Low hypogeous fungal diversity could be offset somewhat by the abundance and diversity of lichens.

The transition from shrubs to forbs is probably the factor underlying the addition of *Microtus oregoni,* an herbivore, to the communities on the Olympic Peninsula. *Microtus oregoni* supplants *Clethrionomys gapperi* in subalpine meadows in Washington (Dragavon 1978) and *Peromyscus maniculatus* in clearcuts dominated by herbaceous cover in the coastal coniferous forests of British Columbia (Petticrew and Sadleir 1974, Sullivan 1980). In Oregon, *M. oregoni* is abundant on clearcut and burned sites with high herbaceous cover (Goertz 1964, Hooven 1973, Hooven and Black 1976) and woodlands, glades, and riparian forests, but rare in mature and old-growth conifer forests (Gashwiler 1959, 1970, 1972; Hooven 1973; Corn et al. 1988). Its tie to herbaceous plants seems clear. Doyle (1985, 1990) and Anthony et al. (1987) found *M. oregoni* to be abundant in streamside conifer forest in the central Oregon Cascades. In addition, they found an increased diversity in the small-mammal communities associated with streamsides as compared to upland, coniferous forests. Streams not only had water-associated small mammals such as *Sorex palustris, Sorex bendirii*, and *Microtus richardsoni*, but also another herbivorous vole, *Phenacomys albipes*, and greater abundances of *Peromyscus maniculatus*, *Clethrionomys californicus*, and *Neurotrichus gibbsii* (and herbaceous vegetation and deciduous shrubs) than upland sites. McComb et al. 1993)

reported similar findings in the Coast Range except *C. californicus* and *M. oregoni* were in greater abundances on upslopes than on streamsides. The moist microclimate around streams in the central Oregon Cascades and Coast Range (and probably elsewhere) appears to increase diversity of communities in a fashion similar to the major moisture-temperature gradient that dominates forest communities in Oregon and Washington. In addition, even small streams have canopy gaps that stimulate understory development (Carey 1988, McGarigal and McComb 1992).

In the warm and relatively dry southwestern Oregon forests other changes take place. *Neotoma fuscipes*, adapted to eating evergreen foliage high in fiber, tannins, and related polypeptides (Atsatt and Ingram 1983) is abundant in the southernmost transition forests in Oregon (Carey 1991, Carey et al. 1992), but does not occur north of the Columbia River. *Neotoma cinerea*, abundant in the warm, dry southwestern Oregon forests, is relegated to rock outcrops in Washington (Carey 1991). Southwestern Oregon is also an area of speciation in *Tamias* and *Phenacomys* [*Arborimus*] (Johnson and George 1991). Thus, it seems that diversity of forest floor small-mammal communities follows a trend opposite that of medium-sized arboreal and semi-arboreal rodents.

Changes in moisture regimes caused by local environmental settings and changes in light regimes caused by forest development from young, closed-canopy forest to open-canopied old growth or to canopy gaps associated with streams, can bring about changes in forest floor small-mammal communities that are similar in Oregon and Washington. However, the regional moisture-temperature gradient seems to cause more profound effects, perhaps even influencing basic ecosystem processes. For example, in warm, dry regions, trees and shrubs root in mineral soils which have a high diversity of hypogeous, ectomycorrhizal fungi (which assist plants in nutrient uptake). Whereas, in cool, moist regions, rooting as in decaying wood, soils are apparently depauperate in hypogeous ectomycorrhizal fungi and are covered with moss, and lichen fall is high and high in nitrogen. Heavy moss cover efficiently intercepts nutrients in through-fall and precipitation, acts as a reservoir of sequestered nutrients, and serves as a barrier to nutrient availability to trees and fungi, limiting production of both. Release of sequestered nutrients depends upon drying events that kill mosses and subsequent rewetting (Carleton and Read 1991). Even common forest structures may differ in function along the gradient. In the dry, southwestern Oregon forests, large fallen trees act as moisture reservoirs and refugia for hypogeous ectomycorrhizal fungi during and after drought and wildfire (Amaranthus et al. 1989) and serve as important foraging sites and travelways for *Clethrionomys californicus* (Hayes and Cross 1987). But, these fallen trees do not seem as important as reservoirs and refugia in the more mesic forests to the

north. There, *C. gapperi* is less tied to fallen trees and fungi and can even become abundant in clearcuts where logging slash and the attendant lichens are abundant (Gunther et al. 1983).

