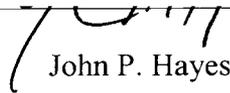


AN ABSTRACT OF THE THESIS OF

Nobuya Suzuki for the degree of Doctor of Philosophy in Forest Science presented on July 19, 2000. Title: Effects of Thinning on Forest-floor Vertebrates and Analysis of Habitat Associations along Ecological Gradients in Oregon Coastal Douglas-fir Forests.

Signature redacted for privacy.

Abstract approved: _____


John P. Hayes

Thinning has the potential to increase structural diversity of managed forests for wildlife. During 1994–1996, I conducted experimental and observational studies using pitfall trapping to assess short-term and potential long-term effects of thinning on abundance and reproduction of forest-floor vertebrates in Douglas-fir (*Pseudotsuga menzeisii*) forests of the Oregon Coast Range. Thinning had positive effects on relative abundances of creeping voles (*Microtus oregoni*) and Pacific jumping mice (*Zapus trinotatus*) in both the short term and the long term. In contrast, relative abundance of western red-backed salamanders (*Plethodon vehiculum*) was lower in stands thinned 7-24 years previously than unthinned stands, suggesting potential negative effects of thinning in the long term. Relative abundance of western red-backed voles (*Clethrionomys californicus*) decreased within 2 years of thinning but was similar in stands thinned 7-24 years

previously and unthinned stands. However, reproductive performance of western red-backed voles was higher in thinned than unthinned stands, suggesting potential positive effects of thinning on reproduction of the voles in the long term.

In 1994, I investigated the influences of ecological gradients on habitat associations of forest-floor vertebrates at microsite and stand scales in 12 Douglas-fir stands in the stem exclusion stage. I examined various gradients of microclimate, stand structure, plant community composition, and downed wood. Among the ecological gradients I examined, the highest number of species was influenced by red alder/herb—conifer/shrub gradient of community composition at both the microsite and stand scales. At the microsite scale, 7 species were associated with red alder/herb communities whereas only 2 species were associated with conifer/shrub communities. Red-alder patches with herb understory, therefore, have a potential role in maintaining biodiversity of forest-floor vertebrate communities in young Douglas-fir dominated stands. Furthermore, I found that habitat associations of 4 shrew species were generally consistent between the microsite and stand scales, whereas those of 3 rodent species were inconsistent between the 2 spatial scales. I hypothesized that this rodent-shrew dichotomy in habitat association occurring at the 2 spatial scales is a result of differences in their ability to explore habitats at multiple spatial scales.

Effects of Thinning on Forest-floor Vertebrates and Analysis of Habitat
Associations along Ecological Gradients in Oregon Coastal Douglas-fir Forests

by

Nobuya Suzuki

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TABLE OF CONTENTS

	<u>Page</u>
CHAPTER 1: GENERAL INTRODUCTION.....	1
CHAPTER 2: EFFECTS OF THINNING ON FOREST-FLOOR VERTEBRATES IN OREGON COASTAL DOUGLAS-FIR FORESTS.....	6
ABSTRACT.....	6
INTRODUCTION.....	8
STUDY AREA.....	13
Experimental Study.....	13
Observational Study.....	16
METHODS.....	18
Thinning in the Experimental Study.....	18
Sampling of Vertebrate Species and Assessment of Small Mammal Reproduction.....	18
Habitat Sampling.....	20
Data Analysis.....	22
RESULTS.....	24
Habitat Characteristics.....	24
Abundance of Forest-floor Vertebrates.....	31
Reproduction of Small Mammals.....	38
The Relationship between Abundance and Reproduction in Small Mammals.....	42
DISCUSSION.....	43
Effects of Thinning on Abundance of Vertebrates.....	43
Relationship between Abundance and Reproduction.....	50
Consistency of Experimental and Observational Approaches.....	51
Management Implications.....	52
Scope and Limitations.....	54
LITERATURE CITED.....	56

TABLE OF CONTENTS (Continued)

	<u>Page</u>
CHAPTER 3: EFFECTS OF ECOLOGICAL GRADIENTS ON HABITAT ASSOCIATIONS OF FOREST-FLOOR VERTEBRATES IN YOUNG DOUGLAS-FIR-DOMINANT STANDS OF THE NORTHERN OREGON COAST RANGE.....	65
ABSTRACT.....	65
INTRODUCTION.....	66
STUDY AREA.....	71
METHODS.....	72
Sampling of Vertebrate Species.....	72
Habitat Sampling.....	73
Data Analysis.....	75
RESULTS.....	79
Abundance of Forest-floor Vertebrates.....	79
Ordination Axes.....	81
Effects of Ecological Gradients on Habitat Associations at the Microsite and Stand Scales.....	86
DISCUSSION.....	117
Plant Community Composition.....	117
Microclimate.....	120
Downed Wood.....	122
Stand Structure.....	124
Generalists vs. Specialists, Patterns of Association at Multiple-Spatial Scales.....	126
CONCLUSIONS.....	131
LITERATURE CITED.....	132
CHAPTER4: CONCLUSIONS.....	139
BIBLIOGRAPHY.....	141

TABLE OF CONTENTS (Continued)

	<u>Page</u>
APPENDICES.....	156
APPENDIX 1.....	157
APPENDIX 2: Interpretation of Ordination Axes.....	159
Microclimate.....	159
Downed Wood.....	160
Tree Species Composition.....	161
Stand Structure.....	163
Understory Composition.....	164
Plant Community Composition.....	166

LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1.	Locations (represented by triangles) of 4 replicate areas, each of which is comprised of control, moderately thinned, and heavily thinned stands, in the experimental thinning study (I), and of 8 replicate areas of thinned and unthinned paired stands in the observational study (II), Oregon Coast Range, 1994-1996.....	15
2.	Arrangement of habitat sampling plots.....	21
3.	Mean numbers of captures/100 trap nights of 6 species of forest-floor vertebrates in control ($n = 4$), moderately thinned ($n = 4$), and heavily thinned stands ($n = 4$) before (1994) and after (1995-1996) thinning was implemented. Error bars represent plus and minus 1 SE.....	34
4.	Changes in reproductive attributes ($\bar{x} \pm 1SE$) of western red-backed voles, creeping voles, and deer mice in control ($n = 4$), moderately thinned ($n = 4$), and heavily thinned ($n = 4$) stands of young Douglas-fir forests (35-45 years old) before (1994) and after thinning (1995-1996), northern Oregon Coast Range.....	40
5	Arrangement of habitat sampling plots.....	74
6.	Habitat association at the microsite scale for 16 species of forest-floor vertebrates along 16 ecological gradients in 12 young-forest stands, northern Oregon Coast Range.....	89

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1.	Characteristics of control (C), moderately thinned (M), and heavily thinned (H) stands in the experimental thinning study before and after thinning; and of unthinned (U) and previously thinned (T) stands (7-24 years previously) in the observational thinning study.....17
2.	Means and 95% confidence intervals of 9 habitat variables, and <i>P</i> -values from 4 orthogonal contrasts in repeated measures ANOVA comparing each habitat variable among control (C), moderately thinned (M), and heavily thinned (H) stands between pre-treatment year (1994) and post-treatment years (1995 and 1996), northern Oregon Coast Range, 1994-1996.....26
3.	Mean frequencies and cumulative lengths of downed logs of 3 size classes, and <i>P</i> -values from 4 orthogonal contrasts in repeated measures ANOVA, as identified in Table 2, comparing log abundances among control (C), moderately thinned (M), and heavily thinned (H) stands between pretreatment year (1994) and post-treatment years (1995 and 1996), northern Oregon Coast Range, 1994-1996.....28
4.	Habitat characteristics of unthinned stands and stands thinned 7-24 years previously in the Oregon Coast Range, 1996.....30
5.	Mean number of captures/100 trap nights and 95% confidence intervals for forest-floor vertebrates in 8 pairs of unthinned and thinned (7-24 years previously) Douglas-fir stands in the Oregon Coast Range, 1995-996.....37
6.	Twenty-four indicator plant species that are indicators of microclimate in the Oregon Coast Range adapted from Hemstorm and Logan (86).....77
7.	Ecological gradients identified at microsite and stand scales using Nonmetric Multidimensional Scaling.....82
8.	Descriptions of the gradients of plant community composition at the microsite scale in 3 vegetative categories: overstory trees, understory shrubs and herbs, and overall plant community of trees, shrubs, and herbs combined.....83

LIST OF TABLES (Continued)

<u>Table</u>	<u>Page</u>
9. Descriptions for the gradients of plant community composition at the stand scale in 3 vegetative categories: overstory trees, understory shrubs and herbs, and overall plant community of trees, shrubs, and herbs combined.....	85
10. Number of species associated with 16 ecological gradients at the microsite scale within 12 young forest stands (35-45 years old) in the northern Oregon Coast Range, 1994.....	87
11. Number of species associated with 13 ecological gradients at the stand scale among the 12 young forest stands (35-45 years old) in the northern Oregon Coast Range, 1994.....	88
12. Habitat associations of 6 insectivore species at the microsite scale along 16 ecological gradients within 12 young-forest stands (35-45 years old) in the northern Oregon Coast Range, 1994.....	94
13. Habitat associations of 5 rodent species at the microsite scale along 16 ecological gradients within 12 young-forest stands (35-45 years old) in the northern Oregon Coast Range, 1994.....	95
14. Habitat associations of 4 amphibian species at the microsite scale along 16 ecological gradients within 12 young-forest stands (35-45 years old) in the northern Oregon Coast Range, 1994.....	96
15. Habitat associations of 6 insectivore species at the stand scale along 13 ecological gradients among the 12 young forest stands (35-45 years old) in the north Oregon Coast Range, 1994.....	98
16. Habitat associations of 3 rodent species at the stand scale along 13 ecological gradients among the 12 young forest stands (35-45 years old) in the northern Oregon Coast Range, 1994.....	100
17. Habitat associations of 6 amphibian species at the stand scale along 13 ecological gradients among the 12 young forest stands (35-45 years old) in the north Oregon Coast Range, 1994.....	102
18. Habitat associations of 5 insectivore species with ecological gradients measured at the microsite and stand scales.....	104

LIST OF TABLES (Continued)

<u>Table</u>		<u>Page</u>
19.	Habitat associations of 3 rodent species with ecological gradients measured at the microsite and stand scales.....	105
20.	Association of 4 amphibian species with ecological gradients measured at the microsite and stand scales.....	107

LIST OF APPENDICES

APPENDIX

Page

1. Mean numbers of captures per 100 trap nights (TN), 95% confidence intervals, and *P*-values from 2 orthogonal contrasts with repeated measures ANOVA comparing abundance of forest-floor vertebrates between control (C) and thinned (T) stands before and after experimental thinning of 35-45 year old Douglas-fir forests, northern Oregon Coast Range, 1994-1996.....157
2. Interpretation of Ordination Axes.....159

CHAPTER 1: GENERAL INTRODUCTION

One of the biggest challenges of forest management in the Pacific Northwest today is to maintain biodiversity and ecological functions of forest ecosystems without suffering from severe negative social and economic consequences (Hansen et al. 1991, McComb et al. 1993, Carey and Curtis 1996, Hayes et al 1997). On federal lands, the Pacific Northwest Forest Plan attempts to provide a solution to this dilemma by protecting a large proportion of late-successional forests in reserves while allowing resource extraction from the matrix of younger forests. Under this plan, the matrix lands are also managed to promote structural diversity for vertebrate habitats and to enhance connectivity among reserves for vertebrate dispersal (Forest Ecosystem Management Assessment Team 1993).

The landscape of the Oregon Coast Range, however, exists in a checkerboard pattern of federal, state, and private ownerships (Hansen et al. 1991, Garman et al. 1999). The largest proportion, 62%, of the land area of the Oregon Coast Range is in private ownership, whereas only 25% and 12% are in federal and state ownerships, respectively (Garman et al. 1999). Under this scenario, the Pacific Northwest Forest Plan plays only a limited role in conservation of the regional biodiversity. Instead, the protection of late-successional forests and reduction in timber harvest on federal lands may increase harvest levels among private ownerships (Greber 1994). Much of the

private and state forestlands in the Oregon Coast Range has already lost large patches of late-successional forests that have been replaced with young plantations (Garman et al. 1999). Furthermore, the plantations on private ownerships are often managed for 40 to 50 year rotations (Carey and Curtis 1996) and harvested before they develop habitat characteristics suitable for vertebrate species associated with late-successional forests (McComb et al. 1993). Because plantations do not have sufficient structural and compositional characteristics to serve as high quality habitats for many vertebrate species, young plantations scattered across the landscape may act as a barrier for dispersal of some species (Hansen et al. 1991). The future of biodiversity in the Oregon Coast Range, therefore, depends on how we improve the stand structure of young forests in relation to various ownerships across the landscape. As a potential solution for biodiversity and timber production in young forests, the Oregon Department of Forestry proposed “structure-based management” (Oregon Department of Forestry 1998). This management plan is intended to maintain shifting mosaics of 5 successional forest habitats in given proportions across the landscape over time. Under this plan, thinning of young stands is encouraged to promote structural diversity within a stand (Oregon Department of Forestry 1998).

In recent years, thinning young Douglas-fir stands has been proposed as means to promote biodiversity in the Pacific Northwest forests (Carey and Curtis 1996, Hayes et al. 1997). Thinning has been widely practiced on private lands to increase wood fiber production; however, biodiversity objectives are seldom incorporated into thinning prescriptions (Carey and Curtis 1996, Hayes et al. 1997). Carey and Curtis

(1996) proposed “biodiversity thinning,” which uses precommercial thinning and a series of variable-density thinnings to stimulate tree growth, promote understory development, recruit coarse downed wood, and provide a continuous flow of wood products and revenue. Biodiversity thinning is intended to minimize area and time in which a stand stays in an ecologically stagnant condition due to stem exclusion (Carey and Curtis 1996).

To incorporate biodiversity objectives into the planning of forest management, development of a large ecological information base for a wide range of organisms is necessary. Until recently, ecological research of forest-management impacts in the region has focused primarily on conservation of rare and endangered vertebrate species and their late-successional habitats (Thomas et al. 1990). In recent years, more ecologists have been trying to assess effects of forest management practices on a wide variety of species and communities of vertebrates, invertebrates, bryophytes, and vascular plants (Marcot 1997). However, only a handful of studies to date have focused on managed forests of the Pacific Northwest and assessed the influence of thinning or silvicultural alternatives to clearcutting on wildlife populations, communities, and habitats (e.g., Hagar et al. 1996, Chambers and McComb 1997, Chambers et. al 1999, Humes et al. 1999).

This dissertation consists of 2 studies of forest-floor vertebrate communities in managed Douglas-fir dominant forests of the Oregon Coast Range. In chapter 2, I present the short- and long-term effects of thinning Douglas-fir stands on abundance and reproduction of forest-floor vertebrates. In chapter 3, I present the effects of

ecological gradients on habitat association of forest-floor vertebrates in managed Douglas-fir dominant forests at a microsite scale within stands and at a stand scale across the landscape.

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CHAPTER 2: EFFECTS OF THINNING ON FOREST-FLOOR VERTEBRATES IN OREGON COASTAL DOUGLAS-FIR FORESTS

ABSTRACT

During 1994–1996, I conducted experimental and observational studies using pitfall trapping to assess effects of thinning on abundance and reproduction of forest-floor vertebrates in Douglas-fir (*Pseudotsuga menzeisii*) forests of the Oregon Coast Range. In the experimental study, I assessed the short-term effects of thinning stands to moderate ($\bar{x} = 267$ trees/ha, 95% CI = 248-286 trees/ha) and to low ($\bar{x} = 193$ trees/ha, 95% CI = 186-201 trees/ha) tree densities on forest-floor vertebrates during the first 2 years following thinning. In the observational study, I assessed potential long-term effects of thinning by comparing relative abundance and reproductive performance of forest-floor vertebrates in previously thinned (7-24 years prior to the study) and unthinned stands. In the short term (≤ 2 years), thinning did not influence total number of small mammals captured, but total number of amphibians captured decreased. Among the 14 species of vertebrates I examined in the experimental study, number of captures increased for 4 species of mammal and 1 species of amphibian and decreased for 1 species of mammal within 2 years of thinning; responses of these vertebrates were similar in moderately and heavily thinned stands. In the observational study, total number of amphibians captured did not differ between thinned and unthinned stands; however, total number of small mammals captured was higher in thinned than in unthinned stands. Among the 10 species I examined in the observational study, numbers of captures were greater for 5 species of mammal and

lower for 1 species of amphibian in thinned than in unthinned stands. Effects of thinning on abundances of creeping voles (*Microtus oregoni*) and Pacific jumping mice (*Zapus trinotatus*) were consistent in the short and long term; numbers of captures for both species increased in the first two years following thinning and were greater in stands thinned 7-24 years previously than unthinned stands. Number of western red-backed voles (*Clethrionomys californicus*) captured decreased within 2 years of thinning but was similar in stands thinned 7-24 years previously and in unthinned stands. In contrast, number of western red-backed salamanders (*Plethodon vehiculum*) captured did not change in response to thinning in the short term but was lower in stands thinned 7-24 years previously than in unthinned stands. Reproductive performances of deer mice (*Peromyscus maniculatus*) and creeping voles improved following thinning in the short term, but differed with thinning intensity; the increase in number and proportion of pregnant deer mice was greater in heavily thinned stands than in moderately thinned stands, whereas the increase in proportion of creeping vole females in breeding condition was greater in moderately thinned stands than in heavily thinned stands. In the observational study, reproductive performance of western red-backed voles was higher in thinned than in unthinned stands. Overall, thinning did not have substantial detrimental effects on any of the species I investigated and had positive effects on several. I suggest that potential negative effects of thinning could be minimized with planning and decisions based on ecological factors, and that thinning can be applied to enhance habitat quality of forest-floor vertebrates.

INTRODUCTION

Because of extensive fires, logging, and silvicultural practices, young forest stands (< 50 years old) of Douglas-fir have become increasingly dominant in the landscape of the Oregon Coast Range (Hayes et al. 1997). Historically, timber production was the primary management goal for most of these young stands in western Oregon and Washington (Oswald et al. 1986). Recently, however, there has been increased interest in incorporating non-timber objectives into management of the forests of the Pacific Northwest, especially conservation of wildlife species and biological diversity (Carey and Curtis 1996). However, relatively little information exists concerning how to incorporate non-timber objectives into even-age management of young Douglas-fir stands.

Thinning has been proposed as a potential approach to provide both for wildlife habitat management and timber production in young Douglas-fir stands (McComb et al. 1993, Carey and Johnson 1995, Carey and Curtis 1996, Hagar et al. 1996, Hayes et al. 1997). Thinning can increase vertical structural diversity of even-age stands for wildlife, while providing a source of wood products before stands complete the rotation (Hunter 1990:227, Oliver and Larson 1990:226). By regulating stand density through thinning, foresters can accelerate volume and diameter growth of trees, create trees with deeper crowns, and promote development of understory herbs and shrubs (Marshall 1990, Barbour et al. 1997, Hayes et al. 1997, Bailey and Tappeiner 1998, Bailey et al. 1998). Thinning with variable intensities, therefore, has

the potential to create diverse habitat conditions for wildlife (Carey and Curtis 1996, Hayes et al. 1997). For example, thinned stands, because of their high structural diversity, often maintain higher abundance and richness of breeding bird communities than unthinned stands in coniferous (Hagar 1992, Hagar et al. 1996) and hardwood forests (DeGraaf et al. 1991, Aigner et al. 1998). Thinning also can improve forage production for ungulates (Doerr and Sandburg 1986, Lyon 1987), and thinned stands are used more frequently by bats than nearby unthinned stands (Humes et al. 1999). In contrast, thinning of young lodgepole pine (*Pinus contorta*) reduced population densities of red squirrels (*Tamiasciurus hudsonicus*, Sullivan and Moses 1986) and did not improve habitat conditions for snowshoe hares (*Lepus americanus*, Sullivan and Sullivan 1988).

There is very little published information concerning responses of forest-floor small mammals (Wilson and Carey 2000) and amphibians (Grialou et al. 2000) to thinning. In the *Tsuga heterophylla* vegetation zone of Washington, small mammals were more abundant in thinned stands than in unthinned legacy stands, even though the legacy stands were managed to retain downed wood, snags, and live legacy trees (Wilson and Carey 2000). On the other hand, thinning did not affect presence and absence of 2 terrestrial amphibian species (red-backed salamanders and ensatinas) and did not reduce captures of these species, although the increase in capture of western red-backed salamanders between pre- and post treatment years was higher in control than in thinned stands (Grialou et al. 2000). These existing studies, however, did not address effects of thinning intensity on forest-floor vertebrates. Furthermore, they

addressed only either the short-term effects of thinning on amphibians using an experimental approach (Grialou et al. 2000) or the potential long-term effects of thinning on small mammals using an observational approach (Wilson and Carey 2000). Because none has addressed both short-term and long-term effects of thinning on a group of forest-floor vertebrates, information on potential long-term effects of thinning on amphibians and on short-term effects of thinning on small mammals is still lacking. Additionally, to my knowledge, no previous study has investigated the effects of thinning on forest-floor small mammals and amphibians in the Oregon Coast Range.

Few researchers have experimentally manipulated stand structure to examine response of species to thinning (Sullivan and Sullivan 1988, Aigner et al. 1998, Grialou et al. 2000). Instead, researchers generally rely on comparative mensurative experiments (Hurlbert 1984), generally referred to as observational studies (Ramsey and Schafer 1997:5-15), to compare abundance of wildlife or use of habitat between unthinned and previously thinned stands (e.g., Doerr and Sandburg 1986, DeGraaf et al. 1991, Hagar et al. 1996, Humes et al. 1999). In observational studies, investigators cannot randomly assign stands to treatment groups, and thus it is not possible to reliably infer causality as observed ecological differences may be due to confounding factors, such as environmental conditions, rather than thinning (Ramsey and Schafer 1997:5-7). Nonetheless, observational comparisons are useful because they require shorter time to conduct than do experimental studies and thus are valuable to evaluate potential long-term effects of management practices (Gauch 1982:68-69, Ramsey and

Schafer 1997:5-7). In this study, I employ both experimental and observational approaches.

A shortcoming of most studies of vertebrate habitat relationships is the failure to evaluate the influence of habitat on individual fitness. With rare exceptions (e.g., Sullivan and Moses 1986, Sullivan and Sullivan 1988, Grialou et al. 2000, Wilson and Carey 2000), conclusions about effects of thinning on wildlife are based on estimates or indices of abundance (e.g., DeGraaf et al. 1991, Hagar et al. 1996, Aigner et al. 1998) or habitat use (e.g., Doerr and Sandburg 1986, Humes et al. 1999). Because abundance or habitat use are not always related to habitat quality (Van Horne 1983), evaluation of measures of fitness is necessary to fully determine the effects of thinning on habitat quality for wildlife.

