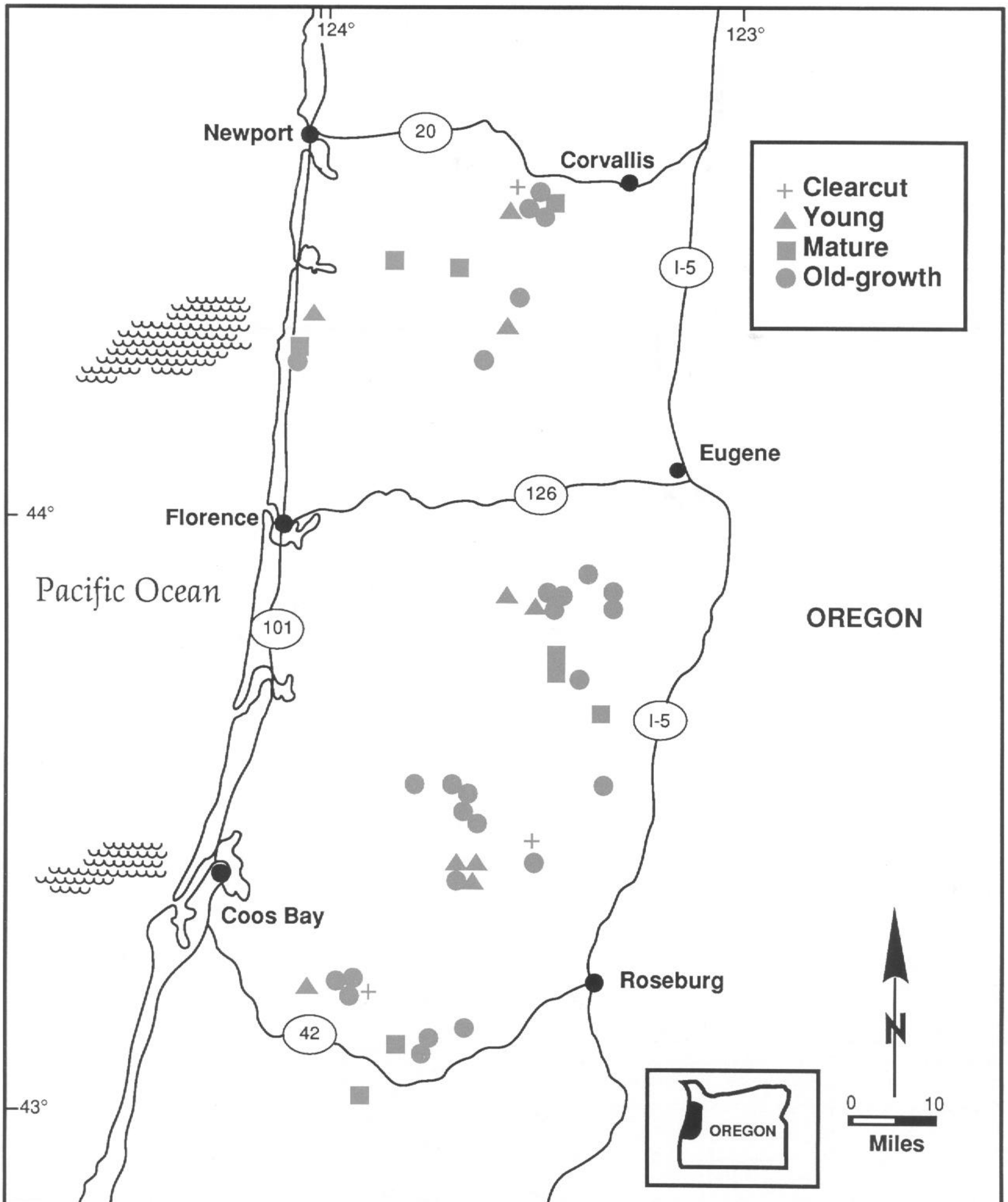
Part 5

Small Mammals of Oregon and Washington



Location of study sites.

Small Mammal Communities in the Oregon Coast Range

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Abstract

We used pitfall trapping to sample small mammals in clearcut, young, mature, and old-growth forests in the Coast Ranges of Oregon in 1984 and 1985. Our objectives were to identify species or groups of species associated with old-growth forests and to identify structural components of the habitat associated with mammal abundance. Trowbridge's shrews, red-backed voles, and Pacific shrews were the most abundant species in forested stands; vagrant shrews, deer mice, and creeping voles were most abundant in clearcuts. Significantly more red tree voles were captured in old-growth stands than in mature and young stands, and Pacific shrews were significantly more abundant in mature stands than in either young or old-growth stands. No significant differences were found in the abundance of any species across a moisture gradient in old-growth stands. No strong correlations were found between habitat variables and the abundance of any mammals. Abundance and diversity of small mammals were greater in mature stands than in young stands, but abundance and diversity in old-growth stands broadly overlapped both mature and young stands. Diversity of small mammals did not display a U-shaped curve relative to stand age (high diversity in young and old-growth stands and low diversity in mature stands).

Introduction

The Pacific Northwest harbors one of the richest communities of small mammals in North America. Several species are endemic to the region, with their distributions restricted to forests west of the Cascade Range in California, Oregon, Washington, and British Columbia (Hagmeier and Stults 1964, Simpson 1964). These species include the Trowbridge's shrew, Pacific shrew, marsh shrew, shrew-mole, western red-backed vole, creeping vole, red tree vole, and white-footed vole (Ingles 1965, Maser and others 1981, van Zyll de Jong 1983). Because a majority of the forests west of the Cascade Range were old growth before logging began (Harris 1984, Spies and Franklin 1988), a logical hypothesis is that many of the unique small mammals of the region would reach their greatest abundance in old-growth forests. Early lists of vertebrates associated with old-growth forests included several small mammals (Franklin and others 1981, Meslow and others 1981), but data on habitat use were scarce for most of them.

Several habitat features of Douglas-fir forests when plotted against stand age have a U-shaped curve (high values in young forests, low values in mature forests, and the highest values in old-growth forests). These features include amount of coarse woody debris, heterogeneity of the understory, and plant species diversity (Spies and Franklin 1988). Because these features (particularly coarse woody debris) may be significant biological components of the habitat of forest mammals, Spies and Franklin (1988) hypothesized that species diversity of mammals follows the same U-shaped distribution with forest age. Raphael (1988c) did not find this distribution of mammals in northern California (diversity of mammals was highest in mature and old-growth forests), but few data existed relating species diversity to age of Douglas-fir forests in Oregon and Washington.

The Old-Growth Program was chartered, in part, to address the lack of information on the abundance of vertebrates and their habitat associations (Ruggiero and Carey 1984). Pilot studies were conducted in the Cascade Range in 1983 (Corn and others 1988), and, in 1984, vertebrate community studies were extended to the Coast Ranges in Oregon. The need for studies of old growth is most acute in the Coast Ranges. Because of fire and logging, little old growth remains (Spies and Franklin 1988), and it is distributed in small, scattered fragments (Harris 1984, Monthey 1984).

In this paper, we report the results of pitfall trapping of small mammals over a large area of the Coast Ranges in 1984 and 1985. Our objectives were to:

- Determine the relative abundance and diversity of small mammals in young, mature, and old-growth forests and across a moisture gradient in old growth;
- Compare the abundance of small mammals to physiographic features and vegetative characteristics important for maintaining diversity of small mammals; and
- Contrast differences in the abundance of small mammals between old-growth forests and clearcuts as a first step in comparing managed and natural forests.

Met hods

Study Areas

We studied 45 closed-canopy forest stands and 3 recently clearcut stands in the Coast Ranges of Oregon (see frontispiece). Three stands were near the coast in the vicinity of Cape Perpetua, but most stands were in the interior or on the eastern flank (valley margin) of the Coast Ranges. Most of the stands were south of Eugene on land managed by the Bureau of Land Management (BLM). One stand near Drain was on land owned by International Paper Company. Stands north of Eugene were on BLM land, the Siuslaw National Forest (including Cape Perpetua and Lost Creek Wilderness Areas), or land managed by the city of Corvallis (Marys Peak).