In summary, the structure and composition of the forest floor small-mammal communities differed more along the north-south moisture-temperature gradient than between young and old-growth forests. Communities in the Olympic Peninsula Western Hemlock Zone forests were more diverse, with a greater number of species and a more even distribution of individuals among species than communities to the south. The increasing complexity in the forest floor small-mammal communities along the south-north gradient was accompanied by a decreasing complexity in the mediumsized, arboreal and semi-arboreal rodent community (*Phenacomys, Neotoma, Tamias, Glaucomys,* and *Tamiasciurus*). Changes in the forest floor plant communities induced by increasing rainfall and decreasing temperature seem to be more compositional and functional than structural.

Managed vs. old-growth forests

The differences between managed and old-growth forests on the Olympic Peninsula were qualitatively similar to those reported by Carey et al. (1991) at the southern extreme of the Western Hemlock Zone in the Oregon Coast Range. Young stands had greater canopy closure, density of trees, and density of small-diameter snags. Old growth had more large trees, large snags, and foliage-height diversity (greater understory and midstory development). But shrub cover and relative abundance of forbs, ferns, and deciduous shrubs (vs. evergreen shrubs) in the Coast Range were more related to local moisture conditions than to stand age. On the Olympic Peninsula, young stands were more likely to have an evergreen shrub (*Gaultheria shallon*) as a major associate than old stands which were more likely to have a deciduous shrub (*Vaccinium alaskaense*) as a major associate. Understory development in managed stands on the Peninsula seemed more related to stand history (species planted or seeded and thinning) than to local site conditions. Stands that regenerated to *Tsuga heterophylla* and had no subsequent management had greater canopy closure, poorer (to absent) understory development, and higher moss cover than stands with *Pseudotsuga menziesii* in the overstory and stands that were thinned. Coarse woody debris in young stands (some managed, most naturally regenerated) in the Coast Range was 94% of that in old growth (Corn and Bury 1991a, b), whereas coarse woody debris in our managed stands averaged only 61 % of that in old growth. Still, mean cover of coarse woody debris did not differ statistically between young and old stands because of high variances, particularly in old growth. In a regional analysis, Spies and Franklin (1991) reported results more similar to our Olympic Peninsula results than to the results from southwestern Oregon.

Spies and Franklin (1991) examined four classes of attributes: overstory, stand condition (degree of decadence), understory, and debris. Old-growth overstories differed from young, natural overstories in having low densities of trees, larger trees, and greater variation in tree diameters due to large, dominant *Pseudotsuga menziesii* and smaller, shade-tolerant species. Our stands differed from those described by Spies and Franklin (1991) in having old-growth overstories composed primarily of shade-tolerant species and in the incorporation of shade tolerants even in the canopies of managed stands. Old-growth stands differed from young, natural stands in having higher levels of decadence (cavities in trees, resinous, broken tree tops), but decadence was highly variable reflecting histories of natural disturbances, such as windstorms, in individual stands. We observed the effects of localized disturbances in our study areas also. Spies and Franklin (1991) found that cover of herbs, deciduous shrubs, and shade-tolerant saplings increased with age. However, total volume of coarse woody debris in young, natural stands was 1.7 times that in old growth, a result much different from ours. The catastrophic disturbances creating the natural stands added large amounts of coarse woody debris that persisted for 100 yr, resulting in a U-shaped distribution of coarse woody debris with the lowest values at 80-120 yr (Spies et al. 1988). Logging, of course, resulted in our managed stands having much less coarse woody debris. Litter depth and arboreal lichens increased with age and latitude (Spies and Franklin 1991). Despite some similarities in forest structure and composition, old growth provides a distinctly different environment than young stands (managed and natural) throughout the Pacific Northwest.

Despite the marked differences in forest structure between old growth and naturally regenerated young stands, forest floor mammal communities differed only in southern Washington where *Peromyscus maniculatus* and *P. oreas* were more abundant in old growth, suggesting that differences in understory development along with differences in plant species composition were responsible for the differences. On the Olympic Peninsula, where compositional differences were more extreme, and where the young, managed stands had less coarse woody debris than old stands, important differences in community composition, community structure, and abundances of species emerged, suggesting influences of plant community composition, understory development, and coarse woody debris abundance. Of particular note is the increased importance of *Neurotrichus gibbsii* and *Microtus oregoni* in the communities. *Neurotrichus gibbsii* might well be responding to increased development of soil organic layers; *M. oregoni* to increasing abundances of herbaceous plants.