One component of fitness of small mammals is reproductive performance. Reproductive performance of small mammals is influenced by local environmental conditions and by availability of resources (Cameron 1977, Kenagy and Bartholomew 1981, Millar and Gyug 1981, Bronson and Pryor 1983, Kenagy and Bartholomew 1985, Millar and Innes 1985, Stenseth et al. 1985, Negus and Berger 1988, McMurry et al. 1994, Wauters and Lens 1995, Slade et al. 1996). In particular, increased availability and quality of food resources often increases reproductive performance of small mammals (Ford and Pitelka 1984, Batzli 1986, Bomford 1987, Dobson 1988, Merson et al. 1983, Heideman and Bronson 1993, McMurry et al. 1994, Duquette and Millar 1995, Slade et al. 1996). When food is scarce or the local environment is unfavorable, small mammals tend to reduce reproductive output to maintain the

probability of survival above some threshold level and thereby increase the probability of future reproduction (Myers and Master 1983, Ludwig 1988, Michener and Locklear 1990, Nichols et al. 1994, Waser and Jones 1991). Therefore, if thinning were to improve quality of habitat for small mammals, their reproductive performance would improve after thinning and would be better in previously thinned than in nearby unthinned stands.

In this study, I examined 1) whether manipulation of stand density through thinning influences abundance of forest-floor vertebrates and reproductive performance of small mammals, 2) whether the influence of thinning on abundance of forest-floor vertebrates and reproductive performance of small mammals differs between 2 thinning intensities (moderate and heavy thinning), 3) whether results from the short-term and long-term responses are similar, and 4) whether there is a relationship between abundance and reproductive performance of each species of small mammals.

Because thinning reduces tree density, increases light input, and stimulates understory growth (Bailey and Tappeiner 1998, Bailey et al 1998), I hypothesized that the habitat conditions of forest-floor following thinning would be beneficial to open-habitat or early- seral associates, such as deer mouse (Verts and Carraway 1998: 270-271) and creeping vole (Goertz 1964, Gashwiler 1972). On the other hand, I hypothesized that thinning would have negative effects on associates of closed canopy forests, such as western red-backed vole (Doyle 1987, Rosenberg et al. 1994, Mills 1995, Verts and Carraway 1998: 298-299). Furthermore, as thinning reduces

suppression mortality of competing overstory trees and recruitment of deadwood (Smith et al. 1997: 69-130), I hypothesized that thinning would have negative effects on associates of dead wood, such as the western red-backed vole (Hayes and Cross 1987, Tallmon and Mills 1994), ensatina, and western red-backed salamander (Aubry et al 1988, Aubry and Hall 1991, Corn and Bury 1991, Butts and McComb 2000).

Based on these hypotheses, I predicted that relative abundances and reproduction of deer mice and creeping vole would increase following thinning and would be higher in previously thinned stands than in unthinned stands and that those of western red-backed voles would decrease following thinning and would be lower in previously thinned stands than in unthinned stands. I further predicted that relative abundances of ensatinas and western red-backed salamanders would decrease following thinning and would be lower in previously thinned stands than in unthinned stands.

STUDY AREA

Experimental Study

As part of a larger study on the effects of thinning on wildlife, 4 replicate areas of 35-45 year-old, unthinned Douglas-fir forests were selected in the northern Oregon Coast Range for the experimental study. The replicates are located within an extensive area of the northern Oregon Coast Range, generally referred as “the Tillamook Burn”. A series of 4 fires burned the Tillamook Burn between 1933 and 1951, and the area

was subsequently reforested with Douglas-fir between 1949 and 1970 (Wells 1999:7-12). Three of the replicates were located in the Tillamook State Forest, Tillamook County, Oregon and one was on adjacent private land, owned by Stimson Lumber Company (Figure 1). Each replicate is comprised of 3 stands selected to minimize differences in initial tree density, proportion of hardwoods, and stand age within a replicate. Stands ranged from 26 to 40 ha ($\bar{x} = 34$ ha) in area and 485 to 849 m ($\bar{x} = 612$ m) in elevation. The climate of the Oregon Coast Range is maritime and is characterized by wet and mild winters and cool, dry summers (Franklin and Dyrness 1988:38-43).

Both the experimental and observational thinning study areas were in the *Tsuga heterophylla* vegetation zone (Franklin and Dyrness 1988:70-93). Douglas-fir was the dominant tree species in the experimental study sites and red alder (*Alnus rubra*) was common in moist or disturbed areas. Other tree species found in the study area included western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), noble fir (*Abies procera*), and Sitka spruce (*Picea sitchensis*). Common understory shrubs were salal (*Gaultheria shallon*), red huckleberry (*Vaccinium parviflorum*), trailing blackberry (*Rubus ursinus*), vine maple (*Acer circinatum*), and dwarf Oregon grape (*Berberis nervosa*). Common species of herbs included Oregon oxalis (*Oxalis oregana*), sword fern (*Polystichum munitum*), and bracken fern (*Pteridium aquilinum*).

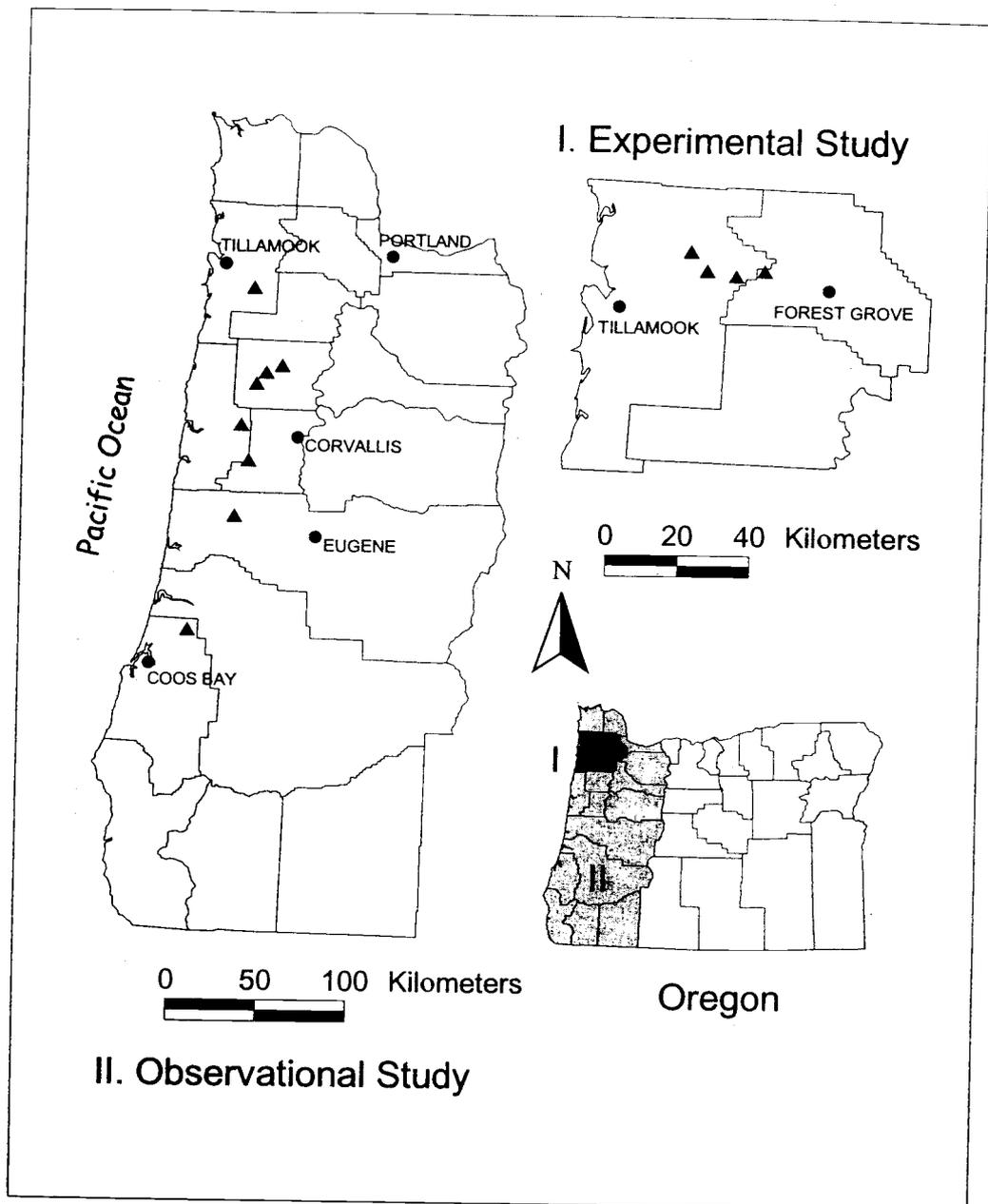


Figure 1. Locations (represented by triangles) of 4 replicate areas, each of which is comprised of control, moderately thinned, and heavily thinned stands, in the experimental thinning study (I), and of 8 replicate areas of thinned and unthinned paired stands in the observational study (II), Oregon Coast Range, 1994-1996.

Observational Study

I selected 8 sites, consisting of 1 previously thinned and 1 unthinned stand for the observational study. These sites were located in the Oregon Coast Range, from Tillamook County in the north to Coos County in the south (Figure 1). Elevations ranged from 303 to 582 m ($\bar{x} = 483$ m). Thinned stands were thinned between 1971 and 1988 (7 to 24 years prior to the study). Ages of thinned and unthinned stands within a pair were the same and ranged from 52 to 100 years at the time of the study. Stand sizes ranged from 10 to 28 ha ($\bar{x} = 20$ ha) for thinned stands and from 20 to 73 ha ($\bar{x} = 46$ ha) for unthinned stands. Tree densities of thinned stands in the observational study averaged slightly higher than those of moderately thinned stands in the experimental study; tree densities of unthinned stands were similar to those of control stands in the experimental study (Table 1). Although stand densities are somewhat higher in the unthinned and thinned stands in the observational study than are the control and moderately thinned stands in the experimental study, basal area, DBH, relative density, and other aspects of stand structure in the observational study stands approximate future conditions likely to occur in the control and moderately thinned stands in the experimental study stands.

Douglas-fir dominated the overstory in all stands with patchy distributions of western hemlock and red alder. Common understory shrubs and herbs were generally similar to those in the experimental thinning sites, although Pacific rhododendron (*Rhododendron macrophyllum*) and evergreen huckleberry (*Vaccinium ovatum*) were also common in 2 southern most sites.

Table 1. Characteristics of control (C), moderately thinned (M), and heavily thinned (H) stands in the experimental thinning study before and after thinning; and of unthinned (U) and previously thinned (T) stands (7-24 years previously) in the observational thinning study.

		Experimental Study (n = 4)				Observational Study		
		Pre-treatment (1994)		Post-treatment (1996)		(n = 8)		
		\bar{x}	95% CI	\bar{x}	95% CI	\bar{x}	95% CI	
Trees/ha	C	559	462-656	500	460-540	U	575	439-711
	M	591	522-660	267	248-286	T	346	292-399
	H	574	452-696	193	186-201			
Basal area (m ² /ha)	C	41.1	38.1-44.1	43.6	41.8-45.5	U	65.8	59.7-71.9
	M	41.6	36.4-46.7	27.2	22.3-32.2	T	47.8	41.9-53.7
	H	43.7	39.0-48.5	18.8	16.7-20.9			
DBH (cm)	C	31.1	28.6-33.7	32.0	29.3-34.7	U	41.5	35.3-47.7
	M	29.9	27.4-32.4	36.1	32.8-39.3	T	50.9	45.8-56.1
	H	31.6	29.9-33.3	37.5	34.3-40.7			
Relative Density ^a	C	0.56	0.50-0.62	0.52	0.50-0.54	U	0.74	0.67-0.80
	M	0.57	0.48-0.65	0.31	0.27-0.36	T	0.52	0.46-0.57
	H	0.59	0.52-0.67	0.21	0.20-0.23			

^a Relative density of a stand was calculated based on the following equation by Curtis (1982):
Relative Density (RD) = [(trees/ha) × (quadratic mean diameter/25)^{1.6}]/1470.

METHODS

Thinning in the Experimental Study

In each replicate in the experimental study, 1 stand was randomly assigned to be left unthinned as a control, 1 to be thinned to a moderate tree density (target relative density [RD] of 0.35, Drew and Flewelling 1979; \bar{x} = 267 trees/ha, 95% CI = 248-286 trees/ha), and 1 stand to be heavily thinned to a low tree density (target RD of 0.20; \bar{x} = 193 trees/ha, 95% CI = 186-201 trees/ha). Tree density ranged from 456 to 713 trees/ha prior to thinning. The stands were thinned from below (Smith et al. 1997:99-102) between August 1994 and April 1995; cables and tractors were used to yard felled trees from the stands.

Sampling of Vertebrate Species and Assessment of Small Mammal Reproduction

I established a grid of 25 sampling stations in each stand with stations spaced at 80-m intervals in experimental study sites and 40-m intervals in observational study sites. I placed 2 pitfall traps (double-deep No. 10 tin can) within 10 m of each station center and added water to the bottom 5 cm of each trap upon opening. Traps were opened for 6 weeks beginning in May before thinning in 1994 and after thinning in 1995 and 1996 in the experimental study sites and were opened in the second week of April in 1995 and in 1996 and operated for 40 consecutive days in each year in the observational study sites. I checked traps weekly. Captured live amphibians were

identified to species, measured for body mass, total length, and snout-vent length, and were released outside the trapping grid. All other vertebrates captured were collected.

I identified individuals to species and measured body mass and length (from tip of nose to base of tail) of small mammals and body mass, snout-vent length, and total length of amphibians. Taxonomy used in this study generally follows Collins (1990) for amphibians and reptiles and Jones et al. (1992) and Wilson and Reeder (1993) for mammals. I followed the taxonomic revisions by Good (1989) for Pacific giant salamanders (*Dicamptodon tenebrosus*) and by Good and Wake (1992) for Columbia torrent salamanders (*Rhyacotriton kezeri*) and southern torrent salamanders (*Rhyacotriton variegatus*). I followed the correction of the specific epithet for Baird's shrew (*Sorex bairdi*) presented by Alexander (1996).

I recorded reproductive characteristics of shrew-moles (*Neurotrichus gibsii*), Pacific shrews (*S. pacificus*), fog shrews (*S. sonomae*), marsh shrews (*S. bendirii*), western red-backed voles, white-footed voles (*Arborimus albipes*), creeping voles, deer mice, and Pacific jumping mice. For females, I recorded size of mammae (small or large) and number of visible embryos or placental scars on uterine horns. A female was classified as in breeding condition if it had large mammae, at least one placental scar, or at least one embryo. A female in breeding condition was classified as parous if it had at least one placental scar but no embryos, or as pregnant if it had at least one embryo. For males I measured length and width of a testis and calculated volume based on the equation for the prolate spheroid (Beyer 1987:162; $\text{volume} = 4/3 \pi \times [\text{length}/2] \times [\text{width}/2]^2$).

Habitat Sampling

I sampled habitat characteristics at each grid point in the experimental study sites from late June through July in 1994, 1995, and 1996 and at 20 randomly selected grid points in each stand in the observational study sites in August, 1996. Sampling plots for understory vegetation and forest-floor structure consisted of two 5 m-radius circular plots, two 1 × 1 m square plots nested within each 5 m-radius circular plot, a 10-m radius circular plot, and a 15-m radius circular plot (Figure 2). Center points of the two 5 m-radius circular plots were located 7 m north and 7 m south from the grid point.

Within each 5 m-radius plot, I ocularly estimated percent cover of tall shrubs (woody plants > 1.4 m tall with stems < 10 cm diameter at breast height [DBH]), low shrubs (woody plants < 1.4 m tall with stems < 10 cm DBH), herbs, and slash (downed woody material with stems < 10 cm in diameter). Percent cover of overstory tree canopy was estimated using a convex spherical densiometer at the center points of the 5-m circular plots and was also ocularly estimated in the 15-m radius plot. Values for habitat variables measured in the 2 5-m radius circular plots were averaged for analysis.

Within each 1 × 1 m square plot I ocularly estimated exposure of mineral soil and percent cover of leaf litter, moss, and rock. I also measured depth of leaf litter at 3 randomly selected points within each square plot and recorded the mean of these values. Estimated values of each variable from the 4 1 × 1 m square plots were averaged used for analysis.

Downed logs were classified by diameter (small, 10-29 cm; medium, 30-49 cm; large, ≥ 50 cm) based on the largest diameter within the 10-m radius plot, and by decay class (decay class 1, 2-3, or 4-5; Maser et al. 1979). Frequency and cumulative length of downed logs in each 10-m radius plot were recorded by decay and diameter class.

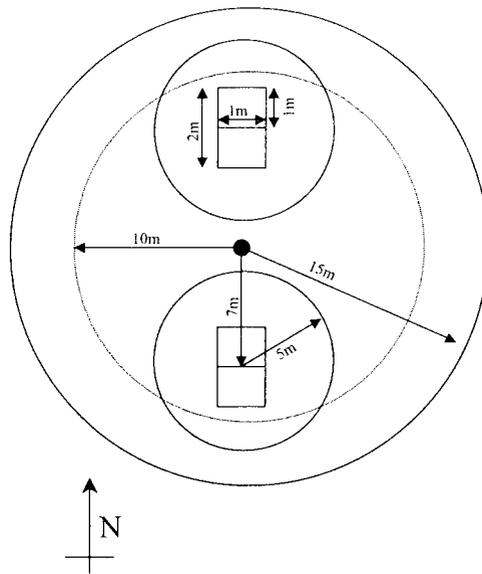


Figure 2. Arrangement of habitat sampling plots.

Data Analysis

For each stand, I used captures of forest-floor vertebrates per 100 trap nights (100TN) as an index of relative abundance. In the experimental study, I used repeated-measures ANOVA with orthogonal contrasts (PROC MIXED; SAS Institute 1997) to assess the influence of thinning and thinning intensity on changes in relative abundance, reproductive parameters, and habitat characteristics. The orthogonal contrasts tested 4 specific null hypotheses for each variable: 1) mean changes in estimated values before and after thinning were equal in control and thinned stands, 2) mean changes in estimated values from the 1st (1995) to the 2nd (1996) post-treatment year were equal in control and thinned stands, 3) mean changes in estimated values before and after thinning were equal in moderately thinned and heavily thinned stands, and 4) mean changes in estimated values from the 1st (1995) to the 2nd (1996) post-treatment year were equal in moderately thinned and heavily thinned stands. In the observational study, I used repeated-measures ANOVA to assess whether estimated means for numbers of captures and reproductive parameters differed between thinned and unthinned stands. Because habitat variables were measured only in 1996 on the observational study sites, I used randomized-complete-block ANOVA, using sites as blocks, to compare differences in estimated means of habitat variables between thinned and unthinned stands.

For all ANOVAs, I examined all variables for normality, constant variance, and independence of residuals using normal probability plots, histograms, and residual

plots (Sabin and Stafford 1990, PROC UNIVARIATE; SAS Institute 1990). I transformed variables that did not meet these assumptions of ANOVA. I used logarithmic transformation, $\ln(Y+1)$ or $\ln(Y)$, for analyses of vertebrate captures/100TN, testis size, and lengths of downed logs; logarithmic or arcsine square-root transformations for analyses of proportions of females in different reproductive conditions, sex ratios, and percent cover of habitat variables; and square-root transformation for analyses of frequencies of downed logs.

I used binomial logistic regression analysis (PROC GENMOD; SAS Institute 1997) to test whether odds of females being pregnant, parous, or in breeding condition can be predicted from number of a species captured in stands. In these analyses, I used the odds ratio of each reproductive parameter as dependent variables and captures/100TN of each species and indicator variables for sites as independent variables in the model; data from the experimental and observational studies were analyzed separately.

Because the numbers of replications for the experimental ($n = 4$) and observational studies ($n = 8$) were small, I considered results with $P < 0.1$ as statistically significant in all analyses to reduce the chance of committing type II error. I analyzed number of captures for species with > 30 captures and reproductive attributes of species with > 30 breeding females in each of experimental and observational studies. Because distribution of aquatic habitats was biased in our study

sites, data for two species of amphibians that are strongly associated with aquatic habitat, tailed frogs (*Ascaphus truei*) and rough-skinned newts (*Taricha granulosa*), were excluded from analysis.

RESULTS

Habitat Characteristics

Experimental Study

Canopy cover of overstory trees was significantly reduced in thinned stands ($F_{1,18} = 34.10, P < 0.001$, Table 2), and the reduction was greater in heavily thinned stands than in moderately thinned stands ($F_{1,18} = 4.34, P = 0.052$). Thinning also reduced percent cover of tall shrubs ($F_{1,18} = 10.40, P = 0.005$) and moss ($F_{1,18} = 16.05, P < 0.001$); cover of tall shrubs ($F_{1,18} = 4.21, P = 0.055$) and moss ($F_{1,18} = 6.75, P = 0.018$) decreased more in heavily thinned than in moderately thinned stands.

In thinned stands, cover of low shrubs increased in heavily thinned stands relative to that in moderately thinned stands from 1995 to 1996 ($F_{1,18} = 3.40, P = 0.082$). Percent cover of herbs in thinned stands also increased relative to that in control stands from 1995 to 1996 ($F_{1,18} = 4.69, P = 0.044$); however, the amount of increase did not differ between moderately thinned and heavily thinned stands ($F_{1,18} = 1.79, P = 0.198$).

Thinning increased percent cover of slash ($F_{1,18} = 72.46$, $P < 0.001$), and this increase was greater in heavily thinned stands than in moderately thinned stands ($F_{1,18} = 20.01$, $P < 0.001$). Thinning also increased exposure of mineral soil ($F_{1,18} = 5.89$, $P = 0.026$). Exposure of mineral soil subsequently decreased ($F_{1,18} = 3.50$, $P = 0.078$) as cover ($F_{1,18} = 9.50$, $P = 0.006$) and depth ($F_{1,18} = 4.16$, $P = 0.056$) of litter increased in moderately thinned stands relative to heavily thinned stands in 1996.

Influence of thinning on abundance of downed logs varied among size classes (Table 3). Frequency and cumulative length of small downed logs increased following thinning (frequency, $F_{1,18} = 15.63$, $P < 0.001$; length, $F_{1,18} = 11.92$, $P = 0.003$); in contrast, frequency and length of medium-sized logs decreased (frequency, $F_{1,18} = 7.62$, $P = 0.013$; length $F_{1,18} = 10.28$, $P = 0.005$). There was no difference in frequency of large logs before and after the thinning ($P > 0.1$), although, the cumulative length of large-sized logs decreased in thinned stands following thinning ($F_{1,18} = 3.59$, $P = 0.074$).

Table 2. Means and 95% confidence intervals of 9 habitat variables, and *P*-values from 4 orthogonal contrasts in repeated measures ANOVA comparing each habitat variable among control (C), moderately thinned (M), and heavily thinned (H) stands between pre-treatment year (1994) and post-treatment years (1995 and 1996), northern Oregon Coast Range, 1994-1996. *P*-values for "Pre vs. Post" are for contrasts testing whether changes in means between the pretreatment year and overall post-treatment years differed between control and thinned stands (C vs. T) and between moderately and heavily thinned stands (M vs. H). *P*-values for "95 vs. 96" are for contrasts testing whether changes in means between 1995 and 1996, the 2 post-treatment years, differed between control and thinned stands (C vs. T) and between moderately and heavily thinned stands (M vs. H). The sample size was $n = 4$ for each of control, moderately thinned, and heavily thinned stands.