Stand Selection and Classification

Stands were selected initially to conform to a chronosequence of four categories beginning with 3 clearcut stands (less than 10 years old), 8 closed-canopy young stands (40-75 years), 10 mature stands (80-120 years), and 27 old-growth stands (150-525 years). Except for one young stand, the last three categories were all composed of naturally regenerated forests. Ages of stands were estimated a *posteriori* by increment coring of at least five dominant Douglas-fir trees per stand (young and mature stands), Ages of old-growth stands were estimated from increment cores and by examining stumps in adjacent clearcuts and roadsides (Spies and others 1988).

A moisture gradient (wet, moderate, and dry) was examined for old-growth stands. The initial position on the moisture gradient was determined largely by topographic position, for example, south- or west-facing ridges were generally dry, whereas stands on north-facing slopes were usually moist to wet. Later, a moisture classification was made based on a multivariate ordination of understory vegetation (Spies and Franklin, this volume). In the Coast Ranges, this resulted in five stands originally considered wet being reclassified as moderate, and one stand originally considered moderate being reclassified as dry. We used the revised classifications in this paper.

Pitfall Trapping

We installed 36 pitfall traps, 15 m apart in a square grid, in each stand in summer 1984. Each trap was constructed from two number-10 cans (3.2 1 volume), stacked and joined with duct tape (Bury and Corn 1987). A short plastic funnel (0.45kg margarine tub with the bottom cut out) nested in the top of the trap. Traps were buried flush with the ground and covered with a cedar shingle that was suspended 3 to 4 cm above the opening with twigs or small rocks. Between the time traps were installed and trapping began and at the end of each trapping season, traps were closed with a tight-fitting plastic lid.

Logistics of trapping 48 stands concurrently dictated placement of pitfall grids to some extent. The near comer of each grid was placed about 100 m from the edge of the stand. This distance was a compromise between the need to avoid edge effects and the need for a field crew to be able to check the grids in five to seven stands in one day.

We opened traps during the first week in October and trapped continuously for 50 days in 1984 and for 30 days in 1985. No water was put in traps because this has a deleterious effect on the preservation of amphibians, which were also sampled with pitfall traps (Corn and Bury, this volume b). In practice, most traps accumulated some water and most mammals drowned. Drowning is the method recommended by the American Society of Mammalogists (1987) when pitfall traps are used as kill traps. We checked traps about once a week; trapped animals were removed and any water that had accumulated was bailed out.

We determined sex and age and made standard measurements (total, tail, foot, and ear lengths, and mass) of mammals, which were then preserved whole in lo-percent formalin, or as skulls, skeletons, or skins and skulls. Specimens were deposited in the National Museum of Natural History, Washington, DC, where all species identifications were verified.

Vegetation Sampling

We sampled vegetation at nine points within the pitfall grid, with the center of each sampling plot equidistant from four pitfall traps. We measured or estimated physiographic, coarse woody debris, live tree, and ground-cover variables (appendix, table 6) in two nested circles. Percentage cover was estimated visually; all other variables were direct counts or were measured. Variables in the interior circle (5.6-m radius, 100 m^2) included slope, cover by down wood, numbers of small snags and small trees, and most ground-cover variables. Variables in the outer circle (15-m radius, 707 m^2) included the presence or absence of water, rock outcrops, or talus; the number of medium and large snags and trees, and cover by midstory and canopy trees. Count variables were converted to density (number per hectare). Because no single vegetation measurement was directly related to a single pitfall trap, we averaged the nine values for each variable to produce a single value for each pitfall grid.

Statistical Analyses

All statistical analyses were done on a microcomputer using SYSTAT. Analysis of the chronosequence was originally intended to exclude wet and dry old-growth stands, so comparisons among young, mature, and old-growth stands would not be influenced by the greater range of moisture conditions in old-growth stands (Carey and Spies, this volume). Mature and young stands had much greater variation on the moisture gradient than expected (Spies and Franklin, this volume), however, so only those old-growth stands that were outliers on the moisture gradient were excluded. In the Coast Ranges, all but two old-growth stands were' retained in the chronosequence analyses. Analysis of the moisture gradient was restricted to old-growth stands.

To facilitate comparisons between years and to reduce the effect of migration onto the trap grid, we used only animals captured during the first 32 to 34 days (the closest we could come to 30 days, because traps were not checked daily) in 1984 (but see below). We measured abundance as the number captured per 100 trap-nights. Analysis of the abundance of individual species depended on numbers captured. "Common" species were captured in more than 50 percent of the stands and with more than 50 total captures. "Rare" species occurred in less than 50 percent of stands with less than 50 but more than 10 captures. For some species-for example, flying squirrels-abundance data may reflect bias from the trapping technique rather than the actual density of the species. Differences on the age and moisture gradients for common species were analyzed by analysis of variance (ANOVA) of log-transformed data ($\log_e$ of abundance + 1). We used Tukey's honestly significant difference for unplanned multiple comparisons (Sokal and Rohlf 1981). Because of the low sample sizes, we used all captures of rare species in both years. Differences in numbers captured among age- and moisture-classes were tested using the G-test (log likelihood ratio) for goodness of fit (Sokal and Rohlf 1981).

Physiographic and vegetative variables--Variables measuring percentage cover were arcsin-transformed (Sokal and Rohlf 1981) before analysis. Count variables had large variances which were log-transformed. We computed Pearson product-moment correlation coefficients between the abundance of common species and each physiographic and vegetation variable. For these six species, we performed multiple regression on subsets of physiographic and vegetative variables. We first eliminated highly intercorrelated variables, then chose variables for each regression model using a stepwise procedure with a significance level of 0.10 to add or remove variables. For rare species, we compared mean values of physiographic and vegetation variables between stands where each species was present or absent. We also performed a principal components analysis with a subset of eight vegetation variables (table 1): LOGS (the sum of DLOGSA, DLOGSB, and DLOGSC), LSNAG, DECSNAG, CTREEL, MCTREE, CCTREE, FERN, AND ESHRUB. These variables represent characteristics used in ecological definitions of old-growth Douglas-fir forests (Franklin and Spies 1984, Morrison 1988, Spies and Franklin 1988). The variables were transformed but not standardized because the scales were generally equivalent after transformation. We used factors produced by the principal components analysis with eigenvalues greater than 1 to examine whether the vegetation variables we measured were reflecting differences among habitat types.

Mammal community structure-We examined the relations among stands in small mammal fauna by using nonmetric multidimensional scaling. By using a matrix of similarities among stands, multidimensional scaling analysis computes the coordinates of a set of stands in a few dimensions (usually 2 to 3), so that the distances between pairs of stands fit as closely as possible to their measured similarities (Wilkinson 1988). We measured similarity as the Euclidean distance between pairs of stands using the abundance (number per 100 trap-nights) of Trowbridge's shrews, Pacific shrews, vagrant shrews, marsh shrews, shrew-moles, and red-backed voles. We chose these six species as most likely to have been sampled in an unbiased manner by pitfall traps. Abundance was not standardized, because we were interested in the relative contributions of each species. To interpret the axes produced by multidimensional scaling analysis, we correlated them with the abundance of each species, total abundance (the sum of the six species), species diversity (Berger-Parker index, Magurran 1988), and physiographic and vegetative variables.

We used the abundances of the six species above and the K-MEANS procedure of SYSTAT to generate a specified number of non-overlapping pools (clusters, see Pielou 1984) of stands. We generated five pools because of the *a priori* classification of stands into five habitat types. The stands belonging to each pool were then plotted against the axes generated by the multidimensional scaling analysis to see if any patterns could be identified in the mammal community.

Results

Abundance of Small Mammals

We captured 3047 individuals of 20 species of small mammals in both years (table 1). Total numbers captured in each year were very similar: 1514 in 1984 and 1533 in 1985. Precipitation may affect capture rates of small mammals (Bury and Corn 1987), so we examined data from eight weather stations in the Coast Ranges (U.S. Department of Commerce, Climatological Data). Mean precipitation was slightly higher in 1984 (19.9 cm) than in 1985 (16.6 cm), but patterns of rainfall were similar in both years. The first region-wide rain was recorded 4 October in 1984 and 7 October in 1985, and rain was recorded almost daily in the second half of October in both years.