On the Olympic Peninsula, *Sorex trowbridgii, S. monticolus, Neurotrichus gibbsii,* and *Peromyscus oreas*

were more abundant in old growth than in managed stands. Species biomass and relative productivity also were greater in old growth than in managed stands. Indeed, relative productivity was highly correlated with abundance across all stands. Our regression analyses suggest that coarse woody debris might have limited *Sorex trowbridgii*, *Clethrionomys gapperi*, and *Neurotrichus gibbsii* in young, managed stands, but only *N. gibbsii* in old growth. Development of woody understory vegetation, including tall, deciduous shrubs, leads to increased abundance of S. *trowbridgii* in old stands where coarse woody debris is abundant, and determines, in part, the abundance of *P. oreas* in managed stands. *Clethrionomys gapperi* and *P. maniculatus* showed positive responses to both understory development and coarse woody debris in managed stands, but not old growth. Old growth had 2.4 times the prevalence of tall shrubs and 1.6 times the cover of coarse woody debris in managed stands. Distribution of coarse woody debris and prevalence of low shrubs were similar in old-growth and managed stands. A putative dependence of M. *oregoni* on the abundance of herbaceous plants was reinforced by regression. Prevalence of herbaceous plants was similar in old-growth and managed stands.

These results suggest that the characteristics of the forest floor (including coarse woody debris) and understory vegetation (especially the prevalences of herbs, low shrubs, and tall shrubs) are indeed important influences on the forest floor small-mammal community-that variation that exists in forest stands, even stands of similar age structure, is sufficient to account for marked variation in species abundances (and reproductive attainment). Our results also suggest that, while a multiplicity of environmental factors are important determinants of species abundances, two factors (coarse woody debris and prevalence of shrub cover) play primary roles. Species responses to these factors are nonlinear and conditioned by the greater stand environment, and thresholds for inflection points or asymptotes in response curves differ among species. We found no evidence, in correlations between species abundances, that interspecific competition, even among closely related species, was playing any major organizing role in the communities we studied. While we cannot demonstrate a cause and effect relationship between the habitat variables and population responses we measured, and indeed we doubt that the two primary habitat factors we chose to examine are ultimate determinants of species responses, we have described how these factors might be important to the species we studied. The species comprising the forest floor community all seem to be generalists rather than species tightly tied to some rare or unique habitat element or condition. But we believe we have demonstrated that forest structure and composition play a predictable role in the structure and diversity of small-mammal communities.

Implications for forest management

The results of our regional analyses, comparisons of old-growth and managed stands, and demonstration of species responses to understory vegetation and coarse woody debris have manifold implications for management of second-growth forests in western Washington and Oregon for biodiversity, including restoration of old-growth conditions and enhancing managed stands for species associated with late successional forests. We discuss opportunities for enhancement of habitat quality in Western Hemlock Zone forests beginning with protection of streamside forests. Then we discuss conservation of coarse woody debris and silviculture for managed forests. Our goal is not to provide a silvicultural textbook or cookbook. Comprehensive overviews of silviculture are available (Burns 1983, 1989; Oliver and Larson 1990). Actual management of any specific stand or landscape must be tailored to local ecological conditions and often may have to address multiple objectives. However, we identify practices that our research suggests would be beneficial. The results of managing for diversity will differ geographically in terms of both the plant and animal species benefited, even though the management practices may be the same.

Streamside forests.—Protection of riparian areas stands out as a primary management implication. Not only do streamsides and wetlands in upland forests support small mammals adapted to exploiting aquatic habitats, they also maintain a diversity and abundance of forest floor generalists (Anthony et al. 1987, Doyle 1990, McComb et al. 1993) and arboreal rodents (Carey et al. 1992). Additionally, even small streams in upland forests contribute to the diversity of forest bird communities (Carey 1988) and to bird species such as *Strix occidentalis* (Carey et al. 1992). Small streams are also important to forest bat communities (Thomas and West 1991) and, especially, to forest amphibian communities (Carey 1989, Bury et al. 1991*b*, McComb et al. 1993). Streams and drainages thus provide the template for landscape management systems for maintaining biodiversity.