Variables		Pre-treatment		Post-treatment		<i>P</i>		
		\bar{x}	95% CI	\bar{x}	95% CI	Pre vs. Post	95 vs. 96	
Litter (%)	C	92.3	85.2-97.2	93.5	88.9-96.9	C vs. T	0.254	0.002
	M	93.5	86.8-97.9	92.4	87.5-96.1	M vs. H	0.706	0.006
	H	94.3	88.0-98.4	92.2	87.3-96.0			
Mineral (%)	C	5.2	2.1-9.6	6.0	2.8-10.3	C vs. T	0.026	0.067
	M	3.2	0.9-6.9	7.3	3.8-12.0	M vs. H	0.552	0.078
	H	2.5	0.5-5.7	7.4	3.8-12.1			
Moss (%)	C	19.7	15.3-24.6	19.5	14.6-25.0	C vs. T	0.001	0.660
	M	16.2	12.1-20.7	10.9	7.2-15.4	M vs. H	0.018	0.646
	H	24.4	19.6-29.6	11.8	7.9-16.3			
Herb (%)	C	33.2	17.0-64.6	29.9	15.4-57.8	C vs. T	0.409	0.044
	M	35.7	18.3-69.5	29.7	15.3-57.5	M vs. H	0.942	0.198
	H	38.2	19.6-74.4	32.0	16.6-62.0			
Low shrub (%)	C	25.6	12.8-51.2	20.0	10.2-39.2	C vs. T	0.018	0.663
	M	11.0	5.5-21.9	11.2	5.7-22.1	M vs. H	0.626	0.082
	H	16.4	8.2-32.8	18.0	9.2-35.2			
Tall shrub (%)	C	18.3	8.5-39.3	15.1	7.2-31.6	C vs. T	0.005	0.362
	M	15.5	7.2-33.4	8.7	4.1-18.1	M vs. H	0.055	0.483
	H	14.9	6.9-32.0	5.3	2.5-11.0			

Table 2 (Continued).

Slash (%)	C	9.6	6.9-13.5	3.9	2.9-5.1	C vs. T	<0.001	0.028
	M	14.9	10.6-20.8	18.0	13.6-23.8	M vs. H	<0.001	0.663
	H	7.3	5.2-10.2	22.9	17.3-30.3			
Canopy (%)	C	97.4	95.8-98.6	97.9	96.0-99.2	C vs. T	<0.001	0.736
	M	97.7	96.2-98.8	87.4	83.4-90.9	M vs. H	0.052	0.227
	H	97.0	95.4-98.3	76.9	72.0-81.5			
Litter depth (cm)	C	1.5	1.2-1.9	1.7	1.4-2.1	C vs. T	0.159	0.398
	M	2.1	1.6-2.6	1.8	1.5-2.2	M vs. H	0.568	0.056
	H	2.1	1.7-2.7	2.1	1.7-2.5			

Table 3. Mean frequencies and cumulative lengths of downed logs of 3 size classes, and *P*-values from 4 orthogonal contrasts in repeated measures ANOVA, as identified in Table 2, comparing log abundances among control (C), moderately thinned (M), and heavily thinned (H) stands between pretreatment year (1994) and post-treatment years (1995 and 1996), northern Oregon Coast Range, 1994-1996. The sample size was $n = 4$ for each of control, moderately thinned, and heavily thinned stands.

Size classes	Pre-treatment		Post-treatment		<i>P</i>			
	\bar{x}	95%CI	\bar{x}	95% CI	Pre vs. Post	95 vs. 96		
Frequency (no./ha)								
Small	C	102.6	38.8-196.8	135.3	70.6-220.8	C vs. T	<0.001	0.930
	M	122.8	51.6-224.5	375.4	260.7-510.9	M vs. H	0.606	0.878
	H	136.5	60.6-242.8	361.2	248.9-494.4			
Medium	C	111.6	62.9-174.2	108.1	65.5-161.3	C vs. T	0.013	0.606
	M	127.5	75.0-194.0	76.9	41.8-122.6	M vs. H	0.247	0.585
	H	207.5	139.5-290.3	106.3	64.1-159.1			
Large	C	140.4	103.9-182.4	126.3	97.4-159.0	C vs. T	0.319	0.484
	M	149.7	111.9-192.9	118.1	90.1-149.7	M vs. H	0.713	0.169
	H	202.9	158.5-252.8	155.6	123.2-191.7			
Length (m/ha)								
Small	C	415.0	254.2-677.6	565.8	369.0-867.5	C vs. T	0.003	0.719
	M	476.2	291.7-777.5	1317.5	859.3-2020.0	M vs. H	0.825	0.659
	H	425.3	260.5-694.4	1243.5	811.0-1906.6			
Medium	C	365.0	212.7-626.4	306.5	187.0-502.4	C vs. T	0.005	0.279
	M	394.9	230.1-677.7	207.3	126.5-339.8	M vs. H	0.275	0.591
	H	768.6	447.8-1319.0	317.9	193.9-521.0			
Large	C	647.4	491.9-852.1	555.8	436.3-707.9	C vs. T	0.074	0.766
	M	680.7	517.2-895.9	473.8	372.0-603.5	M vs. H	0.613	0.347
	H	893.1	678.6-1175.5	575.0	451.4-732.4			

Observational Study

Of 23 habitat attributes I measured, mean values of 12 attributes differed between thinned and unthinned stands (Table 4). Thinned stands had lower percent cover of overstory-tree canopy ($F_{1,7} = 15.80, P = 0.005$) and higher percent cover of tall shrubs ($F_{1,7} = 6.43, P = 0.039$), low shrubs ($F_{1,7} = 11.26, P = 0.012$), and herbs ($F_{1,7} = 3.88, P = 0.090$) than did unthinned stands. Thinned stands had higher percent cover of bracken fern ($F_{1,7} = 16.27, P = 0.005$), trailing blackberry ($F_{1,7} = 17.94, P = 0.004$), and salal ($F_{1,7} = 9.15, P = 0.019$) than did unthinned stands. Means of five variables related to downed wood were higher in unthinned stands than in thinned stands: percent cover of slash ($F_{1,7} = 27.06, P = 0.001$), frequency ($F_{1,7} = 8.19, P = 0.024$) and cumulative length ($F_{1,7} = 23.47, P = 0.002$) of small logs, and frequency ($F_{1,7} = 9.73, P = 0.017$) and cumulative length ($F_{1,7} = 11.71, P = 0.011$) of medium logs. Frequency and cumulative length of large logs did not differ between thinned and unthinned stands ($P > 0.1$).

Table 4. Habitat characteristics of unthinned stands and stands thinned 7-24 years previously in the Oregon Coast Range, 1996. *P*-values were from randomized complete block ANOVAs with *n* = 8 pairs of thinned and unthinned stands.

Variables	Unthinned		Thinned		<i>F</i> _{1,7}	<i>P</i>
	\bar{x}	95% CI	\bar{x}	95% CI		
Vegetative and forest-floor characteristics						
Litter (%)	98.5	96.2-99.7	98.6	96.5-99.8	0.17	0.688
Mineral (%)	1.3	0.4-4.2	0.7	0.2-2.4	2.35	0.169
Moss (%)	39.5	26.5-53.3	37.9	25.0-51.6	0.14	0.723
Herb (%)	23.7	7.9-44.7	35.1	15.9-57.2	3.88	0.090
Low shrub (%)	15.5	8.7-27.8	39.9	22.2-71.5	11.26	0.012
Tall shrub (%)	7.6	3.2-17.7	17.3	7.4-40.4	6.43	0.039
Slash (%)	1.9	1.0-3.7	5.7	3.0-11.1	27.06	0.001
Canopy (%)	97.8	96.7-98.6	94.9	93.3-96.2	15.80	0.005
Litter depth (cm)	2.0	1.7-2.5	2.0	1.6-2.4	0.29	0.605
Herb species (%)						
Sword fern	7.2	2.8-18.6	7.9	3.1-20.4	0.09	0.779
Bracken fern	2.5	0.1-8.1	12.7	5.3-22.5	16.27	0.005
Oxalis	5.3	0.0-20.7	6.1	0.0-22.1	0.42	0.538
Shrub species (%)						
Trailing Blackberry	0.7	0.2-1.6	2.8	1.5-4.3	17.94	0.004
Table 4 (continued)						
Salal	4.0	0.9-18.2	15.0	3.3-67.9	9.15	0.019
Dwarf Oregon grape	2.8	0.7-11.1	2.3	0.6-8.9	0.23	0.649
Red huckleberry	2.1	0.8-4.1	2.4	1.0-4.5	0.15	0.709
Vine maple	5.8	0.1-19.2	8.6	0.8-23.7	0.48	0.512
Frequencies of logs (no./ha)						
Small	265.3	188.5-373.3	193.3	137.3-272.0	8.19	0.024
Medium	110.0	65.9-165.2	64.0	31.8-107.5	9.73	0.017
Large	75.4	43.7-115.6	51.8	26.3-85.8	3.02	0.126
Cumulative length of logs (m/ha)						
Small	1165.9	820.9-1656.0	686.9	483.6-975.6	23.47	0.002
Medium	462.2	243.7-876.5	206.1	108.7-390.9	11.71	0.011
Large	268.3	137.9-522.1	204.6	105.2-398.2	1.24	0.302

Abundance of Forest-floor Vertebrates

Experimental Study

Over 3 years and 75,600 trap nights, I captured 9,016 forest-floor vertebrates in the experimental study sites (11.93 captures/100TN), which included captures of 18 species of small mammals, 10 species of amphibians, and 1 species of reptile.

Trowbridge's shrews (*S. trowbridgii*) were caught most frequently (6.77 captures/100TN) and comprised of 56.8% of all captures of forest-floor vertebrates. Other species of mammals with $n > 30$ individuals included Pacific shrews (1.59 captures/100TN, 13.4% of the total capture), Baird's shrews (0.68 captures/100TN, 5.76%), deer mice (0.62 captures/100TN, 5.21%), vagrant shrews (*S. vagrans*; 0.41 captures /100TN, 3.48%), western red-backed voles (0.40 captures/100TN, 3.33%), shrew-moles (0.30 captures/100TN, 2.52%), creeping voles (0.23 captures/100TN, 1.91%), marsh shrews (0.20 captures/100TN, 1.69%), Pacific jumping mice (0.16 captures/100TN, 1.35%), white-footed voles (0.05 captures/100TN, 0.42%), and coast moles (*Scapanus orarius*; 0.04 captures/100TN, 0.35%). Ensatinas (*Ensatina eschscholtzii*) was the most frequently captured amphibian species (0.10 captures/100TN, 0.80%); other species of amphibians with $n > 30$ individuals included tailed frogs (0.09 captures/100TN, 0.78%), western red-backed salamanders (0.09 captures/100TN, 0.74%), and rough-skinned newts (0.06 captures/100TN, 0.54%). Species with < 30 captures included long-tailed vole (*Microtus longicaudus*),

Townsend's vole (*M. townsendii*), mountain beaver (*Aplodontia rufa*), western pocket gopher (*Thomomys mazama*), ermine (*Mustela erminea*), brush rabbit (*Sylvilagus bachmani*), Northwestern salamander (*Ambystoma gracile*), Pacific giant salamander (*Dicamptodon tenebrosus*), Dunn's salamander (*Plethodon dunni*), torrent salamander (*Rhyacotriton* sp.), red-legged frog (*Rana aurora*), Pacific treefrog (*Pseudacris regilla*), and Northern alligator lizard (*Elgaria coerulea*).

Thinning did not affect total number of captures of small mammals ($P > 0.1$), but total number of captures of amphibians decreased following thinning ($F_{1,18} = 3.14$, $P = 0.093$; Figure 3, APPENDIX 1). The total number of captures of amphibians had continuously decreased in heavily thinned stands over both post-treatment years, whereas it increased to the pre-thinning level in moderately thinned stands in 1996 ($F_{1,18} = 11.55$, $P = 0.003$). As I predicted, captures of western red-backed voles decreased following thinning, but remained relatively constant in control stands throughout the study ($F_{1,18} = 3.66$, $P = 0.072$). Number of red-backed voles captured in thinned stands continued to decrease from 0.33 captures/100TN in 1995 to 0.14 captures/100TN in 1996 ($F_{1,18} = 3.13$, $P = 0.094$). The decrease in captures of western red-backed voles did not differ significantly between moderately and heavily thinned stands ($P > 0.1$). In contrast, number of captures of deer mice ($F_{1,18} = 5.49$, $P = 0.031$), creeping voles ($F_{1,18} = 4.10$, $P = 0.058$), and white-footed voles ($F_{1,18} = 4.49$, $P = 0.048$) increased in thinned stands relative to control stands following thinning. The increase in number of captures of deer mice and creeping voles in response to thinning were also consistent with my predictions. The amount and pattern of increases of

these 3 species, however, did not differ between moderately and heavily thinned stands (deer mice, $F_{1,18} = 0.02$, $P = 0.886$; creeping voles, $F_{1,18} = 0.56$, $P = 0.4635$; white-footed voles, $F_{1,18} < 0.01$, $P = 0.979$). I detected delayed responses in abundances of ensatinas and of Pacific jumping mice to thinning; numbers of captures of these species increased in thinned stands relative to control stands from 1995 to 1996 (ensatinas, $F_{1,18} = 6.66$, $P = 0.019$; Pacific jumping mice, $F_{1,18} = 3.03$; $P = 0.098$). The increase in numbers of ensatinas in response to thinning was contrary to my prediction. No differences in the amount or pattern of increases were detected for ensatinas and Pacific jumping mice between moderately and heavily thinned stands during this period (ensatinas, $F_{1,18} = 0.38$, $P = 0.5436$; Pacific jumping mice, $F_{1,18} = 0.08$, $P = 0.774$). Thinning did not significantly affect number of captures of Baird's shrews, marsh shrews, Pacific shrews, Trowbridge's shrews, vagrant shrews, shrew-moles, coast moles, or western red-backed salamanders ($P > 0.1$). The apparent lack of response of western red-backed salamanders to thinning in the short term was not consistent with my predictions.

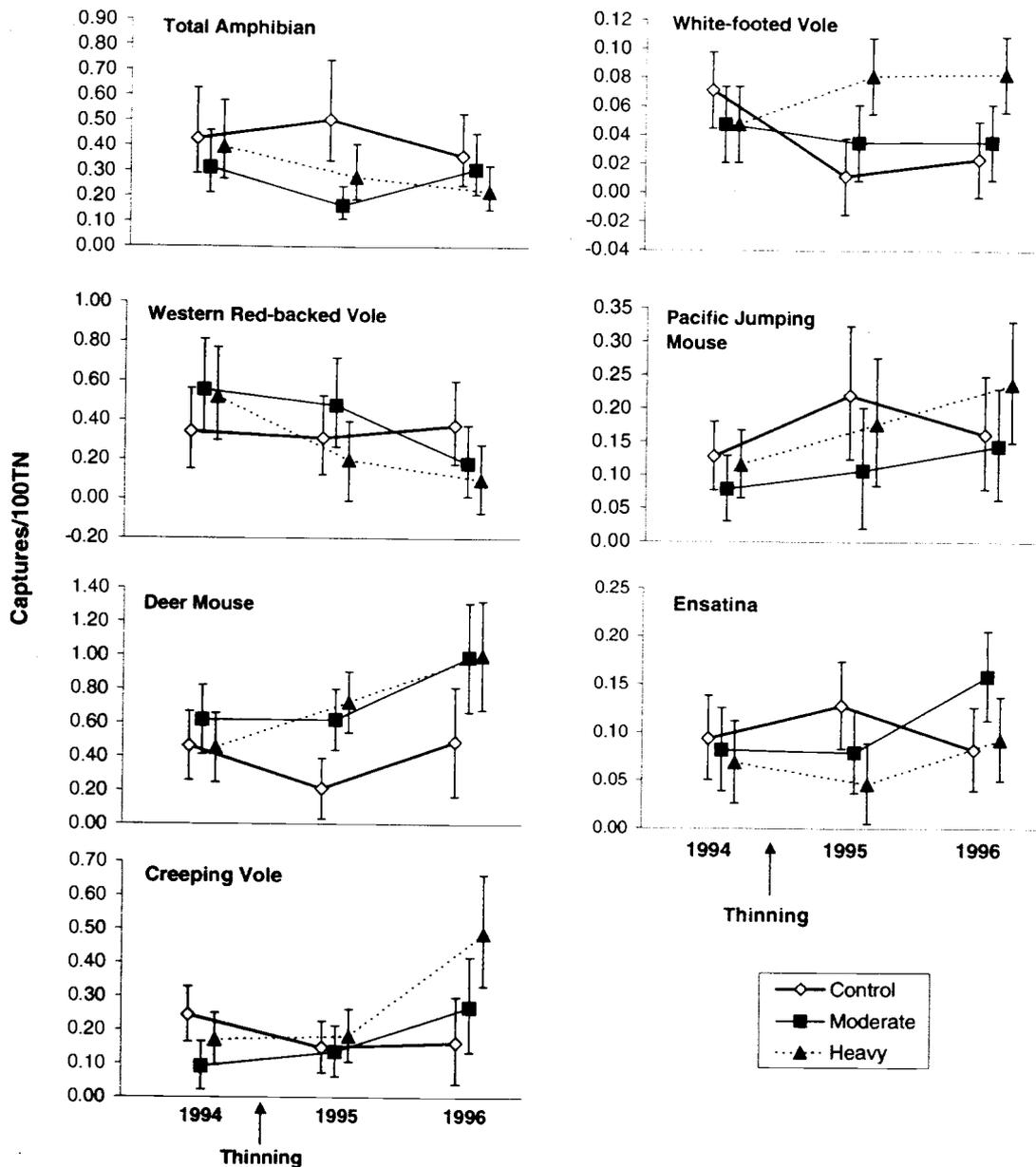


Figure 3. Mean numbers of captures/100 trap nights of 6 species of forest-floor vertebrates in control ($n = 4$), moderately thinned ($n = 4$), and heavily thinned stands ($n = 4$) before (1994) and after (1995-1996) thinning was implemented. Error bars represent plus and minus 1 SE.

Observational Study

Over 2 years and 64,000 trap nights, I captured 5,094 forest-floor vertebrates in the observational study sites (7.96 captures/100TN), which included 18 species of mammals, 10 species of amphibians, and 1 species of reptile. Trowbridge's shrew was the most frequently caught species (5.11 captures/100TN) and comprised 64.25% of the total captures of all forest-floor vertebrates. Other species of mammals with captures $n > 30$ individuals included western red-backed voles (0.79 captures/100TN, 9.95 % of total captures), Pacific shrews (0.51 captures/100TN, 6.47%), fog shrews (0.26 captures/100TN, 3.32%), shrew-moles (0.16 captures/100TN, 1.96%), deer mice (0.13 captures/100TN, 1.64%), vagrant shrews (0.09 captures/100TN, 1.18%), Pacific jumping mice (0.05 captures/100TN, 0.69%), and creeping voles (0.048 captures/100TN, 0.61%). The most frequently captured amphibian was the western red-backed salamander (0.20 captures/100TN, 2.47%). Other species of amphibians with captures $n > 30$ individuals included ensatinas (0.16 captures/100TN, 2.10%), rough-skinned newts (0.12 captures/100TN, 1.53%), and tailed frogs (0.08 captures/100TN, 1.00%). Species with captures $n < 30$ individuals included coast mole, Baird's shrew, marsh shrew, white-footed vole, red tree vole (*A. longicaudus*), Townsend's vole, western pocket gopher, ermine, brush rabbit, Northwestern salamander, Pacific giant salamander, Dunn's salamander, southern torrent salamander (*R. variegatus*), red-legged frog, Pacific treefrog, and Northern alligator lizard.

Total number of amphibians captured did not differ between thinned and

unthinned stands ($P > 0.1$, Table 5), but total number of small mammals captured was higher in thinned stands than in unthinned stands. Of the 12 species of forest-floor vertebrates with > 30 individuals captured, number of captures did not differ between thinned and unthinned stands for four species (shrew-moles, western red-backed voles, deer mice, and ensatinas; $P > 0.1$). These findings for western red-backed voles, deer mice, and ensatinas in thinned and unthinned stands, therefore, were not consistent with my predictions. Five species were captured more frequently in thinned stands than in unthinned stands (creeping voles $F_{1,7} = 5.75$, $P = 0.048$; Pacific jumping mice, $F_{1,7} = 7.03$, $P = 0.033$; Trowbridge's shrews, $F_{1,7} = 4.72$, $P = 0.066$; vagrant shrews $F_{1,7} = 3.85$, $P = 0.091$; and Pacific shrews $F_{1,5} = 4.32$, $P = 0.092$). The higher captures of creeping voles in thinned stands were consistent with my predictions. Although the number of Pacific jumping mice captured showed a slight interaction between treatment and year ($F_{1,14} = 3.32$, $P = 0.090$); it was consistently higher in thinned stands than in unthinned stands in both 1995 ($F_{1,7} = 6.22$, $P = 0.041$) and 1996 ($F_{1,7} = 3.91$, $P = 0.089$). Only western red-backed salamanders were captured less frequently in thinned than in unthinned stands ($F_{1,7} = 3.73$, $P = 0.095$). The lower number of captures of western red-backed salamanders in thinned stands was consistent with my predictions.

Table 5. Mean number of captures/100 trap nights and 95% confidence intervals for forest-floor vertebrates in 8 pairs of unthinned and thinned (7-24 years previously) Douglas-fir stands in the Oregon Coast Range, 1995-1996. *P*-values were from repeated measures ANOVAs: Tr = treatment effect (df 1, 7), Yr = year effect (df 1, 14), Tr × Yr = interaction effect between treatments and years (df 1, 14), except that the degrees of freedom for Pacific shrews were 1 and 5 for Tr, 1 and 12 for Yr, and 1 and 12 for Tr × Yr.

Species	Unthinned		Thinned		<i>P</i>		
	\bar{x}^a	95% CI	\bar{x}	95% CI	Tr	Yr	Tr × Yr
Small Mammals							
Total small mammals	5.39	4.09-7.04	7.61	5.85-9.94	0.031	<0.001	0.541
Pacific shrew ^a	0.44	0.13-0.84	0.81	0.43-1.31	0.092	0.003	0.129
Trowbridge's shrew	3.70	2.75-4.87	5.12	3.89-6.65	0.066	<0.001	0.603
Vagrant shrew	0.05	-0.03-0.13	0.12	0.04-0.22	0.091	0.033	0.147
Shrew-mole	0.13	0.05-0.21	0.17	0.08-0.25	0.449	0.015	0.334
Western red-backed vole	0.66	0.40-0.98	0.84	0.55-1.19	0.282	0.311	0.510
Creeping vole	0.01	-0.01-0.03	0.08	0.06-0.10	0.048	0.455	0.465
Deer mouse	0.10	0.01-0.19	0.15	0.06-0.24	0.293	0.223	0.186
Pacific jumping mouse	0.02	-0.02-0.06	0.08	0.04-0.13	0.033	0.010	0.090
Amphibians							
Total amphibians	0.64	0.41-0.92	0.57	0.35-0.83	0.584	0.916	0.253
Ensatina	0.20	0.11-0.28	0.12	0.04-0.21	0.142	0.043	0.803
Western red-backed salamander	0.23	0.08-0.40	0.13	-0.01-0.28	0.095	0.096	0.464

^a Only 6 of the 8 pairs of stands were within the range of the Pacific shrew.