Deer mice were captured more frequently in 1985 than 1984 (P < O.OOl), but no significant differences were found between years for any other species. All further analyses used the combined abundance (1984 + 1985) of each species. Six common species (Trowbridge's shrew, Pacific shrew, shrew-mole, coast mole, western red-backed vole, and deer mouse) had 55 to 1690 total captures (62-64 trap days). Four other rare species (marsh shrew, vagrant shrew, red tree vole, and flying squirrel) had 17 to 31 total captures (80 trap days). Ten other species had fewer than 10 captures, which was too few for meaningful analysis of differences in habitat types. These included species not well-sampled by pitfall traps (Townsend's chipmunk, Douglas' squirrel, and ermine), species from adjacent grassland habitats (Townsend's mole and California vole), and species most common in riparian habitats (white-footed vole and western jumping mouse).

Table l-Total numbers of small mammals captured by pitfall grids in 45 forest stands in the Oregon Coast Ranges in 1984 and 1985

Species	1984[a]	1985	Total
Insectivores:			
Trowbridge's shrew[b]	896	794	1690
Pacific shrew[b]	187	153	340
Vagrant shrew[c]	12	14	26
Marsh shrew[c]	7	10	17
Shrew-mole[b]	45	41	86
Coast rnole[b]	27	28	55
Townsend's mole[d]	2	1	3
Rodents:			
Western red-backed vole[b]	282	359	641
Red tree vole[c]	5	8	13
White-footed vole[d]	0	2	
Creeping vole[d]	2	7	9
California vole[d]	2	0	2
Long-tailed vole[d]	0	1	
Townsend's vole[d]	0		1
Deer mouse[b]	29	90[e]	119
Western jumping mouse[d]	1	4	5
Northern flying squirrel[c]	11	14	25
Townsend's chipmunk[d]	0	4	4
Douglas' squirrel[d]	0	2	2
Carnivores:			
Ermine[d]	6	0	6
Total (all mammals)	1514	1533	3047
Number of species	14	19	20

[a], Only captures from the first 32 to 34 trap days are listed.
Common species were captured in more than 50 percent of the stands and with more than 50 total captures.
[c] Rare species occurred in less than 50 percent of stands with less than 50 but more than 10 captures. Analyses of abundance used all captures (50 trap days in 1984).
Abundance of species not analyzed.
[e] Trap rate was higher in 1985 than 1984 (P < 0.001).

Sixty-two percent of the Trowbridge's shrews, 61 percent of the Pacific shrews, and 64 percent of the western red-backed voles captured were male. Because the home ranges of small mammal males are usually larger than those of females (Hawes 1977, Van Home 1981), males may have a higher probability of encountering traps. Habitat use by small mammals may not be constant among sex and age groups (Van Home 1981), but our data showed little variation in the proportions of adult male, adult female, and juvenile Trowbridge's shrews, Pacific shrews, and western red-backed voles among young, mature, and old-growth stands (fig. 1). All further analyses did not differentiate among sex and age groups.

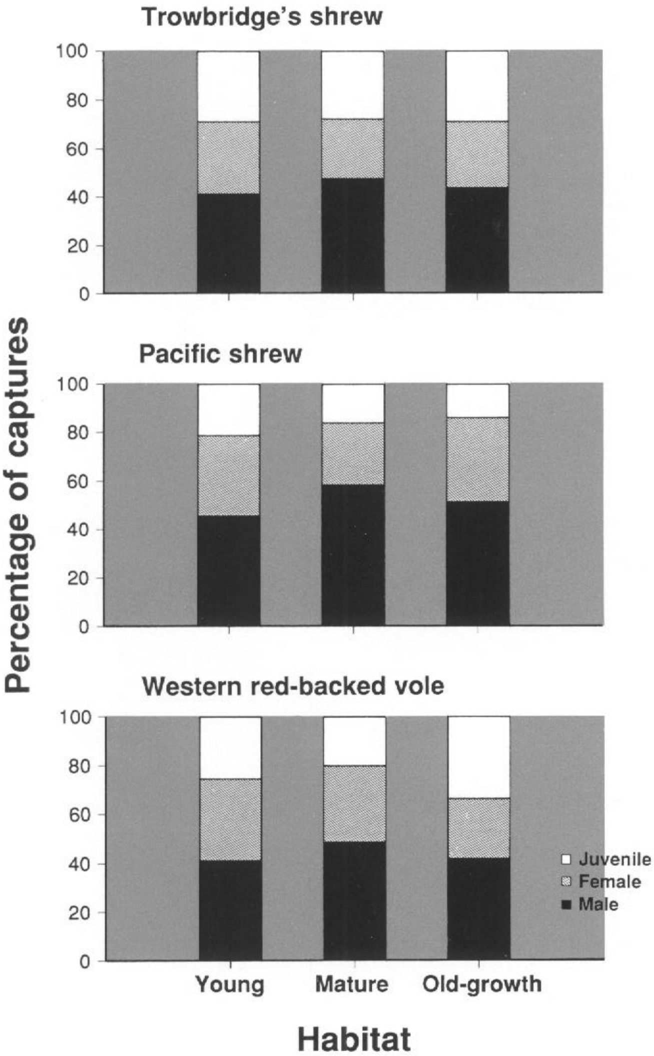

Figure 1—Mean percentage of adult male, adult female, and juvenile Trowbridge's shrews, Pacific shrews, and western red-backed voles captured in young, mature, and old-growth stands.

Variation with stand age—We calculated the mean abundance, relative abundance (percentage of total captures within a stand), and the frequency of occurrence of the six most abundant species in each age-class (table 2). Only Pacific shrews varied significantly among stand types in abundance ($F = 4.86, P = 0.013$). This species was more abundant in mature stands than either old-growth ($P = 0.024$) or young ($P = 0.052$) stands. The two most abundant species, Trowbridge's shrew and the western red-backed vole, were also more abundant in mature stands, but the differences were not statistically significant. Frequency of occurrence was high for all six species in all stand types, ranging from coast moles and deer mice detected in 60 percent of mature stands, to Trowbridge's shrews and western red-backed voles detected

Table 2—Mean abundance, mean relative abundance,[a] and occurrence of common[b] small mammals in different forest types in the Oregon Coast Ranges

		Stand type (N)		
Species	Measure	Old-growth (25)	Mature (10)	Young (8)
Trowbridge's shrew	Number/100 TN[c]	1.660	1.907	1.350
	Relative abundance	57.0	54.2	61.4
	Percentage of stands	100	100	100
Pacific shrew	Number/100 TN	.256	.596*	.251
	Relative abundance	8.4	15.3	10.1
	Percentage of stands	96.0	100	100
Shrew-mole	Number/100 TN	.099	.079	.049
	Relative abundance	3.3	2.3	1.9
	Percentage of stands	68.0	70.0	62.5
Coast mole	Number/100 TN	.060	.040	.044
	Relative abundance	2.1	1.4	1.9
	Percentage of stands	64.0	60.0	37.5
Western red-backed vole	Number/100 TN	.668	.741	.449
	Relative abundance	21.7	21.7	17.7
	Percent of stands	100	100	100
Deer mouse	Number/100 TN	.138	.053	.132
	Relative abundance	4.6	1.5	5.2
	Percentage of stands	96.0	60.0	75.0

* Denotes significant difference among stand ages at $P < 0.05$.
[a] Relative abundance = the percentage of captures contributed by each species in each stand.
[b] Common species were captured in more than 50 percent of the stands and with more than 50 total captures.
[c] TN = trap-nights.

in all stands. Relative abundance of these six species was similar in old-growth and young stands; species ranks in order of abundance were: Trowbridge's shrew > western red-backed vole > Pacific shrew > deer mouse > shrew-mole > coast mole. In mature stands, the order was the same, except that shrew-moles were more abundant than deer mice. This minor variation is probably not significant, because pitfall traps do not sample deer mice well (Bury and Corn 1987).