Conservation of coarse woody debris.—Our empirical data suggest that 15-20% cover of coarse woody debris on the forest floor, well distributed across the site, would be adequate for most small mammals, whereas 5-10% cover would not allow the mammals to reach their potential abundances. But coarse woody debris, especially large, standing and fallen dead trees, is not only an important habitat component for forest floor small mammals, but also provides critical habitat elements for birds (Carey et al. 1991) and amphibians (Bury et al. 1991*a*, Corn and Bury 1991*b*).

Any harvest of overstory trees incurs impacts on the coarse woody debris components of the forest. Not only are trees removed that would eventually contribute to coarse woody debris (as standing dead trees or fallen trees), but the mechanics of tree removal also can have severe effects on the existing coarse woody debris.

Standing dead trees often have to be felled before harvest operations can take place. Moderately- to well-decayed fallen trees are easily broken and crushed. Disrupting intact fallen trees seems to hasten markedly the fragmentation of the remaining bole.

Yarding operations should be designed to minimize overall impacts on coarse woody debris, even at the expense of more severe local impacts. Aerial yarding, of course, would have the least impact. Tractor and cable yarding could utilize corridors to reduce disruption of fallen trees. Retention of unmerchantable logs on site and, if necessary, leaving some large merchantable logs would be of value. Removal of merchantable trees with limbs and tops intact would reduce amount of logging slash left on site and minimize fire hazard and impediments to regeneration. Leaving tall (1-2 m) stumps from large trees can be of particular importance in contributing to coarse woody debris, seedbeds for shade-tolerant trees and understory shrubs such as *Vaccinium* spp., and substrates for epiphytes. Large, decaying stumps in young stands are often used by forest floor and arboreal rodents as nest sites and escape cover (A. B. Carey, *unpublished data*).

Minimizing site preparation (scarification, piling of slash and coarse woody debris, and prescribed burning) after a regeneration harvest would do much to conserve coarse woody debris and other forest floor organic matter. Site preparation in the Pacific Northwest that included prescribed burning removed an average of 34% of woody debris and 29% of the forest floor (Miller and Bigley 1990). While wildfire (crown fires) in old growth may destroy some coarse woody debris, it also kills many standing trees that eventually fall; coarse woody debris accumulations after wildfire are tremendous. Prescribed fire in clearcuts destroys some to all of the existing fallen trees, depending on intensity and type of site preparation, but there are usually no standing live trees to be killed or injured and contribute coarse woody debris.

Regeneration harvests.—Clearcutting probably will remain a method-of-choice for harvest of wood products and regeneration of *Pseudotsuga menziesii* in much of the Pacific Northwest (Fiske and DeBell 1989), but shelterwood and uneven-aged systems are reasonable alternatives when biodiversity and other ecologic and economic values are considered along with timber production (Williamson and Twombly 1983, Fiske and DeBell 1989). Still, in certain types of stands, such as densely stocked stands of trees of small diameters and low live crown-to-height ratios (which suggest trees may not respond to thinnings), removal of the overstory by clearcutting may be the quickest way to create a stand that can be managed to provide old-growth characteristics. In older, more vigorous stands where regeneration harvests are deemed necessary by the landowner, shelterwood and group selection systems (and other methods that retain live trees) can provide more opportunities for continuous

recruitment of coarse woody debris, maintaining biodiversity, and hastening recovery of full ecologic function than clearcutting. Shelterwood and uneven-aged management systems more closely mimic natural disturbance regimes than clearcutting (Fiske and DeBell 1989), particularly when coarse woody debris, live trees, and even patches of intact forest are retained as biological legacies that provide refugia and sources of recolonizers, particularly fungi, lichens, and cryptogams.