Reproduction of Small Mammals

Experimental Study

Deer mice, creeping voles, western red-backed voles, and Pacific shrews had adequate numbers of breeding females ($n > 30$) for statistical analyses of reproductive attributes; however, even for these species, I could not analyze changes in litter size with repeated measures ANOVA because of missing values or inconsistent sample sizes in 1 or more treatments or in time periods. Thinning did not affect any measured reproductive attribute of Pacific shrews or sex ratio and testis size of deer mice, creeping voles, or western red-backed voles ($P > 0.1$). Numbers of captures of pregnant and breeding female western red-backed voles decreased in all stands in 1995; in 1996 these numbers then increased to roughly the original levels in control stands but continued to decrease in thinned stands (Figure 4; number of pregnant females captured, $F_{1,18} = 3.88$, $P = 0.064$; number of breeding females captured, $F_{1,18} = 3.12$, $P = 0.0944$). The decrease in capture of pregnant and breeding western red-backed voles was consistent with my prediction. The amount and pattern of change in these 2 attributes, however, did not differ between moderately and heavily thinned stands ($P > 0.1$). Thinning did not significantly affect proportion of female western red-backed voles that were pregnant or in breeding condition ($P > 0.1$). Proportion of parous western red-backed vole females increased in control stands and slightly decreased in thinned stands ($F_{1,18} = 4.00$, $P = 0.061$); these responses to thinning did

not differ between moderately and heavily thinned stands ($P > 0.1$). Thinning did not affect number of parous western red-backed vole females captured ($P > 0.1$).

Both number ($F_{1,18} = 4.48, P = 0.049$) and proportion ($F_{1,18} = 3.37, P = 0.083$) of pregnant deer mice captured increased in heavily thinned stands relative to moderately thinned stands in 1996; these attributes either decreased or stayed constant in control and moderately thinned stands between 1995 and 1996. Thinning did not affect proportion and number of parous and breeding female deer mice captured ($P > 0.1$).

Proportion of female creeping voles in breeding condition increased in moderately thinned stands whereas it decreased in heavily thinned stands ($F_{1,18} = 3.26, P = 0.088$); the proportion stayed relatively constant in control stands over years. The increase in proportion of breeding females in moderately thinned stands was consistent with my prediction; however, the decrease in heavily thinned was in contrast to my prediction. Thinning did not affect number of captures for breeding females, proportion and number of captures for parous and pregnant females in creeping voles ($P > 0.1$).

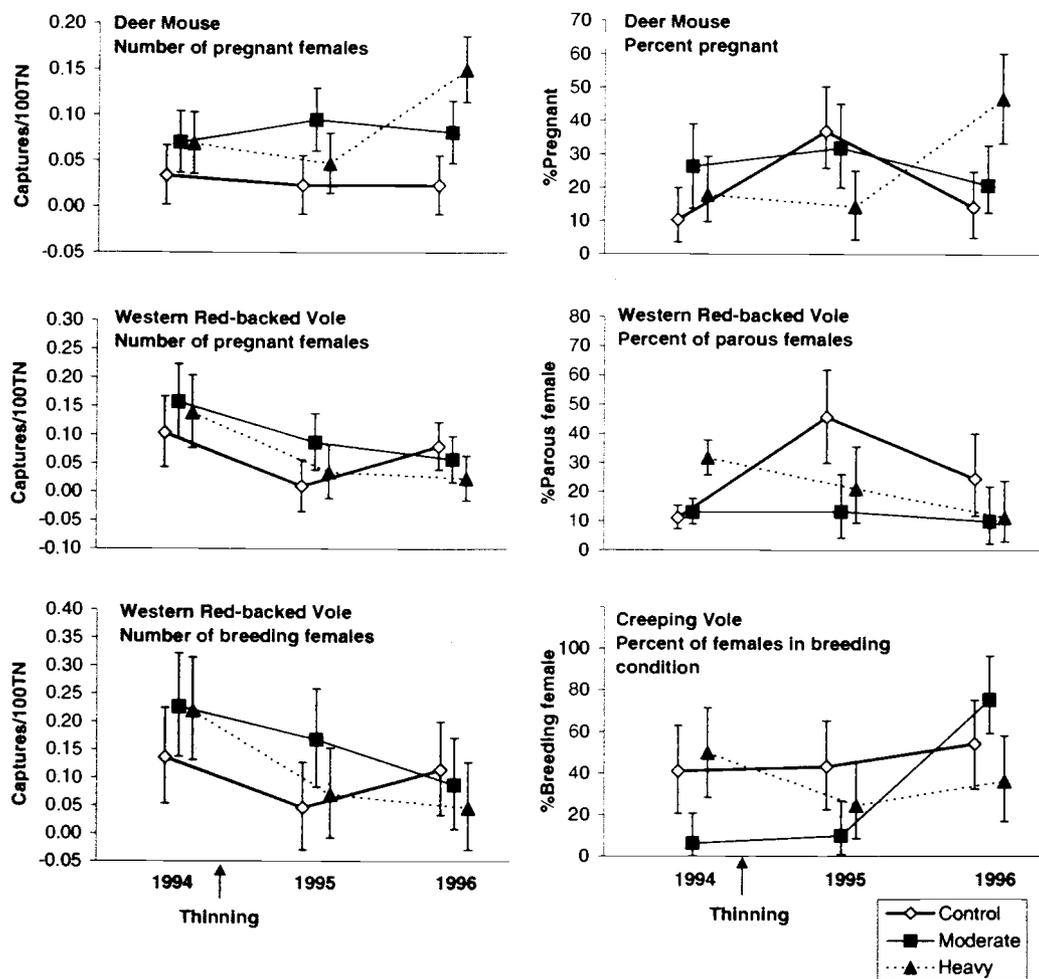


Figure 4. Changes in reproductive attributes ($\bar{x} \pm 1SE$) of western red-backed voles, creeping voles, and deer mice in control ($n = 4$), moderately thinned ($n = 4$), and heavily thinned ($n = 4$) stands of young Douglas-fir forests (35-45 years old) before (1994) and after thinning (1995-1996), northern Oregon Coast Range.

Observational Study

Proportion ($F_{1,7} = 5.38, P = 0.054$) and number ($F_{1,7} = 4.90, P = 0.063$) of pregnant western red-backed voles captured were higher in thinned stands (proportion, $\bar{x} = 6.7\%$, 95% CI = 2.2-17.8%; number of captures, $\bar{x} = 0.04$ captures/100TN, 95% CI = 0.02-0.06 captures/100TN) than in unthinned stands (proportion, $\bar{x} = 1.7\%$, 95% CI = 0.13-5.64%; number of captures, $\bar{x} = 0.02$ captures/100TN, 95% CI = -0.01-0.04 captures/100TN). The higher number and proportion of pregnant western red-backed voles in thinned stands was unexpected and in contrast to my predictions. Proportion and number of parous and of breeding western red-backed vole females captured did not differ between thinned and unthinned stands ($P > 0.1$). Mean size of testes of red-backed vole was greater in thinned stands ($\bar{x} = 117.62 \text{ mm}^3$, 95% CI = 109.28-126.60 mm^3) than in unthinned stands ($\bar{x} = 108.28 \text{ mm}^3$, 95% CI = 100.95-116.13 mm^3 ; $F_{1,7} = 3.71, P = 0.095$). I did not detect differences in sex ratios of western red-backed voles between thinned and unthinned stands ($P > 0.1$). I was unable to analyze reproduction of creeping voles and deer mice because of small sample sizes and too many missing values.

Proportion of pregnant Pacific shrews was higher in unthinned stands ($\bar{x} = 44.9\%$, 95% CI = 20.8-70.3%) than in thinned stands ($\bar{x} = 14.7\%$, 95% CI = 1.8-37.1%; $F_{1,5} = 5.63, P = 0.064$). However, the higher proportion of pregnant females observed in unthinned stands is likely a function of low number of Pacific shrews

captured in unthinned stands, because number of pregnant females captured did not differ between thinned stands ($\bar{x} = 0.05$ captures/100TN, 95% CI = 0.01-0.10 captures/100TN) and unthinned stands ($\bar{x} = 0.06$ captures/100TN, 95% CI = 0.01-0.11 captures/100TN; $F_{1,5} = 0.14$, $P = 0.725$).

On the other hand, both proportion ($F_{1,5} = 7.60$, $P = 0.040$) and number ($F_{1,5} = 6.81$, $P = 0.048$) of parous female Pacific shrews captured were higher in thinned stands (proportion, $\bar{x} = 6.8\%$, 95% CI = 1.4-24.4%; number of captures, $\bar{x} = 0.04$ captures/100TN, 95% CI = 0.02-0.07 captures/100TN) than in unthinned stands (proportion, $\bar{x} = 0.3\%$, 95% CI = -0.6-3.2%; number of captures, $\bar{x} = 0.01$ captures/100TN, 95% CI = -0.02-0.03 captures/100TN). I did not detect differences between thinned and unthinned stands in proportion or number of breeding females captured, or sex ratio of Pacific shrews ($P > 0.1$).

The Relationship between Abundance and Reproduction in Small Mammals

Logistic regression models based on captures/100TN in stands were generally not successful in predicting 3 reproductive odds (odds of being pregnant, parous, or in breeding condition). In the experimental study, none of the reproductive odds for deer mice, western red-backed voles, creeping voles, and Pacific shrews could be predicted from the number of each species captured in stands ($P > 0.1$). In the observational study, reproductive odds of Pacific shrews could not be predicted from their number of captures in stands ($P > 0.1$). Odds of female western red-backed voles being parous decreased with increasing number of voles captured in stands (number of

captures/100TN, $\beta = -0.0746$, $SE = 0.032$, $F_{1,22} = 4.95$, $P = 0.037$); however, odds of female voles being pregnant or in breeding condition were not related to number of voles captures in stands ($P > 0.1$).

DISCUSSION

Effects of Thinning on Abundance of Vertebrates

This study is the first comprehensive examination of the reproductive responses of small mammals and population responses of forest-floor vertebrates to thinning in the Oregon Coast Range. In the short term (≤ 2 years), thinning decreased abundance of amphibians, and the magnitude of effects on abundance was largely dependent on intensity of thinning; abundance of amphibians decreased more following heavy thinning than following moderate thinning. Thinning, however, did not result in short-term decreases in the abundance of any particular species of terrestrial amphibian analyzed. Because of the sampling bias associated with aquatic habitats and of small sample size, 8 species of amphibian (tailed frogs, rough-skinned newts, Pacific giant salamanders, northwestern salamanders, Dunn's salamanders, red-legged frogs, Pacific tree frogs, torrent salamanders) could not be analyzed independently; however, they were still retained in the analysis of total amphibian capture. Consequently, changes in abundances of these 8 species may have been cumulatively contributed to the decrease

in abundance of amphibians. In the long term (7-24 years), thinning did not appear to influence abundance of amphibians and appeared to increase abundance of small mammals.

Thinning Douglas-fir stands had positive effects on associates of early-seral or open habitats, including creeping voles, Pacific jumping mice, and deer mice. Previously, creeping voles and deer mice were found to be more abundant in thinned stands than in unthinned stands dominated by Douglas-fir in the Puget Trough of Washington, even though the unthinned stands were managed to retain large-diameter trees, downed wood, and snags (Wilson and Carey 2000). I observed an increase in the relative abundance of deer mice soon after thinning; however, relative abundance of deer mice did not differ between unthinned stands and stands thinned 7-24 years previously. The initial effects of thinning on abundance of deer mice, therefore, may not persist. Similarly, abundance of deer mice in shelterwood logged stands and in unlogged control stands did not differ 6-7 years following cutting in mixed-fir forests in northern California (Waters and Zabel 1998). In our experimental study, heavy thinning, at least in the short term, positively affected reproduction of deer mice by increasing proportion and number of pregnant females in the population. In other studies, influences of forest management practices on reproduction of deer mice are not always observed. For example, in coastal coniferous forests of British Columbia, population density and demographic characteristics of deer mice, including reproduction, survival, and recruitment, did not differ between mature forests and clearcuts (Petticrew and Sadleir 1974, Sadleir 1974, Sullivan 1979).

Creeping voles and Pacific jumping mice commonly occur in open habitats and early stages of stand development in Douglas-fir forests (Goertz 1964, Gashwiler 1970*a*, 1970*b*, 1972; Hooven 1973, Black and Hooven 1974, Hooven and Black 1976, Borreco et al. 1979, Carraway and Verts 1985, West 1991). The primary diet of creeping voles is grasses and forbs (Hooven 1973, Maser et al. 1981, Verts and Carraway 1998:327) and that of Pacific jumping mice consists of grass seeds (Ingles 1965:304, Jones et al. 1978, Maser et al. 1978, Verts and Carraway 1998:344). Because of their foraging preferences, populations of creeping voles and Pacific jumping mice are influenced by change in cover of herbaceous vegetation (Borreco et al. 1979). Thinning created stands with more open canopies and increased herbaceous cover (Tables 2 and 4). It is likely that the captures of creeping voles and Pacific jumping mice increased following thinning in response to improved condition of their foraging habitats.

In contrast to my prediction, thinning did not have substantial negative effects on western red-backed vole, an associate of closed canopy forests and of downed wood. Although western red-backed voles decreased in abundance after thinning, numbers of red-backed voles in stands thinned 7-24 years previously and unthinned stands were similar. Thus it appears that abundance of western red-backed voles recovers in the long term following thinning. There was no convincing evidence indicating that thinning significantly reduced reproductive potential of red-backed voles in the short term. Observed decreases in numbers of pregnant females and females in breeding condition in the experimental study is probably a function of the

decrease in overall numbers of individuals captured, as proportion of females that were pregnant or in breeding condition was unaffected by thinning. Thus short-term decreases in relative abundance of western red-backed voles in thinned stands are probably not related to reproductive factors, but rather to factors such as emigration or decreases in survival. In the thinned stands in the observational study, western red-backed voles had higher proportions of pregnant females, more pregnant females, and larger testis size of males than in unthinned stands. Based on reproductive parameters and similar numbers of individuals, I conclude that thinned stands probably provide better habitat for western red-backed voles than do unthinned stands in the long term.

Because tree densities of the thinned stands in the observational study ($\bar{x} = 346$ trees/ha) were much greater than those of heavily thinned stands in experimental study ($\bar{x} = 193$ trees/ha), I have no data on the long-term effects of heavy thinning on reproduction and abundance of western red-backed voles. In fir forests in northeastern California, stands logged to very low densities of trees 6 to 7 years earlier using the shelterwood system had lower relative abundances of red-backed voles than did in unlogged stands (Waters and Zabel 1998), and red-backed voles are not usually abundant after clearcutting (Tevis 1956, Gashwiler 1970a; Hooven and Black 1976, Mills 1995). Reduction of stand densities to levels below some threshold likely has long-term negative effects on abundance of western red-backed voles for some years following the operation. Rosenberg et al. (1994) proposed that old-growth Douglas-fir stands provide optimal habitat for western red-backed voles; thinning might accelerate development of these habitat characteristics (Hayes et al. 1997). As old-growth stands

developed at very low tree densities (Tappeiner et al. 1997), I hypothesize that thinning stands to the densities of the heavily thinned stands in my experimental study will have neutral or positive influences on abundance, survival, and reproduction of western red-backed voles in the long term, but this hypothesis remains to be tested.

Thinning had inconsistent effects on abundances of amphibian associates of downed wood; effects of thinning were positive on ensatinas in the short term but were negative on western red-backed salamanders in the long term. Ensatinas occur in Douglas-fir forests of all age classes and opportunistically use wood on the forest floor, such as pieces of bark and downed logs of all sizes, for hiding cover (Aubry et al. 1988, Corn and Bury 1991, Butts and McComb 2000). Therefore, observed increases in relative abundance of ensatinas following thinning may be related to the large amount of coarse and fine wood, including slash and bark piles, left after thinning. Throughout western Oregon and Washington, amount of large downed wood is generally considered as a primary factor influencing abundance of ensatinas (Aubry et al. 1988, Corn and Bury 1991, Butts and McComb 2000). The lack of differences in numbers of captures of ensatinas in thinned and unthinned stands in the observational study may reflect the decrease in abundance of fine wood left after thinning over time through decomposition.

Western red-backed salamanders were the only forest-floor vertebrates that appear to be negatively affected by thinning in the long term. Paradoxically, I did not detect significant changes in numbers of western red-backed salamanders captured in the short term following thinning. Differences in results of the experimental and

observational studies may be related to differences in levels of dead wood in the stands. In southern Washington Cascades, red-backed salamanders were most closely associated with moderately decayed, 10 – 30 cm diameter logs (Aubry et. al 1988). In our observational study, previously thinned stands had lower abundances of small (10 - 29 cm) and medium (30 - 49 cm) logs than did unthinned stands, probably as a result of intensive management practices in the past. The lack of small- and medium-sized logs in previously thinned stands may be responsible for the lower relative abundance of western red-backed salamanders in these stands. Alternatively, western red-backed salamanders may exhibit a delay in population response, and our experimental study may not have been of adequate duration to document declines in the population. In southwestern Washington, thinning did not reduce relative abundance of western red-backed salamander in the short term (< 2years since thinning); however the increase in relative abundance following thinning was lower in thinned than in control stands (Grialou et al. 2000). In contrast, I did not detect a difference in increase in relative abundance of western red-backed salamanders between thinned and control stands in the Oregon Coast Range.

Although I did not make specific predictions, abundances of one other rodent (white-footed vole) and 3 insectivores (Trowbridge's shrew, vagrant shrew, and Pacific shrew) were also influenced by thinning. Relatively little is known about the ecology of white-footed voles; however, thinning seems to have positive effects on abundance of this species at least in the short term. White-footed voles occasionally are found in clearcuts (Maser and Hooven 1969, Verts and Carraway 1998:305) but

appear to be more commonly associated with riparian areas dominated by red alder and salmonberry (Voth et al. 1983, Gomez and Anthony 1998). In our experimental study, conifers were predominantly thinned, and small patches of red alders, especially near small streams, were generally retained. Thinning may enhance habitat characteristics, such as growth of understory vegetation in these red alder patches and adjacent areas, that favor white-footed voles. This may account for observed increases in number of white-footed voles captured following thinning. Because I lack data on white-footed voles from the observational study, long-term effects of thinning on this species are unknown.

Although thinning did not affect relative abundance of any species of shrews in the short term, Trowbridge's shrews, vagrant shrews, and Pacific shrews were more abundant in stands thinned 7 to 24 years previously than in unthinned stands. The higher abundances of shrews in thinned stands are probably a result of the positive responses of shrews to the well-developed understory of herbs, low-shrubs, and tall-shrubs in the long term. The development of understory vegetation immediately following thinning was probably not strong enough for the populations of shrews to respond in the short term. Other factors, such as availability of invertebrates, may also be responsible for the high abundances of shrews in previously thinned stands. Because small- and medium-sized downed logs were less abundant in thinned stands than in unthinned stands, it is unlikely that the abundance of downed logs were the factor influencing the abundances of shrews in thinned stands. The higher abundance of Trowbridge's shrews in thinned stands was unexpected based on the previously

documented association of this species to small-sized downed logs in western Oregon (Butts and McComb 2000). Trowbridge's shrews probably are opportunistic in selecting habitat components based on their availability and may not be strictly associated with downed logs. In the Olympic Peninsula of Washington, the abundance of Trowbridge's shrews in young managed stands was positively and that in old-growth stands was negatively associated with large downed logs; the abundance in the old-growth stands was, instead, positively associated with shrub cover (Carey and Johnson 1995). The higher proportion and number of parous female Pacific shrews captured in stands thinned 7-24 years previously relative to unthinned stands suggests that thinning may improve habitat quality for reproduction of Pacific shrews. Previously, effects of forest management practices, including thinning, on reproduction of Pacific shrew have been largely unknown.

Relationship between Abundance and Reproduction

With one exception, number of captures was not a good predictor of reproductive indicators of small mammals. Strong relationships between abundance or population density and reproductive parameters rarely have been found in field studies of small mammals (Sadleir 1974, Keller 1985, McShea and Madison 1989). Previous studies that have documented associations between abundance and reproduction often report negative relationships, with increased reproduction occurring when abundance is low (e.g., Canham 1969, McShea and Madison 1989, Wauters and Lens 1995, Tkadlec and Zejda 1998). Similarly, I found that odds of female western red-backed

voles being parous was negatively associated with the abundance of individuals in stands. This inverse density-dependent reproduction has been hypothesized to occur when patches of high quality habitat for reproduction are already occupied by dominant females and are not available for subdominant females at high population densities (Wauters and Lens 1995). Because of the lack of positive association between abundance of individuals and reproductive performance of populations, assessment of reproduction is necessary to fully evaluate quality of habitat of small mammals.

Consistency of Experimental and Observational Approaches

Although responses of creeping voles and Pacific jumping mice were consistent between the experimental and observational thinning studies, responses of other species were not. Furthermore, for species for which I had adequate data, responses in reproduction often were not consistent between experimental and retrospective studies. These inconsistencies could result from at least 2 possible factors. First, either the experimental or the observational study failed to accurately portray responses of vertebrate species to thinning due to differences between the 2 approaches. If this were the case, I would have less confidence in the results from our observational study, as extraneous variation unrelated to the variables of interest could confound results (Ramsey and Schafer 1997:5-7). Alternatively, response of species may vary with time since thinning. I contend this is the most likely explanation, as observed differences in response are generally consistent with what is known of the

natural histories of the species studied in relation to changes in habitat through time.

This suggests that inferences of short-term studies should be restricted to the temporal context in which the study was conducted. Although experimental studies conducted over long periods of time (>10 years) are preferable, it is often not feasible to conduct such studies in time frames appropriate to address management issues. As a result, the best alternative initially is often a combination of observational studies to examine long-term responses coupled with experimental studies to evaluate short-term responses. The experimental work established to evaluate short-term responses later could be used over longer time frames as a framework to confirm results and test hypotheses generated in observational studies.

Management Implications

Thinning may be used to accelerate development of some old-growth characteristics in young dense stands of Douglas-fir (Barbour et al. 1997, Hayes et al. 1997, Tappeiner et al. 1997). Stands <100 years old with densities of 100-120 trees/ha seem to have the potential to achieve rates of tree diameter growth that are similar to those achieved by old-growth stands at comparable ages (Tappeiner et al. 1997).

Dense second-growth stands without density management may spend long periods of time (>100 years) in the competitive exclusion stage and may never develop diverse habitats for wildlife (Carey and Curtis 1996). Thinning heavily ($0.15 < RD < 0.25$) or repeatedly, thus, may be an appropriate option if the management objective is to

develop stands with old-growth characteristics. However, there are at least 2 concerns associated with the extensive use of heavy thinning. First, thinning stands to low residual tree densities would make stands highly vulnerable to wind, and as a consequence, the stands might lose too many trees to maintain adequate habitat quality for associates of closed-canopy forests, such as western red-backed voles, over long periods of time. Second, long-term effects (>10 years) of heavy thinning on populations and habitat quality of forest-floor vertebrates are unknown, and it is unclear how quickly initial impacts of heavy thinning on some vertebrates, such as amphibians and red-backed voles, are mitigated. Although the potential to develop old growth characteristics are reduced, our data suggest that moderate thinning ($0.35 < RD < 0.45$) maintains or improves habitat quality for most species of forest-floor vertebrate in the long term. Additionally, the negative influence of thinning on abundance of western red-backed salamanders in the long term may be minimized by reducing salvage of dead wood from stands.