Two rare species were not distributed evenly on the chronosequence (fig. 2). All but one red tree vole were captured in old growth (old growth versus mature plus young: $G = 9.58$, $P < 0.01$), and significantly more vagrant shrews were captured in mature stands than in old-growth and young stands ($G = 29.8, P < 0.001$). Captures of flying squirrels and marsh shrews were evenly distributed among age-classes. Of nine creeping voles captured in forested stands, five were in

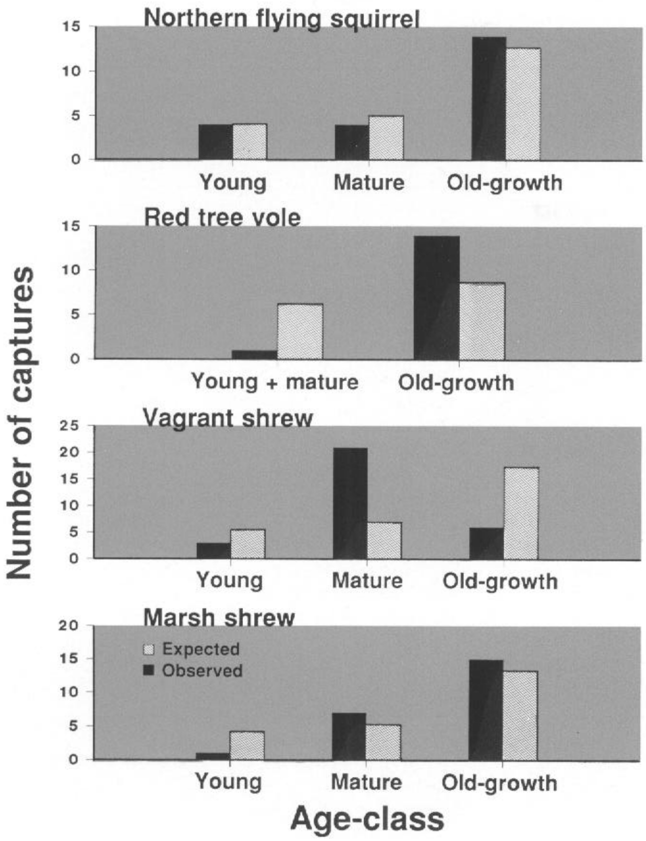

Figure 2—Total captures and expected values of marsh shrews, vagrant shrews, red tree voles, and northern flying squirrels captured in young, mature, and old-growth stands.

Table 3—Mean abundance, mean relative abundance,[a] and occurrence of common[b] small mammals on the moisture gradient in old-growth forests in the Oregon Coast Ranges

Species	Measure	Stand type (N): Wet (5)	Moderate (14)	Dry (8)
Trowbridge's shrew	Number/100 TN[c]	1.591	1.513	1.928
	Relative abundance	57.8	55.1	60.2
	Percentage of stands	100	100	100
Pacific shrew	Number/100 TN	.324	.256	.226
	Relative abundance	11.3	9.2	6.1
	Percentage of stands	100	100	87.5
Shrew-mole	Number/100 TN	.140	.073	.112
	Relative abundance	5.2	2.5	3.2
	Percentage of stands	80.0	64.3	62.5
Coast mole	Number/100 TN	.044	.066	.067
	Relative abundance	1.8	2.5	1.8
	Percentage of stands	60.0	71.4	62.5
Western red-backed vole	Number/100 TN	.467	.692	.678
	Relative abundance	14.2	23.8	20.8
	Percentage of stands	100	100	100
Deer mouse	Number/100 TN	.141	.117	.167
	Relative abundance	5.2	3.9	5.2
	Percentage of stands	100	92.9	100

[a] Relative abundance = the percentage of captures contributed by each species in each stand.
[b] Common species were captured in more than 50 percent of the stands and with more than 50 total captures.
[c] TN = trap-nights.

old-growth stands and four were in mature stands. Three white-footed voles were captured in forested stands, and one each in old-growth, mature, and young stands.

Variation on the moisture gradient—Neither abundance of the common species (table 3) nor number of captures of the rare species (fig. 3) varied significantly across the moisture gradient (only seven vagrant shrews were captured in old growth, too few for analysis on the moisture gradient). The relative abundances suggest some differentiation of the mammal community in wet stands, however. Pacific shrews and shrew-moles contributed a greater percentage of captures and red-backed voles a lower percentage of captures in wet stands than in moderate or dry stands.

Clearcuts versus old growth—We captured nine species in three clearcuts ($\bar{x} = 5.7$ per stand) and 10 species in three adjacent old-growth stands ($\bar{x} = 6.0$ per stand). Total abundance was also not significantly different ($\bar{x} = 2.26$ per 100 trap-nights in old growth; $\bar{x} = 1.95$ per 100 trap-nights in clearcuts), but the species composition of the small mammal fauna was considerably different between clearcuts and old-growth stands. The four small mammals with the greatest mean relative abundance in clearcuts were vagrant shrews, Trowbridge's shrews, deer mice, and creeping voles, but, in the three old-growth stands, the four most abundant species were Trowbridge's shrews, red-backed voles, Pacific shrews, and shrew-moles (fig. 4). Red tree voles, marsh shrews, and ermines were captured in at least one old-growth stand and not in any clearcuts. Creeping voles, pocket gophers, and white-footed voles were captured in at least one clearcut and not in any of the three old-growth stands. White-footed voles and creeping voles were captured in other old-growth stands, however.

Habitat Associations

Physiographic features—None of the physiographic variables we measured varied among the forested stands (table 4). We compared the abundance of common species or the occurrence of rare species to these variables plus latitude, longitude, and stand age, but we observed only six weak associations. Abundance of Trowbridge's shrews was weakly correlated with latitude ($r = 0.37$, $P < 0.05$). Abundance of

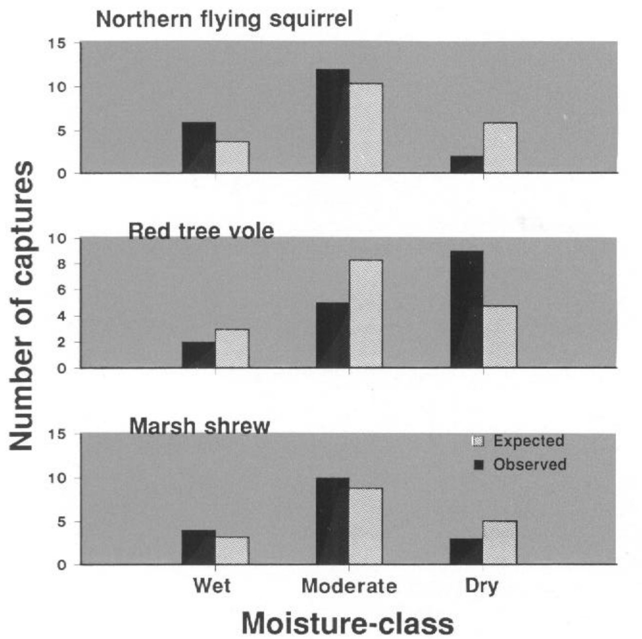

Figure 3—Total captures and expected values of marsh shrews, red tree voles, and flying squirrels captured in wet, moderate, and dry old-growth stands.