Site preparation and planting.—Minimizing site preparation not only conserves coarse woody debris but also many of the shrubs and young trees that existed in the previous stand. Site preparation in the Pacific Northwest, such as burning, has often led to destruction of existing shrubs and establishment of pioneer species. Species such as *Alnus rubra* may become established in amounts sufficient to suppress other shrubs and conifer regeneration. In Washington, excessively dense stands of *Tsuga heterophylla* may become established and preclude any understory development. Burning reduces vegetation cover by 50% for at least the first 3 yr and promotes dominance by *Pseudotsuga menziesii* and hardwoods in the resulting stand; unburned clearcuts produce stands with a greater evenness of conifer species (Miller and Bigley 1990). While burning has not been shown to reduce site productivity (Miller and Bigley 1990), Williamson and Twombly (1983) cautioned that burning may volatilize nitrogen, cause leaching of soil cations, and lead to surface erosion. Current practices of planting widely spaced seedlings (Fiske and DeBell 1989) do not require intensive site preparation and allow for desirable shrubs to be maintained in the early stages of stand development. Prescribed burning of logging slash is being limited by local governments to maintain air quality (Fiske and DeBell 1989); regeneration efforts have not suffered. Incidences of *Alnus rubra* invasion that necessitate control efforts have been reduced. The low numbers of *Alnus rubra* that do become established add an element of diversity and may contribute to the growth of the other plants because of their nitrogen fixation. After clearcutting, planting (as opposed to seeding) is desirable to ensure a mix of conifer species. Planting of *Pseudotsuga menziesii* is often necessary to ensure its presence in the developing stands. Planting other species may or may not be necessary or desirable depending on the site and existing seed sources. A mix of artificial and natural regeneration promotes genetic diversity (Williamson and Twombly 1983). The seeds of *P. menziesii*, the sporocarps of its associated mycorrhizal fungi, and the seeds of *Tsuga heterophylla* are important foods for many small mammals.

In harvests, particularly partial harvests, of overstory trees in stands with poor understory development and high moss cover, scarification may be necessary to remove moss to promote development of understory herbs and shrubs and regeneration of conifers.

Thinnings.—The substantial acreages of second

growth naturally seeded and planted forests in the Pacific Northwest perhaps present the most opportunity for management for biodiversity. Intervention in these stands in both the stand initiation stages and stem exclusion stages (Oliver and Larson 1990) can maintain plant species diversity and eliminate the long interval between the stem exclusion stage and the understory reinitiation stage. Early (stand initiation stage) thinnings may often be necessary to maintain a mix of tree species and continued development of understory herbs and shrubs. These early thinnings can do much to prevent stand stagnation and hasten the development of forest stature and structure.

As the canopy closes in the developing stand (stem exclusion stage), removal of trees (often merchantable) by thinning from below (i.e., removing subordinate and some codominant trees) may be warranted to maintain understory development and a desirable mix of overstory species, to promote the development of shade-tolerant understory trees, and to hasten the development of a fully statured stand. The goal would be to promote a diversity of woody species and a continuous column of vegetation that includes low shrubs, tall shrubs, and midstory trees. Maintaining deciduous tree species further adds to biodiversity, including food (seeds) and shelter (cavities) for wildlife.

At this stage, thinning with variable spacing, as opposed to thinning to even spacing, should be implemented to provide the spatial heterogeneity characteristic of old growth (Carey et al. 1991) that promotes diversity in the understory vegetation (herbs, low shrubs, tall shrubs, shade-tolerant trees). Variable spacing can be done on a scale (0.1-0.5 ha or 40- to 80-m wide strips) that can markedly reduce disturbance of coarse woody debris compared to conventional even spacing. Of course, at this stage, removal or killing of living trees forestalls natural mortality of these trees and their contribution to the coarse woody debris component. Thus, as trees reach a large size (>50 cm diameter), techniques for accelerating the development of cavity trees (Carey and Gill 1983) may have to be applied, and some trees may have to be felled to provide a continuing abundance of coarse woody debris.

Recent research (Curtis 1992) suggests that long rotations and multiple thinnings provide intermediate timber (financial) yields as well as production of high-value timber and that short rotations involve a large loss in potential volume production. Thus, even from a strictly economic standpoint, some of our recommendations for maintaining biodiversity through thinnings should prove attractive to land managers.

Rotation age.—Depending on overall objectives, stands may be maintained for hundreds of years or partially harvested to produce self-perpetuating un

even-aged stands. In other cases, contributions to biodiversity can be maintained through managing stands in the landscape on long (>350 yr) rotations (Harris 1984). But even where the management objective is production of wood products, rotation ages of <150 yr, retention of live trees at harvest combined with coarse woody debris, and understory vegetation enhancement could do much to help preserve biodiversity in the managed landscape.

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