To maintain biodiversity and sustainable ecosystems, the decision to thin a stand should take both stand and landscape scales into account. Factors, such as current spatial distribution of thinned and unthinned stands of different densities, ages, and species compositions should be considered. Thinning extensive areas using single prescription may significantly reduce habitat diversity across the landscape. Consequently, combinations of heavy and moderate thinning should be used to promote diversity across the landscape. Moderate thinning may be used to accelerate overall tree growth in second-growth stands. In some stands or portions of a stand,

heavy thinning can be used to develop large-diameter trees comparable to legacy trees.

Alternatively, some stands previously thinned to a moderate tree density can be thinned for the second time to a low tree density. During this second thinning, managers will have the opportunity to provide large-diameter downed wood and snags to enhance structural diversity of these stands. Carey and Curtis (1996) similarly suggested the use of pre-commercial thinning and variable density thinning to promote habitat diversity across the landscape by developing heterogeneous understory and providing downed wood to the forest floor (Carey and Curtis 1996).

Scope and Limitations

My study was restricted to managed Douglas-fir forests of the Oregon Coast Range. Thus my results may not be applicable to other regions or to different forest types, although it is likely that our results are applicable to other regions with similar species and forest structure. In addition, I did not measure survival or dispersal, and our results relied on a measure of relative abundance rather than estimates of population density. The lack of complete demographic information and population density estimates limits our understanding of the influence of thinning on population dynamics and viability. Furthermore, I did not directly address influences of the landscape context on ecological consequences of thinning in our study design. It is possible that the context of the matrix surrounding a stand influences species response to thinning. As our stands were relatively large in relation to the home ranges of the species studied, I suspect that the influence of larger spatial scales would be relatively

small. However, although landscape structure in the Oregon Coast Range seems to play a minor role in abundance of most forest-floor vertebrates (Martin 1999), the interaction between landscape structure and influence of management activities remains unclear, and landscape context could influence results for some species, especially those with limited vagility.

Finally, inferences from the experimental study were limited to 2 years following thinning; therefore, I could not determine causal relationships for changes in populations over long time periods. Results from our observational study do, however, provide strong hypotheses concerning influences of thinning on forest-floor vertebrates, and I recommend their use to provide management direction until definite causal relationships can be established from long-term experimental studies. I strongly suggest the use of long-term experimental studies (>10 years) to monitor responses of vertebrates to thinning over long periods of time and also to conclusively determine whether thinning is the causal factor of observed long-term ecological responses.

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CHAPTER 3: EFFECTS OF ECOLOGICAL GRADIENTS ON HABITAT ASSOCIATIONS OF FOREST-FLOOR VERTEBRATES IN YOUNG DOUGLAS-FIR-DOMINANT STANDS OF THE NORTHERN OREGON COAST RANGE

ABSTRACT

Microclimate, stand structure, plant community composition, and abundance of downed wood are ecological factors that may influence habitat association of forest-floor vertebrates. In 1994, I investigated the relative influences of these ecological factors on habitat associations of forest-floor vertebrates at microsite and stand scales using relative abundance (captures/100TN) of these vertebrates and ecological variables sampled from 12 Oregon Coastal Douglas-fir stands in the stem exclusion stage. I used nonmetric multidimensional scaling (NMS) with 6 ecological matrices and indirectly measured gradients of microclimate, stand structure, plant community composition, and abundance of downed-wood among microsites within stands and also among 12 stands across the landscape. Among the ecological gradients that I examined, the highest number of vertebrate species was associated with the gradient of plant community composition that changes from red alder-mixed overstory with herb-dominant understory to exclusively conifer overstory with shrub-dominant understory. This pattern was consistent at both the microsite and stand scales. At the microsite scale, 7 species were associated with red alder/herb communities whereas only 2 species were associated with conifer/shrub communities. Patches of red alder with herbaceous understories, therefore, have a potentially important role in maintaining

biodiversity of forest-floor vertebrate communities in young stands dominated by Douglas-fir in the Oregon Coast Range.

Additionally, I tested theoretical habitat-association patterns of 2 habitat generalists and 2 habitat specialists at multiple spatial scales. Trowbridge's shrews (a generalist) and western red-backed voles (a specialist) did not follow the expected theoretical patterns at multiple spatial scales, whereas vagrant shrews (a specialist) and deer mice (a generalist) did. Habitat associations of 4 shrew species remained constant between microsite and stand scales, whereas those of 3 rodent species did not remain consistent between the 2 spatial scales. I hypothesize that this rodent-shrew dichotomy in habitat association occurring at the 2 spatial scales is a result of differences in their ability to explore habitats at multiple spatial scales.

INTRODUCTION

In the past decade, the conservation of biological diversity has emerged as an important consideration in the management of Pacific Northwest forests (Carey and Curtis 1996). To satisfy the information needs to incorporate the biodiversity perspective into management practices, researchers have extensively studied populations and communities of forest-floor vertebrates in the western hemlock zone of Washington and Oregon (e.g., Aubry et al. 1991, Aubry and Hall 1991, Corn and Bury 1991*a*, Corn and Bury 1991*b*, Bury et al. 1991, Gilbert and Allwine 1991*a* and 1991*b*, West 1991, Rosenberg et al. 1994, Carey and Johnson 1995). The emphasis of these studies was to determine the association of vertebrate species to unmanaged old-

growth Douglas-fir forests and to identify biological requirements and ecological relationships of the old-growth associates (Carey and Spies 1991, Ruggiero 1991). These studies failed to identify strong associations of forest-floor vertebrate species to particular age classes of forest stands, suggesting that factors other than age of forest stands significantly contribute to the variability in population and community structure of forest-floor vertebrates among forest stands (Aubry et al. 1991:292, Carey and Johnson 1995).

Previously researchers identified 3 ecological factors, abundance of downed wood, stand structure, and microclimate, as primary determinants of vertebrate populations and communities in the forested habitats of the western hemlock zone (Morrison and Anthony 1988, Aubry and Hall 1991, Bury et al. 1991, Corn and Bury 1991, Gilbert and Allwine 1991, West 1991, Aubry et al. 1991, Carey and Johnson 1995). Among these factors, Carey and Johnson (1995) indicated that microclimate (north-south moisture-temperature gradient among stands within the western hemlock zone) is the prevailing influence on composition and structure of small mammal communities. Along with microclimate, species composition of plant communities as an integral characteristic of forested ecosystems (Spies 1991) and difference in species compositions of plant communities may contribute to the variability in vertebrate populations and communities among stands (Carey and Johnson 1995). However, there are no published comprehensive investigations of the influences of plant species composition on vertebrate populations and communities. Because composition of plant communities is closely related to microclimate (Zobel et al. 1976, Hemstrom and

Logan 1986, Riegel et al. 1992) and defines structural complexity of habitat, vegetative composition may be a better predictor of vertebrate populations and communities than either microclimate or stand structure considered separately, especially when vertebrate communities are influenced by multiplicity of ecological factors (Carey and Johnson 1995).

Although investigators have searched for patterns of vertebrate habitat associations over the years, few previous studies have addressed effects of spatial scales on habitat association of vertebrates. Some researchers, however, have recognized that patterns of habitat association for some species were inconsistent among studies that investigated microhabitat association at small spatial scales (Morris 1987, Jorgensen and Demarais 1999). Inconsistencies in microhabitat associations may be a result of differences in the arbitrarily defined spatial scales and methodologies used among studies, the overriding influence of macrohabitat on microhabitat associations, or other factors (Morris 1987, Jorgensen and Demarais 1999). Alternatively, the scale at which a species responds may vary depending on its resource exploitation strategy; therefore, investigations conducted at a single arbitrarily defined spatial scale may not always accurately reflect true habitat associations of target species (Morris 1996). For example, habitat specialists preferentially use some types of habitat patches over others (coarse-grained exploitation), whereas habitat generalists that are not associated with particular habitat patches exploit habitat patches in proportion to the availability of those patches (fine-grained exploitation, Morris 1987, 1996). For habitat generalists to coexist with

competing specialists in shared environment, a possible strategy is to explore habitats unused or underused by specialist at a larger spatial scale (Morris 1996). If this strategy were true, habitat associations of generalists would be evident at larger spatial scales than would be evident for those of specialists; furthermore, coarse-grained exploitation of habitats by specialists at small spatial scales would likely to remain coarse grained at larger spatial scales (Morris 1996). It is also possible that habitat associations of individuals and of populations are occurring at different spatial scales. For example, individuals may be coarse-grained in habitat use being associated with their preferred microhabitat patches at smaller spatial scales, while populations as a whole may be more closely associated with resource availability or habitat characteristics inherent to larger spatial scales (Morris 1987).

In this study, I examined importance of ecological gradients in habitat associations of forest-floor vertebrates at the stand and microsite scales. I examined the gradients in microclimate, stand structure, plant species composition, and abundance of downed wood in various size and decay classes. The objectives of this study were to determine: 1) whether presence of each species was associated with ecological gradients measured at the microsite scale, 2) whether relative abundance of each species was associated with ecological gradients measured at the forest-stand scale, and 3) patterns of habitat associations of habitat specialists and generalists at 2 spatial scales.

For the first two objectives, I hypothesized that habitat associations of vertebrate species in young managed forests are influenced by multiple ecological

factors and that gradients of plant community composition would describe habitat associations better than other ecological gradients at both microsite and stand scales. For objective 3, I compared habitat associations of 2 specialists and 2 generalists at the microsite and stand scales. I used the vagrant shrew (*Sorex vagrans*), an associate of herbaceous habitats (Hooven et al. 1975, Gashwiler 1970, Borrecco et al. 1979, Morrison and Anthony 1989), and the western red-backed vole, an associate of interior-forest habitats (Mills 1995), as examples of specialists, and used Trowbridge's shrews (*S. trowbridgii*) and deer mice (*Peromyscus maniculatus*) as examples of generalists because they are both well known for their lack of strong association with specific habitat types (Aubry et al. 1991, Corn and Bury 1991a, West 1991, Verts and Carraway 1998: 61, 270). Based on the generalization for habitat associations of specialists and generalists at multiple spatial scales (Morris 1996), I made the following 2 predictions and compared these predicted patterns with the observed habitat associations of the 2 specialists and 2 generalists: 1) habitat specialists, due to their coarse-grained habitat use, would be closely associated with ecological gradients identified at the microsite scale and would maintain similar habitat associations at the stand scale and 2) habitat generalists, which exploit habitat patches unused or underused by specialists at relatively large spatial scales, would be more closely associated with ecological gradients identified at the stand scale than those identified at the microsite scale.

STUDY AREA

I identified 12 young Douglas-fir stands (35-45 years old), 3 stands in each of 4 areas, located in the northern Oregon Coast Range for the study. The stands were artificially regenerated with Douglas-fir after a series of fires burned the area between 1933 and 1951 (Wells 1999). Three of the 4 areas were located in the Tillamook State Forest, Tillamook County, Oregon and one was on adjacent private land, owned by Stimson Lumber Company (Figure 1). Stands ranged from 26 to 40 ha ($\bar{x} = 34$ ha) in size and ranged from 485 to 849 m ($\bar{x} = 612$ m) in elevation. The climate of the Oregon Coast Range is maritime and is characterized by wet and mild winters and cool, dry summers (Franklin and Dyrness 1988:38-43). Mean annual temperature and precipitation in Tillamook between 1994 and 1996 ranged from 10 to 11°C ($\bar{x} = 11$ °C) and from 263 to 311 cm ($\bar{x} = 283$ cm, Oregon Climate Service).

The study was conducted in western hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness 1988:70-93). Douglas-fir (*Pseudotsuga menziesii*) was the dominant tree species in the study sites and red alder (*Alnus rubra*) was common in moist or disturbed areas. Other tree species found in the area included western hemlock, western redcedar (*Thuja plicata*), noble fir (*Abies procera*), and Sitka spruce (*Picea sitchensis*). Common understory shrubs were salal (*Gaultheria shalloon*), red huckleberry (*Vaccinium parviflorum*), trailing blackberry (*Rubus ursinus*), vine maple (*Acer circinatum*), and dwarf Oregongrape (*Berberis nervosa*). Common species of

herbs included Oregon oxalis (*Oxalis oregana*), sword fern (*Polystichum munitum*), and bracken fern (*Pteridium aquilinum*).

METHODS

Sampling of Vertebrate Species

I trapped forest-floor vertebrates in all the 12 stands for 6 weeks beginning in May, 1994. I established a grid of 25 sampling stations with 80 m between stations in each stand. I placed 2 pitfall traps (double-deep No. 10 tin can) within 10 m of each station center and added water to the bottom 5 cm of each trap upon opening. I checked the traps weekly. Live amphibians captured were identified to species, measured for body mass, total length, and snout-vent length, and were released outside the trapping grid; all other vertebrates captured were collected. I identified all captured individuals to species and measured their body mass and total length (from tip of nose to base of tail) of small mammals and snout-vent length and total length of amphibians. Taxonomy used in this study generally follows Collins (1990) for amphibians and reptiles and Jones et al. (1992) and Wilson and Reeder (1993) for mammals. I followed the taxonomic revisions by Good (1989) for Pacific giant salamanders (*Dicamptodon tenebrosus*) and by Good and Wake (1992) for Columbia torrent salamanders (*Rhyacotriton kezeri*) and southern torrent salamanders (*Rhyacotriton variegatus*). I followed the correction of the specific epithet for Baird's shrew (*Sorex bairdi*) presented by Alexander (1996).

Habitat Sampling

I sampled habitat characteristics at each grid point in the 12 stands from late June through July in 1994. Sampling plots consisted of two 5 m-radius circular plots, two 1 × 1 m square plots nested within each 5 m-radius circular plot, a 10-m radius circular plot, and a 15-m radius circular plot (Figure 5).

Within each 1 m x 1m square plot I visually estimated percent cover of each species of herb and shrub less than 0.5 m in height, percent exposure of mineral soil, and percent cover of leaf litter, moss, and rock. Estimated values of each variable from the 4 1 × 1 m square plots were averaged for analysis. Within each 5 m-radius plot, I visually estimated percent cover of each species of shrub (woody plants with stems < 10 cm diameter at breast height [DBH]), tall shrubs (woody plants ≥ 1.4 m tall), low shrubs (woody plants < 1.4 m tall), and herbs. I also estimated percent cover of sword fern, oxalis, and bracken fern, individually. Values for variables measured in the 2 5-m radius circular plots were averaged for analysis. Percent cover of the overstory (all vegetation >10 m in height) was estimated in the 15-m radius plot.

I counted number of trees and pieces of downed wood in the 10-m radius plot. The number of trees was recorded by species in 10 cm-diameter classes. Frequency and cumulative length of downed logs were recorded by diameter (small, 10-29 cm; medium, 30-49 cm; large, ≥ 50cm) based on the largest diameter occurring within the 10-m radius plot, and by decay class (decay class 1, 2-3, or 4-5; Maser et al. 1979).

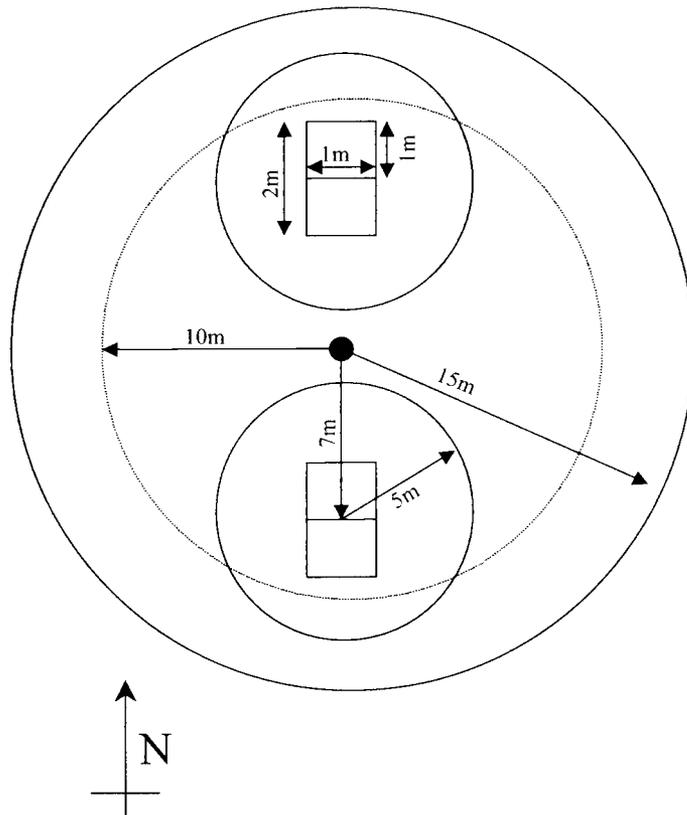


Figure 5. Arrangement of habitat sampling plots.

Data Analysis

Analyses of ecological gradients and associations of vertebrates were conducted at the microsite and stand scales. Analysis at the microsite scale refers to analysis of ecological gradients and vertebrate associations among grid points within stands; whereas, analysis at the stand scale refers to analysis among 12 stands, using the mean of data collected at grid points for each stand.

Using nonmetric multidimensional scaling (NMS, Kruskal and Wish 1978, Clarke 1993, McCune and Mefford 1995), I created ecological gradients for microclimate, stand structure (the physical and temporal distribution of trees, shrubs, and herbs in a stand, Oliver and Larson 1996: 1), plant species composition, and downed wood abundance at the microsite and the stand scales. To create ecological gradients, in each NMS I analyzed a matrix consisted of variables related to one of these 4 factors (the target ecological factor). NMS uses ranked distance among sampling units (either sampling points or stands) and iteratively searches for a placement of sampling units in an ordination space that has smaller dimensions than the space of original ecological variables (McCune and Mefford 1995). The best axes for ordination space are positioned in the directions that minimize stress in placement of the sampling points; the stress is low when ecological relationships among sampling units remain similar between the original multidimensional space and the reduced ordination space (McCune and Mefford 1995). Interpretation of axes was based on evaluations of Pearson's correlation coefficient between NMSscores of each axis and original variables.

In NMS, I reduced the dimensionality in ordination solutions stepping down from 6 dimensions to 1 dimension; I repeated this process for 20 times with a nonrandomized matrix of ecological variables. For each of the 6 dimensions, I also ran a Monte Carlo test in which the original data matrix of ecological variables was randomized across sampling units (either sampling points or stands) 20 times and each randomized matrix was analyzed in a NMS run. I then examined whether the stresses from the 20 NMS runs of nonrandomized data were significantly lower ($P < 0.05$) than those from the 20 NMS runs of randomized data for each dimension. The best dimension was determined by using the criteria of $P < 0.05$ and by visually inspecting the scree plot for a significant reduction in stress between dimensions. I chose the NMS solution with the least stress of the 20 NMS runs for the selected dimensionality.

To create microclimatic gradients, I used a matrix consisting of covers of 24 plant species that are sensitive to microclimatic conditions (Table 6, Hemstrom and Logan 1986). Among these 24 species, 13 were indicators of wet or moist sites, 3 of dry sites, 4 of cool or cold sites, and 8 of warm sites (Table 6). The gradients for stand structure were created using a matrix consisting of measures of overstory cover, tall shrub cover, low shrub cover, herb cover, and moss cover. I created gradients of plant community composition for the following 3 matrices: one matrix consisted of densities of tree species, one of percent covers of understory shrubs and herbs, and one of percent covers of both overstory tree and understory shrub and herb species. The gradients of downed-wood abundance were created using a matrix of cumulative log length in 3 decay and 3 diameter-size classes.

Table 6. Twenty-four indicator plant species that are indicators of microclimate in the Oregon Coast Range adapted from Hemstorm and Logan (1986).

Species	Scientific name	Preferred Microclimate
Devil's club	<i>Oplopanax horridum</i>	Wet
Salmonberry	<i>Rubus spectabilis</i>	Wet
Maidenhair fern	<i>Adiantum pedatum</i>	Wet
Ladyfern	<i>Athyrium filix-femina</i>	Moist, Wet
Wild ginger	<i>Asarum caudatum</i>	Moist
Deerfern	<i>Blechnum spicant</i>	Moist
Pacific breeding heart	<i>Dicentra formosa</i>	Moist
Oak fern	<i>Gymnocarpium dryopteris</i>	Moist
Horsetail	<i>Equisetum</i> spp.	Moist
False solomonseal	<i>Smilacina stellata</i>	Moist
Foamflower	<i>Tiarella unifoliata</i>	Moist
Inside-out-flower	<i>Vancouveria hexandra</i>	Moist, Warm
Pioneer violet	<i>Viola glabella</i>	Moist
Dwarf Oregongrape	<i>Berberis nervosa</i>	Dry, Warm
Baldhip rose	<i>Rosa gymnocarpa</i>	Dry, Warm
Snowberry	<i>Symphoricarpos mollis</i>	Dry, Warm
Red huckleberry	<i>Vaccinium parvifolium</i>	Warm
Trailing blackberry	<i>Rubus ursinus</i>	Warm
California hazel	<i>Corylus cornuta</i>	Warm
Pacific dogwood	<i>Cornus nuttallii</i>	Warm
Fool's huckleberry	<i>Menziesia ferruginea</i>	Cool
Dogwood bunchberry	<i>Cornus canadensis</i>	Cool
Mountain huckleberry	<i>Vaccinium membranaceum</i>	Cool-Cold
Queencup beadlily	<i>Clintonia uniflora</i>	Cool

For matrices having high numbers of variables, I reduced the number of variables in a matrix by removing variables with small numbers of observations (<5-10 % of the total number of sampling units), those with very low coefficients of variation, and those with extreme outliers. For the analysis at the stand scale no more than 8 variables were retained in any matrix.

For the analysis of habitat associations at the microsite scale, combinations of ecological variables measured at 300 sampling points in 12 stands were used in NMS to ordinate the entire 300 points according to similarity in ecological conditions along the gradients of microclimate, downed-wood abundance, stand structure, and plant community composition. This process produced an NMS score (a measure of ecological condition along an ecological gradient) for each sampling point. For each stand, I averaged NMS scores of a particular gradient for the sampling points where I captured a given vertebrate species and for the points where I did not capture that species. I used ANOVA in randomized complete blocks of 12 stands to determine whether average NMS scores of an ecological gradient for each species between capture and non-capture points are the same. Both untransformed and rank-transformed NMS scores were analyzed using ANOVA. I examined the residuals for normality, constant variance, and independence using normal probability plots, histograms, and residual plots (Sabin and Stafford 1990, PROC UNIVARIATE; SAS Institute 1990, Sokal and Rohlf 1997). When *P*-values between untransformed and ranked data differed and the residuals from the untransformed data significantly deviated from the assumptions of ANOVA, I presented *P*-values from the rank-

transformed data; otherwise, I presented *P*-values generated using the untransformed data.

For the analysis of habitat associations at the stand scale, values of each ecological variable measured at 300 points (25 points/ stand) were averaged for each of the 12 stands. I analyzed these averaged ecological values in the NMS to ordinate 12 stands according to their similarity in ecological conditions along particular ecological gradients. I calculated Pearson's correlations between numbers of captures for each species and NMS scores of each ecological gradient for the 12 stands to determine whether there is a significant association ($P < 0.1$) between relative abundance of vertebrate species and ecological gradients at the stand scale.