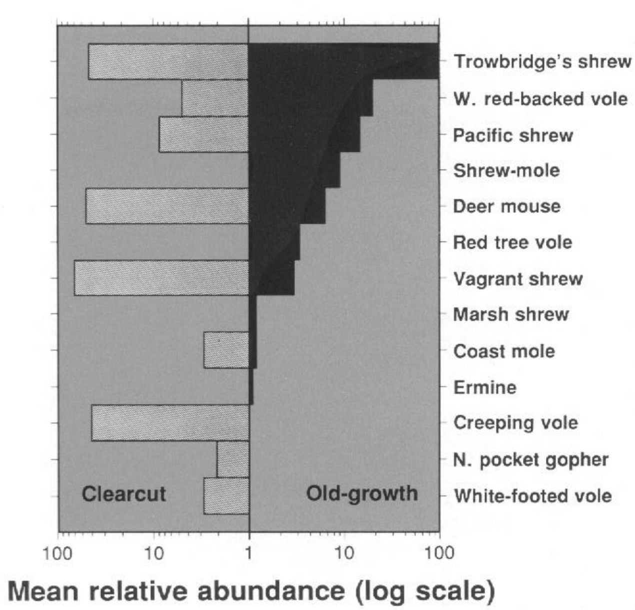

Figure 4—Mean relative abundance (log scale) of small mammals in three old-growth stands and three adjacent clearcuts.

Pacific shrews was weakly correlated with longitude ($r = 0.32$, $P < 0.05$) and negatively correlated with aspect ($r = -0.32$, $P < 0.05$; abundance was lower on southwest-facing slopes). Mean age of 13 stands where red tree voles were present was 294 years; 32 stands without red tree voles averaged 188 years old ($F = 6.75$, $P = 0.013$). Abundance of red-backed voles was 0.67 per 100 trap-nights in 39 stands without surface water and 0.36 per 100 trap-nights in 6 stands with surface water ($F = 4.19$, $P = 0.047$).

Vegetative characteristics—Only a few of the vegetation variables varied significantly ($P < 0.05$) among age-classes of forest stands (table 4). Small and medium-sized snags were most numerous in young stands. Densities of small and large coniferous trees were highest in old-growth stands, but medium-sized conifers were densest in young stands. Cover by broadleaf trees in the midstory was highest in young stands, but cover by conifers in the midstory was highest in old growth. Old-growth stands had the lowest canopy cover by coniferous trees.

Abundances of common species were correlated with few of the vegetation variables. Trowbridge's shrews were negatively correlated with percentage cover of class 3 and 4 down wood (DLOGSB; $r = -0.35$, $P < 0.05$) and cover by conifers in the midstory (MCTREE; $r = -0.30$, $P < 0.05$); they were positively associated with cover by ferns (FERN; $r = 0.32$, $P < 0.05$). Pacific shrews were correlated with the density of medium-sized snags (MSNAG; $r = 0.30$, $P < 0.05$) and cover by berry shrubs (BSHRUB; $r = 0.40$, $P < 0.01$). Coast moles were negatively correlated with canopy cover by broadleaf evergreens (CBTREE; $r = -0.31$, $P < 0.05$). Western red-backed voles were negatively correlated with cover by moss (MOSS; $r = -0.32$, $P < 0.05$) and positively correlated with cover by berry shrubs ($r = 0.33$, $P < 0.05$). Abundances of two species, shrew-moles and deer mice, were not significantly correlated with any vegetative variables.

Similarly, only a few vegetative variables varied between stands with rare species present or absent. In the 18 stands where marsh shrews were captured, mean canopy cover by conifers (CCTREE) was lower (41.3 percent versus 50.4 percent, $P = 0.009$) than in the 27 stands where they were not captured. Mean density of all deciduous trees and broadleaf evergreen trees (BTREES+BTREEM+BTREEL) was lower (45 per ha versus 145 per ha, $P = 0.002$) in 13 stands where vagrant shrews were collected versus 32 stands without vagrant shrews. In 13 stands where we captured red tree voles, there were more large coniferous trees (CTREEL: 34 per ha versus 17.4 per ha; $P = 0.014$) than in 32 stands where we did not capture this species. In 15 stands where flying squirrels were caught, mean density of large snags (LSNAG) was greater (9.2 per ha versus 4.9 per ha, $P = 0.032$), mean cover by fine litter (FLITTER) was greater (71.6 percent versus 58.6 percent, $P = 0.005$), but mean cover by moss (MOSS) was lower (19.2 percent versus 33.2 percent, $P = 0.005$) than in 30 stands without flying squirrels.

Table 4—Mean values of physiographic and vegetative variables (standard deviations in parentheses) measured at pitfall grids in the Oregon Coast Ranges[a]

		Stand type (N)			
Variable	Units	Old-growth (27)	Mature (10)	Young (8)	*P*
Physiographic:					
TRASPECT		1.03 (.62)	1.25 (.40)	1.20 (.70)	
SLOPE	Percent	38.4 (19.2)	46.1 (22.4)	32.1 (23.0)	
WATER	Percent present	22.2	0	0	
OUTCROP	Percent present	14.8	20.0	25.0	
TALUS	Percent present	48.2	50.0	50.0	
Coarse woody debris:					
DLOGSA	Percentage cover	1.9 (1.55)	2.3 (2.23)	1.8 (1.19)	
DLOGSB	Percentage cover	4.7 (2.65)	4.0 (3.38)	3.5 (2.10)	
DLOGSC	Percentage cover	1.5 (1.48)	1.6 (1.77)	1.4 (1.42)	
STUMP	Number/ha	20.6 (22.6)	61.1 (57.4)	62.5 (100.2)	
SSNAG	Number/ha	62.1 (79.5)	68.9 (74.4)	154 (91.3)	0.047
MSNAG	Number/ha	37.0 (38.0)	131 (129)	146 (66.3)	.001
LSNAG	Number/ha	7.2 (5.44)	6.7 (6.2)	2.9 (2.13)	
DECSNAG	Number/ha	8.4 (16.8)	22.6 (22.7)	14.1 (19.5)	
Live tree:					
CTREES	Number/ha	531 (644)	260 (344)	81.9 (106)	.012
CTREEM	Number/ha	271 (138)	321 (156)	501 (198)	.007
CTREEL	Number/ha	32.8 (13.1)	8.0 (6.73)	4.3 (9.31)	<.001
BTREES	Number/ha	30.0 (39.3)	109 (187)	86.1 (86.0)	
BTREEM	Number/ha	58.9 (50.8)	30.0 (39.0)	94.0 (71.1)	
BTREEL	Number/ha	.1 (.30)	.3 (.99)	.2 (.56)	
MDTREE	Percentage cover	8.2 (9.1)	4.3 (6.90)	4.7 (5.86)	
MBTREE	Percentage cover	.8 (1.61)	.8 (2.20)	3.9 (5.32)	.048
MCTREE	Percentage cover	22.3 (11.1)	10.5 (13.3)	5.1 (2.54)	<.001
CDTREE	Percentage cover	.6 (1.08)	.6 (1.90)	1.4 (3.27)	
CBTREE	Percentage cover	.1 (.30)	.1 (.23)	.3 (.65)	
CCTREE	Percentage cover	41.4 (8.38)	52.4 (13.5)	57.9 (6.98)	<.001
Ground cover:					
LITDEPTH	cm	3.6 (2.98)	6.0 (7.74)	3.1 (1.22)	
SOIL	Percentage cover	2.2 (2.12)	3.1 (6.48)	2.1 (1.92)	
ROCK	Percentage cover	.4 (.46)	1.5 (3.98)	.3 (.42)	
FLITTER	Percentage cover	65.9 (11.8)	56.3 (22.9)	61.2 (10.5)	
MOSS	Percentage cover	26.5 (13.4)	31.6 (24.9)	31.8 (12.4)	
FORB	Percentage cover	4.3 (4.41)	6.4 (7.1)	3.8 (7.86)	
GRASS	Percentage cover	.4 (.62)	1.0 (1.33)	.2 (.12)	
FERN	Percentage cover	28.1 (25.5)	18.1 (27.1)	5.8 (3.74)	
ESHRUB	Percentage cover	23.8 (19.8)	22.2 (31.4)	36.6 (20.4)	
DSHRUB	Percentage cover	7.5 (8.5)	5.5 (5.93)	7.8 (6.93)	
BSHRUB	Percentage cover	1.9 (3.02)	4.6 (5.19)	5.1 (9.31)	
MSHRUB	Percentage cover	16.4 (15.6)	9.2 (8.82)	12.1 (8.9)	

[a] Where a significant difference occurred among age-classes, solid lines indicate pairs of age-classes that were not significantly different at $P = 0.05$.

Multiple regression models of abundance of common species on vegetative variables usually included the same variables that were significant in the simple correlations plus one or two additional variables, but the predictive power of the models was low (table 5). Shrew-moles and deer mice, which did not have any significant simple correlations, both had multiple-regression models that contained four variables, but each model accounted for only about a third of the variance

Table 5-Stepwise multiple regression of the abundance of common[a] species on vegetative variables

Species and variable	Coefficient	SE	t	Multiple r^2	SE of the estimate	*F*	*P*
Trowbridge's shrew				0.428	0.163	5.845	<0.00l
constant	1.124	0.126	8.902				
DLOGSB	-1.639	.408	-4.015				
FERN	.272	.082	3.310				
SLOPE	-.308	.112	-2.753				
LITDEPTH	.129	.053	2.444				
MDTREE	.313	.154	2.024				
Pacific shrew				.331	.170	4.951	.002
constant	-.142	.105	-1.361				
DECSNAG	.049	.020	2.404				
FERN	.203	.088	2.289				
SHRUB[b]	.157	.088	1.783				
BSHRUB	.480	.273	1.756				
Shrew-mole				.324	.076	4.802	.003
constant	.232	.057	4.093				
HERB	.355	.111	3.192				
DECSNAG	-.030	.010	-2.942				
MOSS	-.173	.068	-2.544				
MDTREE	-.149	.077	-1.939				
Western red-backed vole				.395	.177	6.531	<.00l
constant	.479	.117	4.080				
BSHRUB	.909	.275	3.311				
MOSS	-.444	.148	-3.012				
TRASPECT	-.059	.027	-2.165				
CTREEL	.038	.022	1.728				
Deer mouse				.366	.084	5.767	.OOl
Constant	.381	.068	5.638				
DLOGSC	-.949	.255	-3.722				
SLOPE	-.186	.060	-3.123				
BSHRUB	-.297	.125	-2.371				
TRASPECT	-.024	.013	-1.858				

[a] Common species were captured in more than 50 percent of the stands and with more than 50 total captures.
[b] ESHRUB+BSHRUB.

in abundance. Most of the variables that were included in the regression models reflected ground cover at or below the shrub layer (less than 2 m above the ground). Abundance of Trowbridge's and Pacific shrews appeared to be associated with denser growth of shrubs and ferns, but the abundance of shrew-moles was associated with herbaceous vegetation, which indicates a more open shrub layer.

Multivariate analyses-A principal components analysis of eight vegetation variables with no rotation of factors produced three factors with eigenvalues greater than 1.0; these accounted for 67.6 percent of the variance. We interpret factor 1 (33.1 percent of the variance) as describing the structure of live trees; it was positively correlated with cover by conifers in the midstory, numbers of large conifers and large snags, and negatively correlated with cover by conifers in the canopy. Factors 2 (19.3 percent) and 3 (15.2 percent) together accounted for only about one-third of the variance. Factor 2 appears to represent coarse woody debris. It was positively correlated with numbers of well-decayed snags and cover by down wood. Factor 3 was associated with the shrub layer. It was positively correlated with cover by evergreen shrubs and negatively correlated with cover by ferns.

Young stands differed from old-growth stands mainly on factor 1 (fig. 5), which would be expected, because young stands lacked large Douglas-fir trees and a well-developed midstory layer. Most young stands had Factor 1 scores less than zero, and most old-growth stands had scores greater than zero. Factor 1 scores for mature stands, however, overlapped young and old-growth stands, so the three age-classes did not form discrete groups.

Mammal Community Structure

Multidimensional scaling of the similarity of 45 stands and K-MEANS clustering based on the abundance of six species of small mammals revealed differences among stands that do not fall in a simple gradient from young forests to old growth (fig. 6). The first multidimensional scaling axis (dimension 1) was strongly correlated with the abundance of Trowbridge's shrews ($r = 0.96$), Pacific shrews ($r = 0.60$), and with the sum of the abundance of all six species ($r = 0.93$, fig. 7). The second multidimensional scaling axis (dimension 2) was strongly correlated with the abundance of red-backed voles ($r = 0.80$) and the Berger-Parker index of species diversity ($r = 0.86$, fig. 8). This index measures dominance (Magurran 1988), so in stands with a low value, Trowbridge's shrews were a high proportion of captures. Stands with higher diversity indices had relatively fewer captures of Trowbridge's shrews and greater contributions from other species. Dimensions 1 and 2 define a gradient in the complexity of the mammal community. Stands with low abundance and species diversity (less complex) had low scores on both dimensions, and stands with high abundance and species diversity (more complex) had high scores on both dimensions.

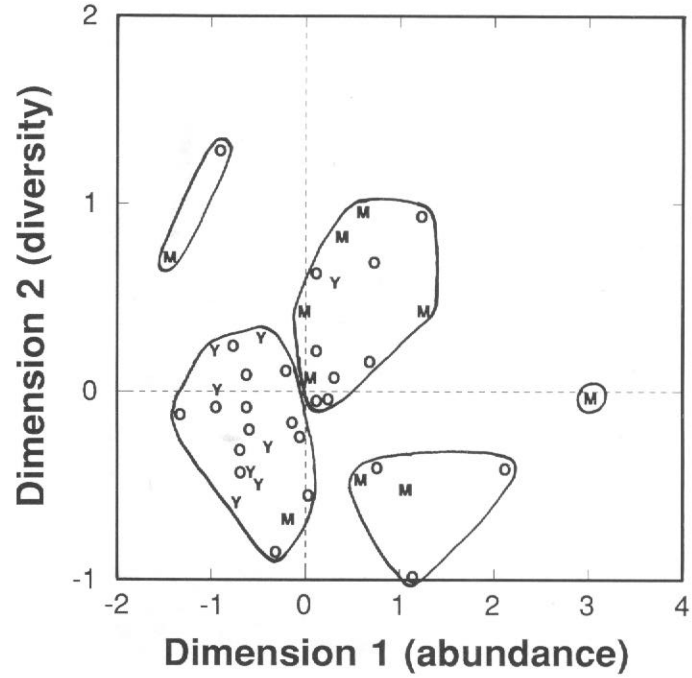

Figure 6—Multidimensional scaling of Coast Range stands based on abundance of six species of mammals (see text). Lines enclose non-overlapping clusters of stands, and symbols indicate habitat type (O = old-growth, M = mature, Y = young).

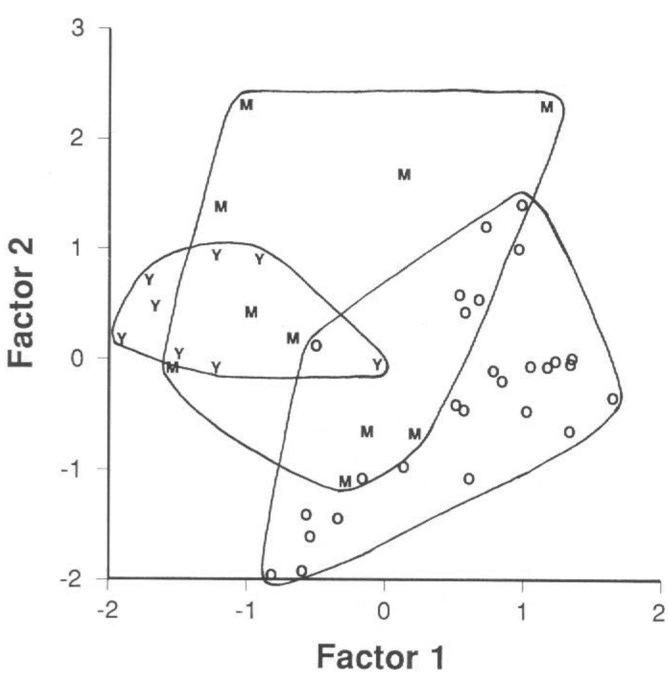

Figure 5—Position of different forest stands on the first two factors of a principal components analysis of eight selected vegetation variables. Habitat types are identified by O (old-growth), M (mature), and Y (young).