RESULTS

Abundance of Forest-floor Vertebrates

I captured a total of 3,202 forest-floor vertebrates in the 12 stands (12.71 captures/100TN) over 25,200 trap nights, which included captures of 17 species of mammals (3093 captures) and 9 species of amphibians (109 captures). Trowbridge's shrews (*Sorex trowbridgii*) were caught most frequently (7.73 captures/100TN) and comprised of 58.4 % of all captures of forest-floor vertebrates. Other species of mammals with > 20 individuals included Pacific shrews (*Sorex pacificus*; 1.68 captures/100TN, 13.21% of the total vertebrate capture), Baird's shrews (*Sorex bairdi*; 0.72 captures/100TN, 5.65%), vagrant shrews (*Sorex vagrans*; 0.44 captures/100TN,

3.59%), western red-backed voles (*Clethrionomys californicus*; 0.54 captures/100TN, 4.28%), deer mice (*Peromyscus maniculatus*; 0.51 captures/100TN, 4.02%), shrew-moles (*Neurotrichus gibbsii*; 0.34 captures/100TN, 2.66%), marsh shrews (*Sorex bendirii*; 0.20 captures/100TN, 1.56%), creeping voles (*Microtus oregoni*; 0.18 captures/100TN, 1.40%), and Pacific jumping mice (*Zapus trinotatus*; 0.11 captures/100TN, 1%). Species of mammal with <20 captures included coast moles (*Scapanus orarius*), brush rabbits (*Sylvilagus bachmani*), Townsend's voles (*Microtus townsendii*), white-footed voles (*Arborimus albipes*), Townsend's chipmunk (*Tamias townsendii*), western pocket gophers (*Thomomys mazama*), and ermines (*Mustela erminea*).

No species was dominant in the amphibian capture. Species with >20 individuals included western red-backed salamanders (*Plethodon vehiculum*; 0.12 captures/100TN, 27% of total amphibian capture), Tailed frogs (*Ascaphus truei*; 0.11 captures/100TN, 26.1%), Rough-skinned newts (0.09 captures/100TN, 20.2%), and Ensatinas (*Ensatina eschscholtzi*; 0.08 captures/100TN, 19.27%). Species of amphibian with < 20 captures included Northwestern salamanders (*Ambystoma gracile*), Pacific giant salamanders (*Dicamptodon tenebrosus*), Dunn's salamanders (*Plethodon dunni*), torrent salamanders (*Rhyacotriton*. spp.), and red-legged frogs (*Rana aurora*).

Ordination Axes

In the analysis of ecological gradients at the microsite scale, ecological matrices of microclimate and tree species composition each produced 2-axis solutions and the 4 remaining matrices produced 3-axis solutions (Table 7). In the analysis of ecological gradients at the stand scale, 5 ecological matrices produced 2-axis solutions and 1, the stand structure matrix, produced a 3-axis solution. For each solution, the average stress for 20 NMS runs with non-randomized original data was lower than the average stress for 20 NMS runs with randomized data in the Monte-Carlo simulations ($P < 0.05$). Final stress ranged from 11.7 to 18.2 at the microsite scale and ranged from 2.2 to 3.5 at the stand scale. Furthermore, these reduced ordination axes of all the NMS solutions retained $> 80\%$ of variability in ecological relationship among stands and also among microsites from the original multi-dimensional space. Details of NMS-axis interpretation are described in APPENDIX 2.

Table 7. Ecological gradients identified at microsite and stand scales using Nonmetric Multidimensional Scaling. r^2 indicates coefficients of determination for correlations between ordination distances and distances in the original n-dimensional space. Refer to Table 8 (microsite scale) and Table 9 (stand scale) for detailed descriptions of gradients in tree species composition, understory species composition, and overall plant community composition. The detailed process of NMS-axis interpretation is described in APPENDIX 2.

Microsite Scale	r^2	Stand Scale	r^2
MICROCLIMATE		MICROCLIMATE	
Temperature (Cool—Warm)	0.19	Temperature (Cool—Warm)	0.60
Moisture (Moist—Dry)	0.39	Moisture (Moist—Dry)	0.26
TREE SPECIES COMPOSITION		TREE SPECIES COMPOSITION	
Douglas-fir—Red alder	0.32	Douglas-fir—Mixed conifer	0.10
Douglas-fir—Mixed conifer	0.33	Mixed conifer—Mixed alder/ Douglas-fir	0.87
STAND STRUCTURE		STAND STRUCTURE	
Herb—Low/Tall shrub (Vertical Understory Structure)	0.54	Herb—Low/Tall shrub (Vertical Understory Structure)	0.86
Herb—Low shrub/Moss (Near-ground Understory Structure)	0.23	Low shrub/Moss—Herb (Near-ground Understory Structure)	0.12
Herb—Moss (Near-ground Understory Structure)	0.15		
UNDERSTORY SPECIES COMPOSITION		UNDERSTORY SPECIES COMPOSITION	
Moist shrub/herb—Dry upland shrub	0.31	Maple/Hemlock seedling/Mountain huckleberry—Ferns/Oxalis	0.32
Boreal shrub—Temperate herb	0.24	Maple/Hemlock seedling—Huckleberries/Oxalis	0.26
Vine maple—Bracken fern/Red huckleberry	0.21	Sword.fern/Oxalis—Salal/Oregongrape/Maple/Hemlock seedling	0.39
DOWNED WOOD		DOWNED WOOD	
Increase in small-diameter wood	0.33	Increase in small-diameter wood	0.16
Increase in medium-diameter wood	0.29	Increase in medium-and large-diameter wood	0.82
Increase in large-diameter wood	0.23		
OVERALL PLANT COMMUNITY COMPOSITION		OVERALL PLANT COMMUNITY COMPOSITION	
Herb community—Low/Tall shrub community	0.16	Salal/Oregongrape—Sword fern/Oxalis	0.48
Mixed conifer/shrub—Alder/shrub	0.21	Alder/Sword fern/Oxalis—Mixed conifer/Maple/Salal/Seedling	0.50
Alder/Herb—Douglas-fir/shrub	0.39		

Table 8. Descriptions of the gradients of plant community composition at the microsite scale in 3 vegetative categories: overstory trees, understory shrubs and herbs, and overall plant community of trees, shrubs, and herbs combined. The detailed process of NMS-axis interpretation was described in the APPENDIX 2.

Compositional Gradients of Plant Community at the Microsite Scale

TREE SPECIES COMPOSITION

Douglas-fir—Red alder

Along this gradient overstory composition changed from uniform Douglas-fir to increasing dominance of red alder.

Douglas-fir—Mixed conifer

Along this gradient overstory composition changed from uniform Douglas-fir to mixed conifer, which included mainly Douglas-fir and western hemlock in the overstory and regeneration of western hemlock, noble fir, and western redcedar seedlings in the understory.

UNDERSTORY COMPOSITION

Moist shrub/herb—Dry upland shrub

Along this gradient, cover of oxalis, Siberian miner's lettuce (*Claytonia sibirica*), false-lily of the valley, mountain huckleberry, and salmonberry increased in one direction (moist shrub/herb community), whereas cover of salal, Oregongrape, vine maple, bald-hip rose, and oceanspray increased in the other direction (dry upland shrub community).

Boreal shrub—Temperate herb

Along this gradient, cover of mountain huckleberry, twin flower, salal, dwarf Oregongrape, and bunchberry increased in one direction (boreal shrub community), whereas cover of sword fern, Siberian miner's lettuce, oxalis, hedge nettle, and thimbleberry in the other direction (temperate-herb community).

Vine maple--Bracken fern/Red huckleberry

Along this gradient, cover of vine maple increased in one direction, whereas cover of bracken fern, red huckleberry, and trailing blackberry increased in the other direction.

Table 8 (Continued).

OVERALL PLANT COMMUNITY COMPOSITION (TREES, SHRUBS, AND HERBS)Herb community—Low/Tall shrub community

Along this gradient, cover of herb species, including oxalis, Smith's fairlybell (*Disporum smithii*), sword fern increased in one direction (Herb community) and that of low- and tall-shrub species, including salal, dwarf Oregongrape, red huckleberry, mountain huckleberry, and bunchberry increased in the other direction (Low/Tall shrub community).

Mixed conifer/Tall shrub/Herb—Alder/shrub

Along this gradient, overstory cover of noble fir and western hemlock and understory cover for mountain huckleberry, twin flower, vanilla leaf (*Achlys triphylla*), bunchberry, three leaved anemone (*Anemone deltoidea*), and sweet cicely (*Osmoriza chilensis*) increased in one direction (mixed conifer/tall shrub/herb community), whereas overstory cover of red alder and understory cover for thimbleberry increased in the other direction (alder/shrub community).

Alder/Herb—Douglas-fir/shrub

Along this gradient, overstory cover of red alder and understory cover for oxalis, sword fern, sweet-scented bedstraw (*Galium triflorum*), and hedge nettle (*Stachys cooleyae*) increased in one direction (Alder/herb community), whereas overstory cover of Douglas-fir and understory cover for salal, vine maple, dwarf Oregongrape, and western hemlock seedling increased in the other direction (Douglas-fir/shrub community).

Table 9. Descriptions for the gradients of plant community composition at the stand scale in 3 vegetative categories: overstory trees, understory shrubs and herbs, and overall plant community of trees, shrubs, and herbs combined. The detailed process of NMS-axis interpretation is described in the APPENDIX 2.

Compositional Gradients of Plant Community at the Stand Scale

TREE SPECIES COMPOSITION

Douglas-fir—Mixed conifer

Along this gradient, tree density of Douglas-fir increased in one direction and that of western hemlock increased in the other direction as species composition of stands shift from uniform Douglas-fir to mixtures of Douglas-fir and western hemlock.

Mixed conifer—Mixed alder/Douglas-fir

Along this gradient, tree densities of both Douglas-fir and western hemlock increased in one direction and that of red alder increased in the other direction as species composition of stands shift from mixtures of Douglas-fir and western hemlock to mixtures of Douglas-fir and red alder.

UNDERSTORY SPECIES COMPOSITION

Maple/Hemlock seedling/M. huckleberry—Ferns/Oxalis

Along this gradient, covers of vine maple, mountain huckleberry, and western hemlock seedling increased in one direction and covers of sword fern, bracken fern, and oxalis increased in the other direction.

Maple/Hemlock seedling—Huckleberries/Oxalis

Along this gradient, covers of vine maple and western hemlock seedling increased in one direction and covers of both mountain huckleberry and red huckleberry, and of oxalis increased in the other direction.

Sword fern/Oxalis--Salal/Oregongrape/Maple/Hemlock seedling

Along this gradient, covers of sword fern and oxalis increased in one direction and covers of salal, dwarf Oregongrape, vine maple and western hemlock seedling increased in the other direction.

OVERALL PLANT COMMUNITY COMPOSITION (TREES, SHRUBS, AND HERBS)

Salal/Oregon.grape—Sword.fern/Oxalis

Along this gradient, covers of salal and Oregongrape increased in one direction and covers of sword fern and oxalis increased in the other direction.

Alder/Sword fern/Oxalis(Alder/Herb)—Mixed conifer/Maple/Salal/Seedling (Conifer/Shrub)

Along this gradient, overstory cover of red alder and understory covers of sword fern and oxalis increased in one direction and overstory covers of Douglas-fir and western hemlock and understory covers of vine maples, salal, and shade-tolerant conifer seedling increased in the other direction.

Effects of Ecological Gradients on Habitat Associations at the Microsite and Stand Scales.

A gradient of overall plant community composition had the most prevailing effects on habitat associations of forest-floor vertebrates at both the microsite and at the stand scales. At the microhabitat scale, the highest number of vertebrate species (9 of 16) was associated with Alder/Herb—Douglas-fir/Shrub compositional gradient (Table 10,12, 13, and 14; Figure 6P). Similarly, at the stand scale, the highest number of vertebrate species (8 of 16) was associated with Alder/S.fern/Oxalis—Mixed conifer/Maple/Salal/Seedling gradient (Table 11,15,16, and 17). Furthermore, at the stand scale, a gradient of overstory tree composition (Mixed conifer—Mixed alder/Douglas-fir gradient) alone could describe the associations of the same 8 species that were associated with Alder/S.fern/Oxalis—Mixed conifer/Maple/Salal/Seedling gradient (Tables 11,15,16, and 17).

Table 10. Number of species associated with 16 ecological gradients at the microsite scale within 12 young forest stands (35-45 years old) in the northern Oregon Coast Range, 1994.

ECOLOGICAL GRADIENTS AT THE MICROSITE SCALE	Number of Species Associated^a				
	Insectivores	Rodents	All Mammals	Amphibians	All Vertebrates
<i>MICROCLIMATE</i>					
Temperature (Cool—Warm)	1	2	3	0	3
Moisture (Moist—Dry)	1	1	2	0	2
<i>TREE SPECIES COMPOSITION</i>					
Douglas-fir—Red alder	2	1	3	2	5
Douglas-fir—Mixed conifer	1	0	1	1	2
<i>STAND STRUCTURE</i>					
Herb—Low/Tall shrub (Vertical Understory Structure)	2	0	2	2	4
Herb—Low shrub/Moss (Near-ground Understory Structure)	3	2	5	2	7
Herb—Moss (Near-ground Understory Structure)	0	0	0	1	1
<i>UNDERSTORY SPECIES COMPOSITION</i>					
Moist shrub/herb—Dry upland shrub	2	3	5	1	6
Boreal shrub—Temperate herb	3	1	4	2	6
Vine maple—Bracken fern/Red huckleberry	0	0	0	1	1
<i>DOWNED WOOD</i>					
Small-sized wood (Less—More)	2	0	2	0	2
Medium-sized wood (Less—More)	3	0	3	0	3
Large-sized wood (Less—More)	0	1	1	1	2
<i>PLANT COMMUNITY COMPOSITION</i>					
Herb community—Low/Tall shrub community	1	0	1	0	1
Mixed conifer/shrub—Alder/shrub	0	0	0	2	2
Alder/herb—Douglas-fir/shrub	4	2	6	3	9

^aNumber of species whose presence and absence were significantly differentiated along each ecological gradient determined by ANOVA using sites as blocks ($P < 0.1$).

Table 11. Number of species associated with 13 ecological gradients at the stand scale among the 12 young forest stands (35-45 years old) in the northern Oregon Coast Range, 1994.

ECOLOGICAL GRADIENTS AT THE STAND SCALE	Number of Species Associated ^a				
	Insectivores	Rodents	All Mammals	Amphibians	All Vertebrates
MICROCLIMATE					
Temperature: Cool—W arm	1	1	2	2	4
Moisture: Moist—Dry	2	3	5	2	7
TREE SPECIES COMPOSITION					
Douglas-fir—Mixed conifer	2	1	3	2	5
Mixed conifer—Mixed alder/Douglas-fir ^b	4	2	6	2	8
STAND STRUCTURE					
Herb—Low/Tall Shrub (Vertical Understory Structure)	3	1	4	2	6
Low shrub/Moss—Herb (Near-ground Understory Structure)	1	0	1	0	1
UNDERSTORY SPECIES COMPOSITION^c					
Maple/HemlockS/M. huckleberry—Ferns/Oxalis	1	2	3	1	4
Maple/HemlockS—Huckleberries/Oxalis	0	0	0	3	3
S.fern/Oxalis—Salal/O.grape/Maple/HemlockS	3	1	4	1	5
DOWNED WOOD^d					
Increase in medium- and large-sized wood	1	0	1	3	4
Increase in small-sized wood	0	0	0	1	1
PLANT COMMUNITY COMPOSITION^e					
Salal/O.grape—S.fern/Oxalis	2	0	2	1	3
Alder/S.fern/Oxalis—Mixed conifer/Maple/Salal/Seedling (Alder/Herb) (Conifer/Shrub)	4	2	6	2	8

^a Number of species that had significant association with each gradient determined by Pearson's r at $P < 0.1$.

^b Mixed conifer included Douglas-fir and western hemlock in the overstory; densities of western hemlock increased in one direction and those of red alder increased in the other direction along this gradient as species composition of stands become mixtures of red alder and Douglas-fir.

^c Maple = Vine Maple, HemlockS = western hemlock seedlings in the understory, Huckleberries = red huckleberry and mountain huckleberry, M. huckleberry = mountain huckleberry, Ferns = both Sword fern and bracken fern, S. fern = sword fern, O. grape = dwarf Oregongrape.

^d small, 10-29 cm; medium, 30-49 cm; large, ≥ 50 cm.

^e Seedlings included western hemlock, noble fir, and western redcedar.

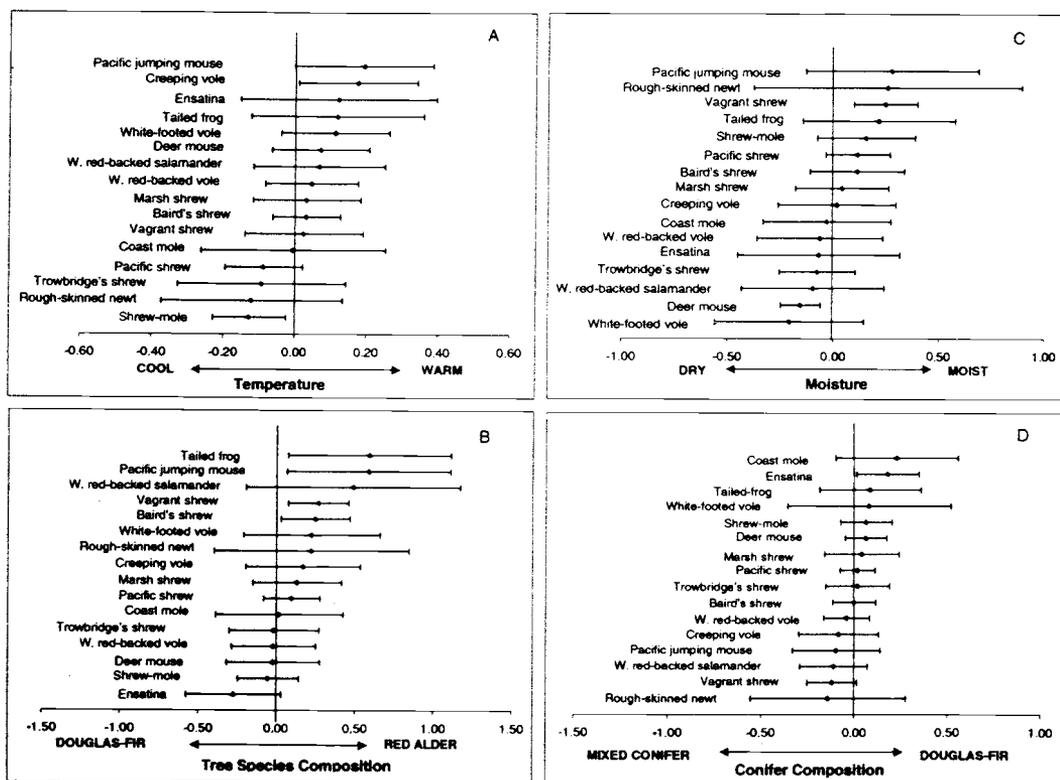


Figure 6. Habitat association at the microsite scale for 16 species of forest-floor vertebrates along 16 ecological gradients in 12 young-forest stands, northern Oregon Coast Range. Graphs indicated mean differences in ordination scores between capture and non-capture microsites and 95% confidence intervals. The ordination scores were based on Nonmetric Multidimensional Scaling.

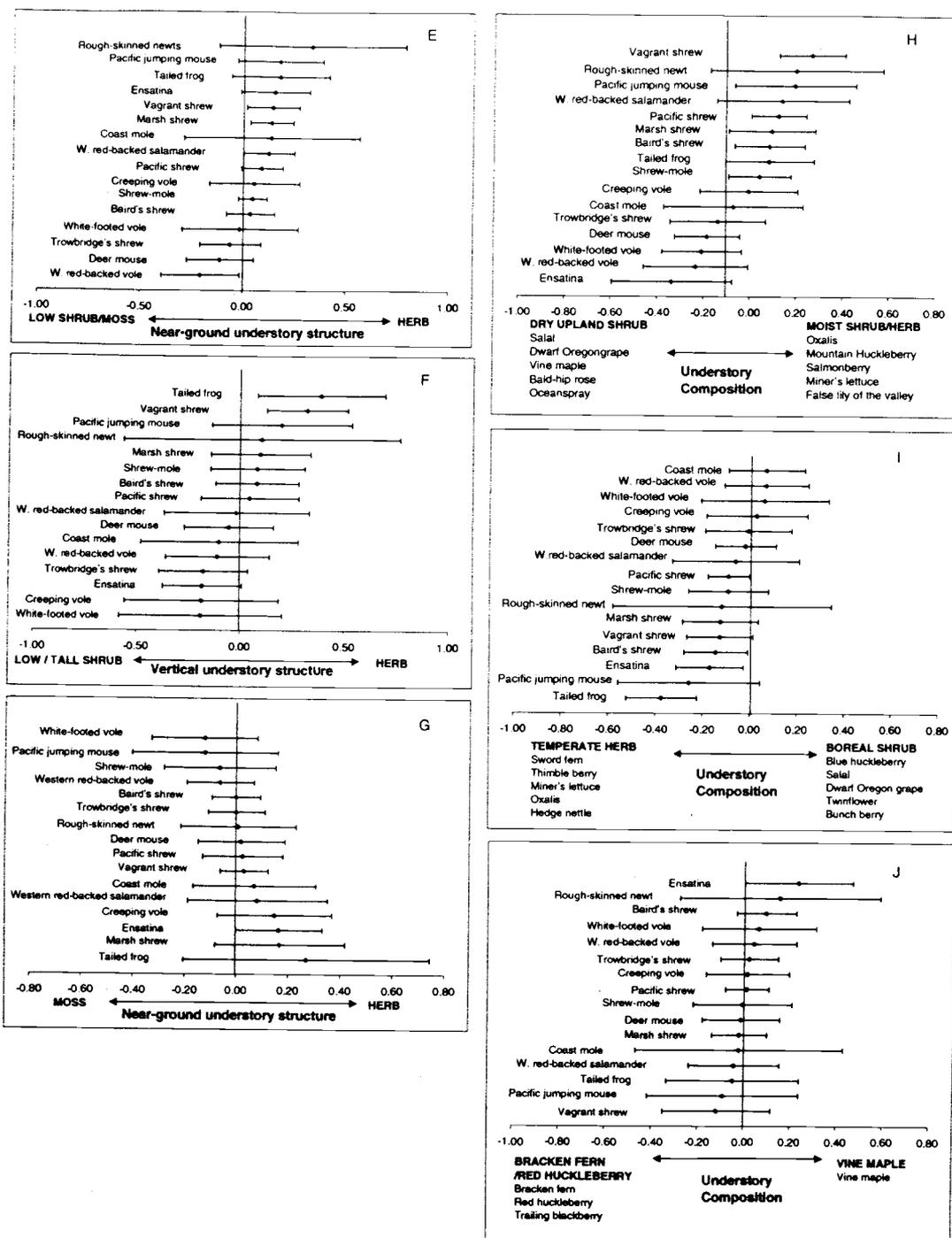


Figure 6 (Continued).