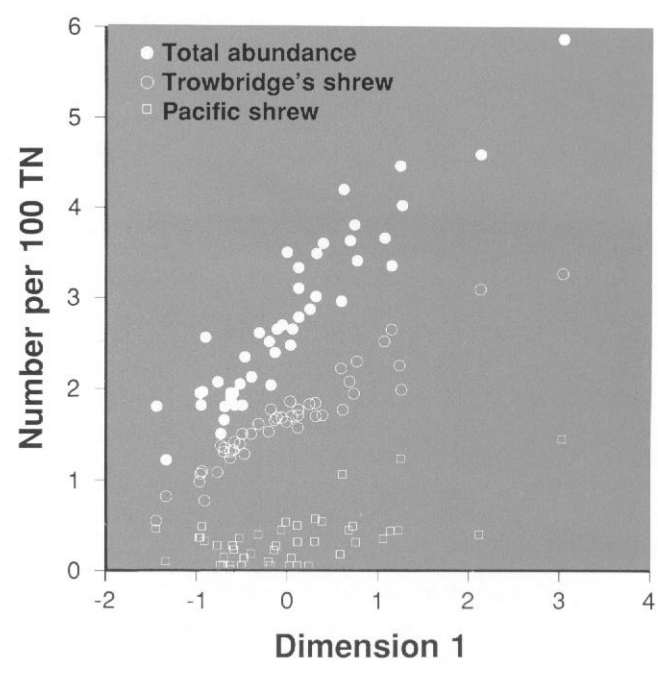

Figure 7—Total abundance of six small mammals and abundance of Trowbridge's and Pacific shrews versus multidimensional scaling axis 1.

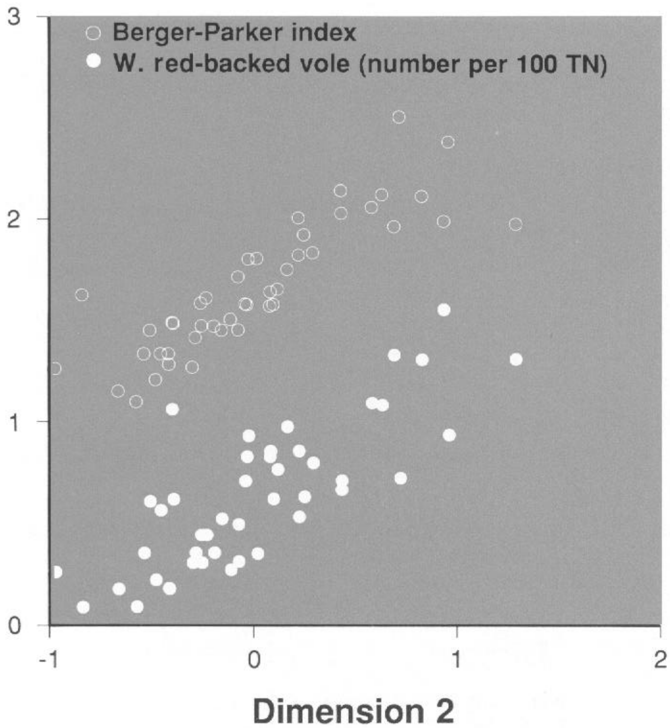

Figure 8—Abundance of western red-backed voles and species diversity (Berger-Parker index) versus multidimensional scaling axis 2.

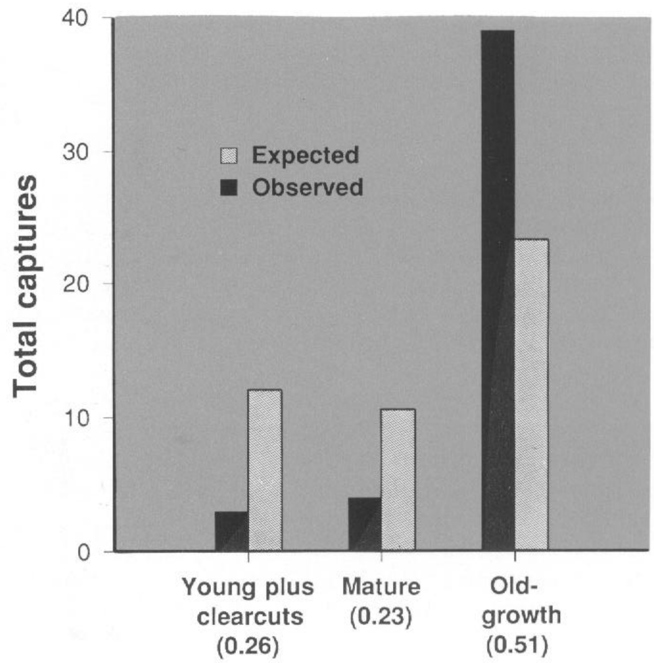

Figure 9—Total captures of red tree voles in the Oregon Cascade Range and Coast Ranges during old-growth community studies, 1983-85. The proportion of the total trapping effort in each age-class is listed in parentheses.

Nonhierarchical clustering generated pool 1 containing 23 stands, pool 2 containing 14 stands, pool 3 containing 5 stands, and two outlying pools with 2 and 1 stands (fig. 6). Pools 1 and 2 orient on the gradient from lower to higher complexity. Membership in pools 1 and 2 was not random with respect to age-class (G = 7.93, 2 df, P = 0.02). Old-growth stands were evenly distributed between pool 1 and pool 2, but seven of eight young stands were in pool 1 and five of six mature stands were in pool 2. The remaining four mature stands were in pools with either high diversity or high abundance.

No strong correlations were found between dimensions 1 and 2 and any of the physiographic or vegetation variables. Dimension 1 was weakly correlated with latitude (r = 0.32, $P < 0.05$), and dimension 2 was weakly correlated with longitude (r = 0.38, $P < 0.05$).

Discussion

Species Associated With Old-Growth Forests

One species, the red tree vole, was significantly more abundant in old-growth forests than in young or mature forests in the Oregon Coast Ranges. This small, arboreal rodent was seldom captured on the ground until we began using large numbers of pitfall traps (Corn and Bury 1986). Red tree voles are an important prey of spotted owls (Forsman and others 1984), and they were listed as a species potentially dependent on old-growth forests (Meslow and others 1981). Anecdotal reports have long indicated an affinity for large Douglas-fir trees (Bailey 1936, Howell 1926, Maser and others 1981), and we found greater density of large conifers in stands where we caught red tree voles. Recent searches for nests of red tree voles support the notion that old-growth trees are preferred as nest sites (Gillesberg and Carey, this volume); Meiselman and Doyle, in press), although nests have also been observed occasionally in young second-growth trees (Carey 1989, Maser 1966).

The 17 red tree voles we trapped in the Coast Ranges constitute a small sample, but since 1983, 46 red tree voles have been trapped in the Coast and Cascade Ranges of Oregon by old-growth researchers (this study; Corn and Bury 1986; Gilbert and Allwine, this volume a). Most (39) were captured in old-growth stands (fig. 9), and, because the trapping effort was about evenly split between old-growth stands and younger stands, a significant excess of captures was in old growth (G = 24.0, 2 df, $P < 0.001$). Raphael (1988c) captured an additional 19 red tree voles in pitfall traps in Douglas-fir forests in northwestern California. Although the difference in relative abundance among stand age-classes was not significant, most red tree voles were captured in stands older than 100 years. Meiselman and Doyle (in press) located several nests of red tree voles in northwestern California, and a statistically significant majority were in old-growth forests. These results indicate that red tree voles are strongly associated with old-growth Douglas-fir forests.

Aside from red tree voles and Pacific shrews (most abundant in mature stands), no statistically significant relations were found between stand age and the abundance of small mammals. Our results agree with other old-growth research from Oregon and Washington that found few species of terrestrial small mammals associated with older forests (Anthony and others 1987; Corn and others 1988; Gilbert and Allwine, this volume a; West, this volume).