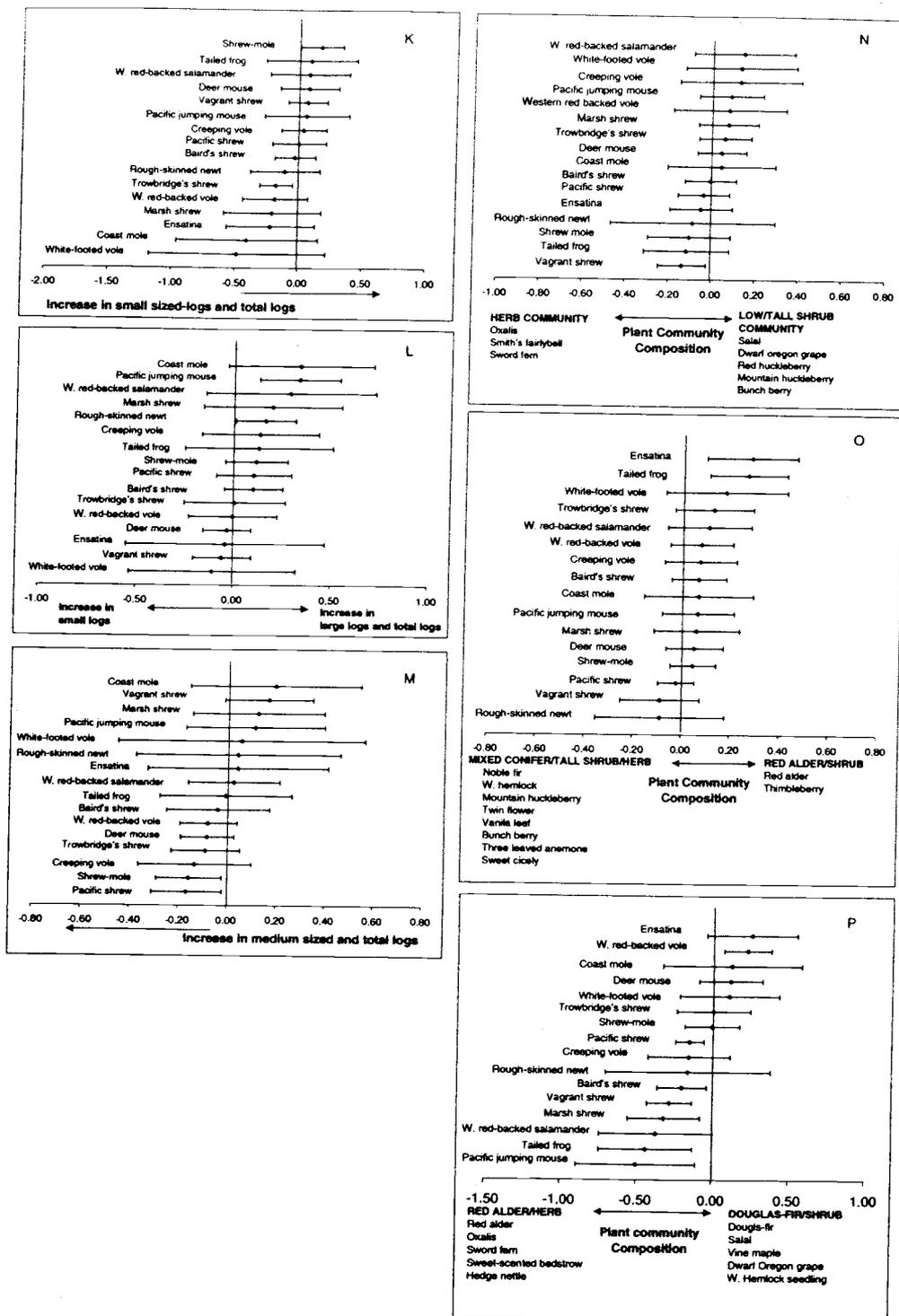


Figure 6 (Continued).

The 2 gradients of microclimate, moisture and temperature, were more important at the stand scale than at the microsite scale. At the stand scale, 7 species and 4 species were associated with the moisture gradient and the temperature gradient; whereas, at the microsite scale, only 3 species and 2 species were associated with the moisture gradient and the temperature gradient (Tables 10 and 11).

Association of vertebrate species with stand structure also differed between the 2 spatial scales. At the microsite scale, more species were associated with the gradient of near-ground understory structure than with that of vertical understory structure (Table 10; near-ground structural gradient of Herb—Low shrub/Moss, 7 species; vertical structural gradient of Herb—Low/Tall Shrub, 4 species); however, this trend was reversed at the stand scale; more species were associated with the gradient of vertical understory structure than with that of near-ground understory structure at the stand scale (Table 11; near-ground structural gradient, 1 species; vertical structural gradient, 6 species).

Microclimate

Presence of 5 species of mammals was associated with the 2 gradients of microclimate among microsites within the stands ($P < 0.1$, Tables 12 and 13; Figures 6A, C). Along the moisture gradient, vagrant shrews occurred at wetter microsites, whereas deer mice occurred at drier microsites. Along the temperature gradient, creeping voles and Pacific jumping mice occurred at warmer microsites, whereas shrew-moles occurred at cooler microsites along the temperature gradient. No species

of amphibian was associated with the microclimatic gradients at the microsite scale ($P > 0.1$, Tables 10 and 14).

The association of vertebrates with microclimatic condition was the strongest at the stand scale; abundances of 9 species were associated with 2 gradients of microclimate among the 12 stands (Tables 15, 16, and 17). Among these, abundances of 7 species were associated with the moisture gradient and those of 4 species were associated with the temperature gradient. Along the moisture gradient, western red-backed voles, deer mice, and coast moles were more abundant in drier stands, whereas Pacific jumping mice, Baird's shrews, Dunn's salamanders, and western red-backed salamanders were more abundant in wetter stands. Furthermore, along the temperature gradients, Pacific shrews, western red-backed voles, and northwestern salamanders were more abundant in cooler stands, whereas western red-backed salamanders were more abundant in warmer stands. The association of deer mice with dry habitats was consistent at both the microsite and stand scales (Tables 13, 16, and 19). However, associations of other species with the microclimatic gradients were inconsistent between the microsite and stand scales (Tables 18, 19, and 20).

Table 12. Habitat associations of 6 insectivore species at the microsite scale along 16 ecological gradients within 12 young-forest stands (35-45 years old) in the northern Oregon Coast Range, 1994. *P*-values were based on comparisons of ordination scores (Nonmetric Multidimensional Scaling) between the present and absent sites with ANOVA using stands as blocks. The letters within the parentheses indicates specific associations of species along the gradients.

Ecological Gradients at the Microsite Scale	<i>P</i> -values					
	Baird's shrew	Marsh shrew	Pacific shrew	Trowbridge's shrew	Vagrant shrew	Shrew-mole
Microclimate						
Temperature (Cool—Warm)						0.021 (Cool)
Moisture (Moist—Dry)					0.004 (Moist)	
Tree species composition						
Douglas-fir (Df)—Red alder (Ra)	0.030 (Ra)				0.011 (Ra)	
Douglas-fir (Df)—Mixed conifer (Mc)						
Stand structure						
Herb—Low/Tall shrub (Vertical Understory Structure)				0.096 (Shrub)	0.004 (Herb)	
Herb—Low shrub/Moss (Near-ground Understory Structure)		0.013 (Herb)	0.062 (Herb)		0.028 (Herb)	
Herb—Moss (Near-ground structure)						
Understory Composition						
Moist shrub/herb (Msh)—Dry upland shrub (Dus)			0.042 (Msh)		0.002 (Msh)	
Boreal shrub (Bs)—Temperate herb (Th)	0.042 (Th)		0.049 (Th)		0.077 (Th)	
Vine maple—Bracken fern/Red huckleberry						
Downed-wood Density						
Small-sized wood/10-29 cm in diameter (Less—More)				0.012 (Less)		0.047 (More)
Medium-sized wood/30-49 cm in diameter (Less—More)			0.031 (More)		0.066 (Less)	0.028 (More)
Large-sized wood/≥50 cm in diameter (Less—More)						
Plant Community Composition						
Herb community—Low/Tall shrub community					0.022 (Herb)	
Mixed conifer/shrub (Ms)—Alder/shrub (As)						
Alder/Herb (Ah)—Douglas-fir/shrub (Ds)	0.020 (Ah)	0.013 (Ah)	0.004 (Ah)		0.002 (Ah)	

Table 13. Habitat associations of 5 rodent species at the microsite scale along 16 ecological gradients within 12 young-forest stands (35-45 years old) in the northern Oregon Coast Range, 1994. *P*-values were based on comparisons of ordination scores (Nonmetric Multidimensional Scaling) between the present and absent sites with ANOVA using stands as blocks. The letters within the parentheses indicates specific associations of species along the gradients.

Ecological Gradients at the Microsite Scale	<i>P</i> -values				
	Western red-backed vole	White-footed vole	Creeping vole	Deer mouse	Pacific jumping mouse
Microclimate					
Temperature (Cool—Warm)			0.039 (Warm)		0.050 (Warm)
Moisture (Moist—Dry)				0.004 (Dry)	
Tree species composition					
Douglas-fir (Df)—Red alder (Ra)					0.032 (Ra)
Douglas-fir (Df)—Mixed conifer (Mc)					
Vegetation structure					
Herb—Low/Tall shrub (Vertical Understory Structure)					
Herb—Low shrub/Moss (Near-ground Understory Structure)	0.038 (Shrub/Moss)				0.077 (Herb)
Herb—Moss (Near-ground Understory Structure)					
Understory composition					
Moist shrub/herb (Msh)—Dry upland shrub (Dus)	0.045 (Dus)	0.025 (Dus)		0.015 (Dus)	
Boreal shrub (Bs)—Temperate herb (Th)					0.084 (Th)
Vine maple—Bracken fern/Red huckleberry					
Downed-wood Density					
Small-sized wood/10-29 cm in diameter (Less—More)					
Medium-sized wood/30-49 cm in diameter (Less—More)					
Large-sized wood/≥50 cm in diameter (Less—More)					0.006 (More)
Plant Community Composition					
Herb community—Low/Tall shrub community					
Mixed conifer/shrub (Ms)—Alder/shrub (As)					
Alder/Herb (Ah)—Douglas-fir/shrub (Ds)	0.008 (Ds)				0.020 (Ah)

Table 14. Habitat associations of 4 amphibian species at the microsite scale along 16 ecological gradients within 12 young-forest stands (35-45 years old) in the northern Oregon Coast Range, 1994. The *P*-values were based on comparisons of ordination scores (Nonmetric Multidimensional Scaling) between the present and absent sites with ANOVA using stands as blocks. The letters within the parentheses indicates specific associations of species along the gradients.

Ecological Gradients at Microsite Scale	<i>P</i> -values			
	Ensatina	Western red-backed salamander	Rough-skinned newt	Tailed frog
Microclimate				
Temperature (Cool—Warm)				
Moisture (Moist—Dry)				
Tree species composition				
Douglas-fir (Df)—Red alder (Ra)	0.072 (Df)			0.030 (Ra)
Douglas-fir (Df)—Mixed conifer (Mc)	0.039 (Df)			
Stand structure				
Herb—Low/Tall shrub (Vertical Understory Structure)	0.059 (Shrub)			0.02 (Herb)
Herb—Low shrub/Moss (Near-ground Understory Structure)	0.064 (Herb)	0.044 (Shrub/Moss)		
Herb—Moss (Near-ground Understory Structure)	0.052 (Herb)			
Understory Composition				
Moist shrub/herb (Msh)—Dry upland shrub (Dus)	0.018 (Dus)			
Boreal shrub (Bs)—Temperate herb (Th)	0.026 (Th)			<0.001 (Th)
Vine maple—Bracken fern/Red huckleberry	0.049 (Vine maple)			
Downed-wood Density^a				
Small-sized wood/10-29 cm in diameter (Less—More)				
Medium-sized wood/30-49 cm in diameter (Less—More)				
Large-sized wood/≥50 cm in diameter (Less—More)			0.042 (More)	
Plant Community Composition				
Herb community—Low/Tall shrub community				
Mixed conifer/shrub (Ms)—Alder/shrub (As)	0.008 (Ms)			0.005 (As?)
Alder/Herb (Ah)—Douglas-fir/shrub (Ds)	0.085 (Ds)	0.052 (Ah)		0.011 (Ah)

The association of vertebrates to microclimatic condition was most prevalent at the stand scale; abundances of 9 species were associated with 2 gradients of microclimate among the 12 stands (Tables 15, 16, and 17). Among these, abundances of 7 species were associated with the moisture gradient and those of 4 species were associated with the temperature gradient. Along the moisture gradient, western red-backed voles, deer mice, and coast moles were more abundant in drier stands, whereas Pacific jumping mice, Baird's shrews, Dunn's salamanders, and western red-backed salamanders were more abundant in wetter stands. Furthermore, along the temperature gradients, Pacific shrews, western red-backed voles, and Northwestern salamanders were more abundant in cooler stands, whereas western red-backed salamanders were more abundant in warmer stands. The association of deer mice with dry habitats was consistent at both the microsite and stand scales (Tables 13, 16, and 19). However, the habitat associations of other species with the microclimatic gradients were inconsistent between the microsite and stand scales (Tables 18, 19, and 20).

Table 15. Habitat associations of 6 insectivore species at the stand scale along 13 ecological gradients among the 12 young forest stands (35-45 years old) in the north Oregon Coast Range, 1994. Pearson's correlation coefficients indicated correlations between number of captures of species and ordination scores of ecological gradients based on Nonmetric Multidimensional Scaling.

Ecological Gradients	Pearson's r^a					
	Baird's Shrew	Pacific Shrew	Trowbridge's Shrew	Vagrant Shrew	Shrew Mole	Coast Mole
MICROCLIMATE						
Temperature: Cool (-)—Warm (+)		-0.501*				
Moisture: Moist (-)—Dry (+)	-0.675**					+0.663**
TREE SPECIES COMPOSITION						
Douglas-fir (-)—Mixed conifer (+)				-0.566*		+0.590**
Mixed Conifer (-)—Mixed alder/Douglas-fir (+) ^b	+0.516*			+0.881***	+0.694**	-0.558*
STAND STRUCTURE						
Vertical Understory Structure: Herb (-)—Low/Tall Shrub (+)			+0.549*	-0.804**		+0.637**
Near-ground Understory Structure: Low shrub/Moss (-)—Herb (+)		+0.743**				
UNDERSTORY SPECIES COMPOSITION^c						
Maple/HemlockS/M. huckleberry (-)—Ferns/Oxalis (+)				+0.847*****		
Maple/HemlockS (-)—Huckleberries/Oxalis (+)						
S.fern/Oxalis (-)—Salal/O.grape/Maple/Hemlock (+)		-0.525*		-0.621**		+0.576**
DOWNED WOOD^d						
Increase (+) in medium- and large-sized wood	-0.541*					
Increase (+) in small-sized wood						
PLANT COMMUNITY COMPOSITION^e						
Salal/O.grape (-)—S.fern/Oxalis (+)		0.614**				-0.612**
Alder/S.fern/Oxalis (-)—Mixed Conifer/Maple/Salal/Seedling (+) (Alder/Herb) (Conifer/Shrub)	-0.514*			-0.837*****	-0.561*	+0.498*

^a * $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$, **** $P < 0.001$

Table 15 (Continued)

^b Mixed conifer included Douglas-fir and western hemlock in the overstory; densities of western hemlock increased in one direction and those of red alder increased in the other direction along this gradient.

^c Maple = vine maple, HemlockS = western hemlock seedlings in the understory, Huckleberries = both red huckleberry and mountain huckleberry, M. huckleberry = mountain huckleberry, Ferns = both sword fern and bracken fern, S. fern = sword fern, O. grape = dwarf Oregongrape.

^d small, 10-29 cm; medium, 30-49 cm; large, ≥ 50 cm.

^e Seedlings included western hemlock, noble fir, and western redcedar.

Table 16. Habitat associations of 3 rodent species at the stand scale along 13 ecological gradients among the 12 young forest stands (35-45 years old) in the northern Oregon Coast Range, 1994. Pearson's correlation coefficients indicated the correlations between number of captures of species and ordination scores of ecological gradients based on Nonmetric Multidimensional Scaling. No significant associations with these ecological gradients were detected for creeping voles and white-footed voles.

Ecological Gradients	Pearson's r^a		
	Western red-backed vole	Deer mouse	Pacific jumping mouse
MICROCLIMATE			
Temperature: Cool (-)—Warm (+)	-0.672***		
Moisture: Moist (-)—Dry (+)	+0.783***	+0.537*	-0.594**
TREE SPECIES COMPOSITION			
Douglas-fir (-)—Mixed conifer (+)		+0.512*	
Mixed conifer (-)—Mixed alder/Douglas-fir (+) ^b	-0.769***	-0.919****	
STAND STRUCTURE			
Vertical Understory Structure: Herb (-)—Low/Tall shrub (+)		+0.668**	
Near-ground Understory Structure: Low shrub/Moss (-)—Herb (+)			
UNDERSTORY SPECIES COMPOSITION^c			
Maple/HemlockS/M.huckleberry (-)—Ferns/Oxalis (+)	-0.795***	-0.785***	
Maple/HemlockS (-)—Huckleberries/Oxalis (+)			
S.fern/Oxalis (-)—Salal/O.grape/Maple/HemlockS (+)		+0.518 *	
DOWNED WOOD^d			
Increase (+) in medium- and large-sized wood			
Increase (+) in small-sized wood			
PLANT COMMUNITY COMPOSITION^c			
Salal/O.grape (-)—S.fern/Oxalis (+)			
Alder/S.fern/Oxalis (-)—Mixed conifer/Maple/Salal/Seedling (+)			
(Alder/Herb) (Conifer/Shrub)	+0.647**	+0.826****	

^a * $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$, **** $P < 0.001$

Table 16 (Continued).

^b Mixed conifer included Douglas-fir and western hemlock in the overstory; densities of western hemlock increased in one direction and those of red alder increased in the other direction along this gradient.

^c Maple = vine maple, HemlockS = western hemlock seedlings in the understory, Huckleberries = both red huckleberry and mountain huckleberry, M. huckleberry = mountain huckleberry, Ferns = both sword fern and bracken fern, S. fern = sword fern, O. grape = dwarf Oregon-grape.

^d small, 10-29 cm; medium, 30-49 cm; large, ≥ 50 cm.

^e Seedlings included western hemlock, noble fir, and western redcedar.

Table 17. Habitat associations of 6 amphibian species at the stand scale along 13 ecological gradients among the 12 young forest stands (35-45 years old) in the north Oregon Coast Range, 1994. Pearson's correlation coefficients indicated the correlations between number of captures of species and ordination scores of ecological gradients based on Nonmetric Multidimensional Scaling.

Ecological Gradients	Pearson's r^a					
	North-western Salamander	Pacific Giant Salamander	Dunn's Salamander	Western red-backed Salamander	Rough-skinned Newt	Tailed Frog
MICROCLIMATE						
Temperature: Cool (-)—Warm (+)	-0.510*			+0.543*		
Moisture: Moist (-)—Dry (+)			-0.535*	-0.608**		
TREE SPECIES COMPOSITION						
Douglas-fir (-)—Mixed conifer (+)	+0.557*				+0.577**	
Mixed conifer (-)—Mixed alder/Douglas-fir (+) ^b				+0.579**	-0.522*	
STAND STRUCTURE						
Vertical Understory Structure:						
Herb (-)—Low/Tall shrub (+)				-0.560*	+0.735***	
Near-ground Understory Structure:						
Low shrub/Moss (-)—Herb (+)						
UNDERSTORY SPECIES COMPOSITION^c						
Maple/HemlockS/M. huckleberry (-)—Ferns/Oxalis (+)				+0.517*		
Maple/HemlockS (-)—Huckleberries/Oxalis (+)		+0.681**			-0.668**	+0.667**
S.fern/Oxalis (-)—Salal/O.grape/Maple/HemlockS (+)					+0.775***	
DOWNED WOOD^d						
Increase (+) in medium- and large-sized wood	+0.669**			-0.714***	+0.627**	
Increase (+) in small-sized wood	-0.514*					
PLANT COMMUNITY COMPOSITION^e						
Salal/O.grape (-)—S.fern/Oxalis (+)					-0.697**	
Alder/S.fern/Oxalis (-)—Mixed Conifer/Maple/Salal/Seedling (+)				-0.577**	+0.766***	
(Alder/Herb) (Conifer/Shrub)						

Table 17 (continued).

^a * $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$, **** $P < 0.001$

^b Mixed conifer included Douglas-fir and western hemlock in the overstory; densities of western hemlock increased in one direction and those of red alder increased in the other direction along this gradient.

^c Maple = vine maple, HemlockS = western hemlock seedlings in the understory, Huckleberries = both red huckleberry and mountain huckleberry, M. huckleberry = mountain huckleberry, Ferns = both sword fern and bracken fern, S. fern = sword fern, O. grape = dwarf Oregon grape.

^d small, 10-29 cm; medium, 30-49 cm; large, ≥ 50 cm.

^e Seedlings included western hemlock, noble fir, and western redcedar.

Table 18. Habitat associations of 5 insectivore species with ecological gradients measured at the microsite and stand scales.

ECOLOGICAL GRADIENTS	Insectivores									
	Baird's Shrew		Pacific Shrew		Trowbridge's Shrew		Vagrant Shrew		Shrew-mole	
	Stand	Micro	Stand	Micro	Stand	Micro	Stand	Micro	Stand	Micro
MICROCLIMATE	Moist	--	Cool	--	--	--	--	--	--	Cool
TREE SPECIES COMPOSITION	Mixed alder/D-fir	Alder	--	--	--	--	Mixed alder/D-fir	Alder/D-fir	Mixed alder/D-fir	--
VERTICAL UNDERSTORY STRUCTURE^a	--	--	--	--	L/Tshrub	L/Tshrub	Herb	Herb	--	--
NEAR-GROUND UNDERSTORY STRUCTURE	--	--	Herb	Herb	--	--	--	--	--	--
UNDERSTORY COMPOSITION^b	--	Temp Herb	S.fern/Oxalis	Moist Shrub/Herb or Temp Herb	--	--	Fern/Oxalis or S.fern/Oxalis	Mois Shrub/Herb or Temp Herb	--	--
LARGE-DOWNED WOOD^c	Less	--	--	--	--	--	--	--	--	More
MEDIUM-DOWNED WOOD	Less	--	--	More	--	--	--	Less	--	More
SMALL-DOWNED WOOD	--	--	--	--	--	Less	--	--	--	--
PLANT COMM. COMPOSITION^d	Alder/S.fern/Oxalis	Alder/Herb	S.fern/Oxalis	Alder/Herb	--	--	Alder/S.fern/Oxalis	Alder/Herb	Alder/S.fern/Oxalis	--

^aL/Tshrub indicates the association of species to mixture of low- and tall shrubs.

^bTemp Herb indicates temperate-herb community, which typically included sword fern, Siberian miner's lettuce, oxalis, hedge nettle, and thimbleberry. Moist Shrub/Herb community typically includes oxalis, Siberian miner's lettuce, false-lily of the valley, mountain huckleberry, and salmonberry. S.fern indicates sword fern and fern includes both sword fern and bracken fern.

^cSmall-downed wood, 10-29 cm in diameter; medium-downed wood, 30-49 cm in diameter; large-downed wood, ≥ 50 cm in diameter.

^dAlder/Herb community is characterized by red alder overstory with herb dominated understory, which includes oxalis, sword fern, sweet-scented bedstraw, and hedge nettle. S.fern indicates sword fern.