The lack of strong correlations between habitat features and mammal abundance was somewhat surprising, considering that studies of insectivores (Hawes 1977, Terry 1981). earlier studies from the old-growth program (Corn and others 1988), and studies in California (Raphael 1988c, Raphael and Barrett 1984) found several significant habitat associations. One possibility is that by trapping only in the fall, we were sampling populations composed of high proportions of subadult animals (Sullivan 1979, Van Home 1981), which might be transients in habitat of lower quality. Abundance data, then, would give a misleading indication of habitat quality (Sullivan 1979, Van Home 1983). Our data did not reveal any marked differences in the proportions of subadult Trowbridge's and Pacific shrews and red-backed voles among young, mature, and old-growth forests. Hawes (1977) found that home ranges of subadult vagrant and montane shrews in British Columbia were smaller subsets of the areas they occupied when breeding the next spring. This finding suggests that subadult shrews have the narrowest habitat requirements and that trapping in the fall would reveal important habitat associations.

A more likely explanation for finding few habitat associations is that threshold values for critical habitat features to small mammals are exceeded in naturally regenerated forests after the canopy is reestablished (West, this volume). Understory plant communities in Douglas-fir forests are resilient and rapidly return to the composition found in old growth after disturbance (Halpern 1988). In the Coast Ranges, structural features likely to be associated with terrestrial mammals did not differ among different ages of stands. For example, no difference was found in the Coast Ranges in the percentage cover by down wood among young, mature, and old-growth stands (Spies and others 1988). Different age-classes of naturally regenerated forest represent a single habitat type for most small mammal species. This conclusion is supported by the observation that neither abundance nor diversity of small mammals displayed the predicted U-shaped pattern (Spies and Franklin 1988) when compared to stand age. No decline occurred in abundance or diversity in mature stands in the Cascade Range (Gilbert and Allwine, this volume a; West, this volume). In the Coast Ranges, the trend was opposite of the prediction; abundance and diversity of six species of mammals were greater in mature stands. These studies provide little support for a U-shaped pattern of diversity of small mammals.

Managed Forests

Many studies have examined the effects of logging on small mammals in the Pacific Northwest, and they have documented major changes in the composition of the mammal community. In general, populations of deer mice, creeping voles, vagrant shrews, and Townsend's chipmunks increase after logging, while red-backed voles and Trowbridge's shrews decline (Anthony and Morrison 1985; Corn and others 1988; Gashwiler 1959, 1970b; Hooven and Black 1976; Raphael 1988c; Sullivan and Krebs 1980; Tevis 1956; West, this volume). Some of these changes represent increased abundance by species adapted to open habitats, but for other species, clearcuts may act as dispersal sinks and the increased abundance is transitory (Sullivan 1979).

Species composition of mammal communities in clearcuts is less predictable than that of old-growth forests. Considering both this study and the earlier study in the Oregon Cascades (Corn and others 1988), Trowbridge's shrews (76 percent of captures in forested stands) and vagrant shrews (71 percent of captures in clearcuts) had similar relative abundances in forests and clearcuts, respectively. But while Trowbridge's shrews were always the most abundant insectivore in forested stands, vagrant shrews were the most abundant insectivore in only three of six clearcuts. Abundance of creeping voles and deer mice also varied widely among clearcuts. The low predictability of mammal populations in clearcuts may be related to the rapid succession occurring in the plant communities (Halpern 1988, Schoonmaker and McKee 1988), which may generate greater variability in food resources and microclimates than is found in closed-canopy forests.

The apparent low habitat quality and unpredictibility of clearcuts for many mammal species means that, as naturally regenerated forests are converted into managed forests, the long-term survival of many species will depend on whether managed forests provide essential habitat features. For example, modem logging practices greatly reduce both the amount of coarse woody debris carried over into a stand after harvest and the amount accumulated before the next harvest (Spies and Franklin 1988, Spies and others 1988). The results of our studies, however, provide little insight into this question. We did not investigate managed stands after closure of the canopy, and the range of variation of habitat variables in naturally regenerated stands is probably insufficient to make predictions about habitats and small mammal communities in intensively managed forests.

Recommendations

The studies of old-growth forests reported in this volume have provided baseline data on the occurrence of vertebrate species in natural Douglas-fir forests in the Pacific Northwest. In general, however, more questions have been created than answers supplied. We offer the following suggestions for high-priority research in the Coast Ranges of Oregon:

Determine the abundance of red tree voles in old-growth, mature, young, and managed forests. The data collected so far suggest that this species may depend on old growth, but the sample size is small. The red tree vole is probably the most difficult small mammal in the Pacific Northwest to study, but recently developed techniques (Gillesberg and Carey, this volume; Meiselman and Doyle, in press) show promise.

Compare small mammal populations in naturally regenerated and intensively managed forests. The changes in forest structure predicted between managed and natural forests are of a much greater magnitude than we measured in a natural sere. Although we found few differences among different-aged forests, the same prediction cannot be made for a comparison of managed and natural forests. Some work along this line has begun; more is needed.

Determine the effects of forest fragmentation on small mammal populations. We did not deal with fragmentation in this paper, and, currently, little evidence indicates that small-mammal populations are strongly influenced by stand size or degree of fragmentation (Raphael 1984, Rosenburg and Raphael 1986). Few data have been collected so far on the effects of fragmentation in western forests, however, and any effects are likely to be severe in the Coast Ranges, where most old growth exists as small, isolated patches (Harris 1984, Monthey 1984, Spies and Franklin 1988).

The lack of a unique community of small mammals in old-growth forests does not reduce the value of these habitats. Old growth is a nonrenewable resource (Schoen and others 1981) with numerous other intrinsic assets. In the Coast Ranges, our results suggest that the biological integrity of isolated blocks of old growth may be enhanced if tracts of younger, naturally regenerated forest are contiguous.

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Appendix

Table 6-Vegetative variables measured at 9 points within pitfall grids

Variable	Description
Physiographic:	
TRASPECT	Transformed aspect (cosine transformation [NE=O, SW=2])
SLOPE	Percent slope
WATER	Presence or absence of open water (seeps, ponds, permanent or intermittent streams) on grid
TALUS	Presence or absence of exposed talus on grid
Coarse woody debris:	
DLOGSA	Percentage cover by decay class 1 and 2 down wood
DLOGSB	Percentage cover by decay class 3 and 4 down wood
DLOGSC	Percentage cover by decay class 5 down wood
STUMP	Number of stumps per hectare
SSNAG	Number of small snags (<10 cm d.b.h.) per hectare
MSNAG	Number of medium snags (l0-50 cm d.b.h.) per hectare
LSNAG	Number of large snags (>50 cm d.b.h.) per hectare
DECSNAG	Number of well-decayed (class 4 and 5) medium and large snags per hectare
Live tree:	
CTREES, CTREEM, CTREEL	Number of small (<l0 cm d.b.h.), medium (≥ 10 cm and <l m d.b.h.), and large (>1 m d.b.h.) coniferous trees per ha
BTREES, BTREEM, BTREEL	Number of broadleaf trees (same size-classes) per ha
MDTREE	Percentage cover by deciduous midstory trees
MBTREE	Percentage cover by broadleaf evergreen midstory trees
MCTREE	Percentage cover by coniferous midstory trees
CDTREE	Percentage canopy cover by deciduous trees
CBTREE	Percentage canopy cover by broadleaf evergreen trees
CCTREE	Percentage canopy cover by coniferous trees
Ground cover:	
LITDEPTH	Depth (cm) of organic litter layer
SOIL	Percentage cover by bare soil
ROCK	Percentage cover by exposed rock
FLITTER	Percentage cover by fine organic litter
MOSS	Percentage cover by moss
HERB	Percentage cover by forbs
GRASS	Percentage cover by grasses
FERN	Percentage cover by ferns
ESHRUB	Percentage cover by evergreen shrubs
DSHRUB	Percentage cover by deciduous shrubs
BSHRUB	Percentage cover by ***berry*** shrubs ***(Rubus*** spp. and ***Vaccinium*** spp.)
MSHRUB	Percentage cover by midstory shrubs (>2 m high)

Continue