Table 19. Habitat associations of 3 rodent species with ecological gradients measured at the microsite and stand scales.

ECOLOGICAL GRADIENTS	Rodents					
	Western red-backed vole		Deer mouse		Pacific jumping mouse	
	Stand	Micro	Stand	Micro	Stand	Micro
<i>MICROCLIMATE</i>	Dry/Cool	--	Dry	Dry	Moist	Warm
<i>TREE SPECIES COMPOSITION^a</i>	Mixed conifer	--	Mixed conifer	--	--	Alder
<i>VERTICAL UNDERSTORY STRUCTURE^b</i>	--	--	L/Tshrub	--	--	--
<i>NEAR-GROUND UNDERSTORY STRUCTURE^c</i>	--	Lshrub/Moss	--	--	--	Herb
<i>LARGE-DOWNED WOOD^d</i>	--	--	--	--	--	More
<i>MEDIUM-DOWNED WOOD</i>	--	--	--	--	--	--
<i>SMALL-DOWNED WOOD</i>	--	--	--	--	--	--
<i>UNDERSTORY SPECIES COMPOSITION^e</i>	Vine maple /M. huckleberry /Hemlock seedling	Dry upland Shrub	Vine maple /M. huckleberry /Hemlock seedling or Salal/Oregon rape /Vine maple /Hemlock seedling	Dry upland Shrub	--	Temp Herb
<i>PLANT COMMUNITY COMPOSITION^f</i>	Mixed conifer /Vine maple /Salal /Conifer seedling	Douglas-fir /shrub	Mixed Conifer /Vine maple /Salal /Conifer seedling	--	--	Alder /herb

^aMixed conifer includes Douglas-fir and western hemlock in the overstory.

^bL/Tshrub indicates the association of species to mixture of low- and tall shrubs.

^cLshrub/Moss indicates the association of species to mixture of low-shrub and moss ground cover.

^dSmall-downed wood, 10-29 cm in diameter; medium-downed wood, 30-49 cm in diameter; large-downed wood, ≥ 50 cm in diameter.

Table 19 (Continued).

[°] **M. huckleberry** indicates mountain huckleberry. **Dry-upland-shrub** community typically includes salal, Oregongrape, vine maple, bald-hip rose, and oceanspray. **Temp Herb** indicates temperate-herb community, which typically includes sword fern, Siberian miner's lettuce, oxalis, hedge nettle, and thimbleberry.

^f **Alder/Herb** community was characterized by red alder overstory with herb dominated understory, which includes oxalis, sword fern, sweet-scented bedstraw, and hedge nettle. **S.fern** indicates sword fern. **Douglas-fir/Shrub** community is characterized by Douglas-fir overstory with shrub dominated understory, which includes salal, vine maple, dwarf Oregongrape, and western hemlock seedlings.

Table 20. Association of 4 amphibian species with ecological gradients measured at the microsite and stand scales.

ECOLOGICAL GRADIENTS	Amphibians							
	Ensatina		Western red-backed Salamander		Rough-skinned		Tailed Frog	
	Stand	Micro	Stand	Micro	Stand	Micro	Stand	Micro
<i>MICROCLIMATE</i>	--	--	Moist/Warm	--	--	--	--	--
<i>TREE SPECIES COMPOSITION</i> ^a	--	D-fir	Mixed alder/D-fir	--	Mixed conifer	Mixed conifer	--	Alder
<i>VERTICAL UNDERSTORY STRUCTURE</i> ^b	--	L/Tshrub	Herb	--	L/Tshrub	--	--	Herb
<i>NEAR-GROUND UNDERSTORY STRUCTURE</i> ^c	--	Herb	--	Lshrub/Moss	--	--	--	--
<i>LARGE-DOWNED WOOD</i> ^d	--	--	Less	--	More	More	--	--
<i>MEDIUM-DOWNED WOOD</i>	--	--	--	--	More	--	--	--
<i>SMALL-DOWNED WOOD UNDERSTORY COMPOSITION</i> ^e	--	Temp Herb or Dry upland shrub or Vine maple	Fern/Oxalis	--	Vine maple /HemlockS or Salal /OregonGrape /Maple /HemlockS	--	Huckleberries /Oxalis	Temp Herb
<i>PLANT COMM. COMPOSITION</i> ^f	--	Mixed conifer /Shrub or Douglas-fir /Shrub	Alder/S.fern/ Oxalis	Alder/Herb	Salal/Oregon-grape or Hemlock /Vine maple /Salal /Conifer seedling	--	--	Alder/Shrub Or Alder/Herb

Table 20 (continued).

^aMixed conifer includes Douglas-fir and western hemlock in the overstory.

^bL/Tshrub indicates the association of species to mixture of low- and tall shrubs.

^cLshrub/Moss indicates the association of species to mixture of low-shrub and moss ground cover.

^dSmall-downed wood, 10-29 cm in diameter; medium-downed wood, 30-49 cm in diameter; large-downed wood, ≥ 50 cm in diameter.

^eDry-upland-shrub community typically includes salal, Oregongrape, vine maple, bald-hip rose, and oceanspray. Temp Herb indicates temperate-herb community, which typically includes sword fern, Siberian miner's lettuce, oxalis, hedge nettle, and thimbleberry. HemlockS indicates the presence of western hemlock seedlings in the understory. Huckleberries indicates the presence of either mountain huckleberries or red huckleberries in the understory.

^fMixed Conifer/Shrub community is characterized by mixture of Douglas-fir and either western hemlock, noble fir, or both in the overstory with shrub dominated understory, which includes mountain huckleberry, twin flower, vanilla leaf, bunchberry, three leaved anemone, and sweet cicely. Douglas-fir/Shrub community is characterized by Douglas-fir overstory with shrub dominated understory, which includes salal, vine maple, dwarf Oregongrape, and western hemlock seedlings. Alder/Herb community is characterized by red alder overstory with herb dominated understory, which includes oxalis, sword fern, sweet-scented bedstraw, and hedge nettle. S.fern indicates sword fern. Alder/shrub community is characterized by red alder overstory with understory dominated by thimbleberry.

Downed Wood

Six species (5 mammals and 1 amphibian) were associated with the 3 gradients of downed wood abundance at the microsite scale ($P < 0.1$, Tables 12, 13, and 14; Figures 6K, L, M). Among these, 4 species showed positive and 2 showed negative associations with downed wood. In comparison to the non-capture sites, Pacific jumping mice and rough-skinned newts occurred at microsites with larger amounts of large downed wood (Tables 13 and 14; Figure 6L), whereas Pacific shrews occurred in microsites with a larger amounts of medium downed wood (Table 12; Figure 6M). Shrew-moles occurred in microsites with larger amounts of downed wood in either small or medium size classes. In contrast, Trowbridge's shrews and vagrant shrews occurred in microsites with less downed wood in the small- and in the medium-size classes, respectively.

Fewer species were associated with downed wood at the stand scale than at the microsite scale. Abundances of 4 species (3 species of amphibian and 1 species of mammal) were associated with 2 gradients of downed wood abundance among the 12 stands (Tables 15, 16, and 17); 2 species were associated positively and 2 were associated negatively with the abundance of downed wood. Northwestern salamanders and rough-skinned newts were more abundant in stands with more medium- and large-sized downed wood; however, northwestern salamanders were less abundant in stands with more small-sized downed wood. In contrast, Baird's shrews and western red-backed salamanders were more abundant in stands with fewer

medium and large-sized downed wood. The association of rough-skinned newts with large downed wood was consistent between the microsite and stand scales; however, for other species, their associations to downed wood were inconsistent between the 2 spatial scales (Tables 18, 19, and 20).

Tree Species Composition

There was no strong association of vertebrates to increasing densities of western hemlock trees among microsites within stands ($P > 0.1$); however, presence and absence of 5 species (3 species of mammal and 2 species of amphibian) was associated with Douglas-fir—red alder gradient at the microsite scale ($P < 0.1$, Tables 12, 13, and 14; Figure 6B). Presence of 4 species (Baird's shrews, vagrant shrews, Pacific jumping mice, and tailed frogs) was associated positively with increasing density of red alder, and presence of 1 species (ensatinas) was associated positively with increasing density of Douglas-fir.

Abundances of 9 species (6 mammals and 3 amphibians) were associated with tree species composition at the stand scale ($P < 0.1$, Tables 15, 16, and 17). Eight species were associated with the Mixed conifer—Mixed alder/Douglas-fir gradient. Abundances of Baird's shrews, vagrant shrews, shrew-moles, and western red-backed salamanders were positively related to increasing densities of red alder, whereas abundances of coast moles, western red-backed voles, deer mice, and rough-skinned newts were positively related to with increasing densities of western hemlock. Only 1 species was associated with the Douglas-fir—Mixed conifer gradient; northwestern

salamanders were more abundant in stands with increasing densities of western hemlock trees. The positive associations of 2 species (Baird's shrews and vagrant shrews) to increasing red alder trees were consistent between the microsite and stand scales (Table 18).

Stand Structure

Presence and absence of 9 species (6 mammals and 3 amphibians) was associated with stand structure at the microsite scale ($P < 0.1$; Tables 12, 13, and 14; Figure 6). Presence and absence of 7 species (5 mammals and 2 amphibians) was associated with Herb—Low shrub/Moss gradient, a gradient of near-ground understory structure (Figure 6E). Along this near-ground structural gradient, presence of 6 species (marsh shrews, Pacific shrews, vagrant shrews, Pacific jumping mice, ensatinas, and western red-backed salamanders) was positively associated with increasing herb cover, whereas that of 1 species (western red-backed voles) was associated positively with increasing low-shrub and moss cover. Furthermore, presence of 4 species was associated with Herb—Low/Tall shrub gradient, a gradient of vertical understory structure. Along this gradient, presence of Trowbridge's shrews and ensatinas was positively associated with increasing mixture of low- and tall-shrub cover, whereas vagrant shrews and tailed frogs were associated positively with increasing herbaceous cover. In addition, presence of ensatinas was associated negatively with a near-ground gradient in increasing moss cover (Herb—Moss gradient; Figure 6G).

At the stand scale, abundances of 7 species (5 species of mammal and 2 species of amphibian) were associated with stand structure (Tables 15, 16, and 17). Six species were associated with changes in the vertical understory structure, Herb—Low/Tall Shrub gradient (Figure 6F) whereas only 1 species (Pacific shrew) was associated with changes in the near-ground understory structure (Low shrub/Moss—Herb gradient, Table 11). In contrast to the microsite scale, more species were associated with the gradient in vertical understory structure than with near-ground understory structure at the stand scale. Trowbridge's shrews, coast moles, deer mice, and rough-skinned newts were more abundant in stands with more complex vertical structure with increasing low-shrub and tall-shrub covers, whereas vagrant shrews and western red-backed salamanders were more abundant in stands with less complex vertical structure with increasing herb cover. Pacific shrews were associated with the gradient in near-ground understory structure and were more abundant in stands with increasing herb cover and decreasing low-shrub and moss cover on the forest-floor. The associations of Pacific shrews and vagrant shrews with herbs and of Trowbridge's shrews with low and tall shrubs were consistent between the microsite and stand scales (Table 18).

Understory Species Composition

Presence of 9 species (7 mammals and 2 amphibians) was associated with the 3 gradients of understory plant community composition at the microsite scale ($P < 0.1$; Tables 12, 13, and 14). Six (5 mammals and 1 amphibians) were associated with

Moist shrub/herb—Dry upland shrub gradient (Figure 6H). Along this gradient, presence of 4 species (deer mice, white-footed voles, western red-backed voles, and ensatinas) were positively associated with increasing cover of upland-shrub species (salal, dwarf Oregongrape, vine maple, bald-hip rose, and oceanspray), whereas 2 species (vagrant shrews and Pacific shrews) were positively associated with increasing cover of shrubs and herbs typically associated with moist habitats (oxalis, mountain huckleberry, salmonberry, miner's lettuce, and false-lily of the valley). Similarly, 6 species were associated with Boreal shrub—Temperate herb gradient (Figure 6I). Along this gradient, Pacific shrews, marsh shrews, vagrant shrews, Baird's shrews, ensatinas, and tailed frogs occurred in microsites with increasing cover of plant species that are characteristic of temperate herb communities (sword fern, thimbleberry, miner's lettuce, oxalis, and hedge nettle). Presence of only 1 species was associated with Vine maple—Bracken fern/Red huckleberry gradient; ensatinas occurred in microsites with increasing cover of vine maple.

At the stand scale, abundances of 9 species (5 species of mammal and 4 species of amphibian) were associated with understory plant community composition ($P < 0.1$; Tables 15, 16, and 17). Four species (3 mammals and 1 amphibian) were associated with Maple/Hemlock seedling/Mountain huckleberry—Ferns/Oxalis gradient. Along this gradient, abundances of vagrant shrews and western red-backed salamanders were associated with increasing cover of oxalis, sword fern, and bracken fern, whereas abundances of western red-backed voles and deer mice were associated

with increasing covers of vine maple, mountain huckleberry, western hemlock seedling, and salal.

Three species of amphibian were associated with Maple/Hemlock seedling—Huckleberry/Oxalis gradient. Pacific giant salamanders and tailed frogs were most abundant in stands with high covers of red huckleberry, mountain huckleberry, and oxalis (mixed tall-shrub herb communities), whereas rough-skinned newts were most abundant in stands with high cover of salal, vine maple, and western hemlock seedling (mixed tall- and low-shrub communities). Five species (4 species of mammal and 1 species of amphibian) were associated with Sword fern/Oxalis—Salal/Oregongrape/Maple/Hemlock seedling gradient. Along this gradient, Pacific shrews and vagrant shrews were most abundant in stands with high cover of sword fern and oxalis, whereas coast moles, deer mice, and rough-skinned newts were most abundant in stands with high cover of salal, Oregongrape, vine maple, and hemlock seedling.

Although the interpretations of axes differed slightly between microsite and stand scales, I found a similarity between the 2 scales in the association of vagrant shrews and Pacific shrews with understories dominated by herbs and in the association of western red-backed voles and deer mice with understories dominated by shrubs (Tables 18 and 19).

Plant Community Composition

Presence of 9 species (6 mammals and 3 amphibians) was associated with the 3 gradients of overall plant community composition (trees, shrubs, and herbs combined) at the microsite scale ($P < 0.1$; tables 12, 13, and 14). All 9 species were associated with the Alder/herb—Douglas-fir/shrub gradient (Figure 6P). More species were associated with this gradient than any other gradient examined (Table 10). Among the 9 species, 7 (Baird's shrews, marsh shrews, Pacific shrews, vagrant shrews, Pacific jumping mice, western red-backed salamanders, and tailed frogs) were positively associated with increasing cover of plant species characteristic of red alder-herb communities (red alder, oxalis, sword fern, sweet-scented bedstraw, and hedge nettle), whereas 2 (western red-backed voles and ensatinas) were positively associated with increasing cover of plant species characteristic of Douglas-fir/shrub communities (Douglas-fir, salal, vine maple, dwarf Oregongrape, and western hemlock seedlings). Two species of amphibian (ensatinas and tailed frogs) were associated with the Mixed conifer/shrub—Alder/shrub gradient (Figure 6O). Along this gradient, ensatinas and tailed frogs were positively associated with increasing covers of red alder and thimbleberry. Only 1 species (vagrant shrews) was associated with the Herb—Low/Tall shrub gradient. Vagrant shrews were associated positively with increasing covers of herbs, such as oxalis, Smith's fairly-bell, and sword fern.

At the stand scale, abundances of 9 species were cumulatively associated with plant community composition ($P < 0.1$; Tables 15, 16, and 17). Eight species were associated with Alder/Sword.fern/Oxalis—Hemlock/Maple/Salal/Seedling gradient.

Along this gradient, Baird's shrews, vagrant shrews, shrew-moles, and western red-backed salamanders were more abundant in stands with higher covers of red alder, sword fern, and oxalis, whereas coast moles, western red-backed voles, deer mice, and rough-skinned newts were more abundant in stands with higher cover of western hemlock, vine maple, salal, and western hemlock seedling. Furthermore, abundances of 3 species were associated with Salal/Oregongrape—Sword fern/Oxalis gradient; Pacific shrews were more abundant in stands with higher covers of sword fern and oxalis, whereas coast moles and rough-skinned newts were more abundant in stands with higher cover of salal and Oregongrape. The associations of Baird's shrews, vagrant shrews, and western red-backed salamanders with red alder communities with herb understory were consistent between the 2 spatial scales (Tables 18 and 20).

Generalists vs. Specialists

Among the habitat generalists I investigated, deer mice were consistently associated with dry microclimate and shrubby understory at both the microsite and stand scales; however, their association with mixed conifer overstory and with an overall plant community type detected at the stand scale was not evident from analyses at the microsite scale (Table 19). These associations of deer mice with greater number of ecological gradients at the larger spatial scale, therefore, followed the predicted pattern of habitat generalist. On the other hand, the habitat association of Trowbridge's shrews with low- and tall-shrubs was almost identical between the microsite and stand scales, and no other association was evident at the stand scale;

therefore, Trowbridge's shrews did not follow the predicted pattern of habitat generalist (Table 18).

Among the 2 habitat specialists, vagrant shrews were consistently associated with red alder overstory and herbaceous understory at both the microsite and stand scales; therefore, they followed the predicted pattern of specialist habitat association (Table 18). Western red-backed voles, on the other hand, were inconsistent in their associations with microclimate, tree species composition, and plant community composition between the microsite and stand scales (Table 19). In addition, their habitat associations with other ecological gradients at the microsite scale were not particularly more evident than those at the stand scale. The pattern I observed for western red-backed voles, therefore, did not follow the pattern predicted for a habitat specialist.

DISCUSSION

Plant Community Composition

Among all the ecological gradients I examined (16 gradients at the microsite scale and 13 gradients at the stand scale), the gradient of overall plant community composition that changes from a red-alder mixed overstory with an herb-dominant understory to a conifer-dominant overstory with a shrub-dominant understory (Alder/Herb—Conifer/Shrub) had the strongest influence on the association of vertebrate species at both microsite and stand scales. At the stand scale, all the stands

were dominated by Douglas-fir, and varying densities of red alder and western hemlock trees mainly contributed to the gradient of overstory tree composition among stands. During early spring, red alder canopies allow more light to reach forest-floor than do conifer canopies; therefore, unique gradients of understory vegetation develop due to differences in shade-tolerance of understory plants in response to varying densities of Douglas-fir and red alder (Pabst and Species 1997). Consequently, at the stand scale, even without considering understory species composition, overstory tree composition (Mixed alder/Douglas-fir—Mixed conifer) alone can describe habitat associations of the same 8 vertebrate species (Baird's shrew, vagrant shrew, shrew-mole, coast mole, western red-backed vole, deer mouse, western red-backed salamander, and rough-skinned newt) that were associated with the Alder/Herb—Conifer/Shrub gradient.

In stands dominated by even-aged, Douglas-fir overstory, red alder patches with herb-dominant understories provided habitat for several species of forest-floor vertebrates especially at the microsite scale in my study. Neitlich and McCune (1997) defined patches of hardwood in conifer-dominant stands as “hardwood gaps,” which supported higher diversity of epiphytic lichen communities than the surrounding conifer matrix in young managed forests of the Oregon Coast Range. Hardwood gaps were also critical foraging habitats for cavity-nesting birds in my study site (Weikel and Hayes 1999), probably due to a high diversity and abundance of arthropod communities associated with red alder trees (Furniss and Carolin 1977, Oboyski 1995). Despite the potential of red alder community as a key wildlife habitat

component in the Pacific Northwest Forests (McComb 1994), only a few researchers have investigated the association of forest-floor vertebrates with red alder community (McComb et al. 1993, Gomez and Anthony 1998). Gomez and Anthony (1996, 1998) found that the total captures of small mammals and amphibians were greater in deciduous stands dominated by red alder and big-leaf maple than in stands dominated by Douglas-fir or shrubs.

The red-alder/herb community was particularly important for insectivores in my study; 5 out of 7 species of insectivores were associated with red-alder/herb communities at either the microsite or stand scale. I hypothesize that these shrews were attracted to a high abundance and diversity of invertebrates in red alder patches and that multiple species may be able to coexist by feeding on different species of invertebrates. Currently, very little is known about abundance and diversity of invertebrate communities associated with the forest-floor of deciduous or red alder forests in western Oregon. Alder communities generally maintain productive detrital invertebrate communities by providing higher abundance of litter with higher nitrogen concentration relative to conifers; therefore, they have the potential to support greater biomass of insectivores (Bormann et al. 1994).

The habitat associations of vagrant shrews, Pacific shrews, marsh shrews, shrew-moles, Pacific jumping mice, and western red-backed salamanders with deciduous microhabitats or stands with a red alder component are consistent with previously reported work in the Oregon Coast Range (Gomez 1992, Gomez and Anthony 1996, 1998). In addition, I found that Baird's shrews and tailed frogs are

associated with the red alder/herb community at the microsite scale. This habitat association of tailed frogs is probably due to the proximity of red alder/herb patches to seeps and streams. The association of Baird's shrews with red alder/herb community has not been documented previously; to my knowledge, this is the first study to quantify habitat association of Baird's shrews at any spatial scale (Verts and Carraway 1998: 48-49).

Microclimate

At the stand scale, the moisture gradient influenced habitat associations of 7 vertebrate species. Among these, 6 were associated with Alder/Herb—Conifer/Shrub gradient, indicating that there is a considerable overlap between the effects of moisture and Alder/Herb—Conifer/Shrub gradients on habitat associations of vertebrates. Because low winter temperature and lack of precipitation during growing season limit the range of red alder and the local distributions of red alder were highly influenced by soil moisture (Harrington et al. 1994: 4), it may be unrealistic to attempt to separate the moisture gradient from the Alder/Herb—Conifer/Shrub gradient. In fact, many of the red alder/herb communities in my study sites occurred near seeps, ephemeral streams, and small perennial streams, suggesting that moisture gradient also was a factor contributing to the development of the Alder/Herb—Conifer/Shrub gradient.

Variation in microclimate, specifically gradients of moisture and temperature within the region, has been described as an underlying factor affecting various ecological processes and biological communities in western Oregon and Washington,

including fire (Agee 1993), accumulation and decay of dead wood (Spies et al. 1988), plant species composition (Spies and Franklin 1991, Ohmann and Spies 1998), and small mammal species composition (Carey and Johnson 1995). Carey and Johnson (1995) suggested that the moisture-temperature gradient and habitat components associated with this gradient interactively influence small mammal community structure across the western hemlock zone from the southern Oregon to the northern Washington. At the spatial scale of their investigation, the moisture-temperature gradient seemed to interact with diversity of conifers rather than the abundance or diversity of deciduous trees (Carey and Johnson 1995). Either deciduous trees, especially red alder, were not abundant in their study sites or the gradient of red alder-conifer, which interacts with the moisture gradient, can only be recognized at a smaller localized spatial scales, such as among different forest stands within northern Oregon coast range. At the scale of microsites within stands, the influence of microclimatic gradients on habitat associations seems to either diminish, due to the small spatial scale, or to be incorporated into the compositional gradients of plant community or other ecological gradients.

In the western hemlock zone of the Pacific Northwest, regional changes in small mammal community structure along the moisture-temperature gradient from warm-dry southern latitudes in Oregon to cold-wet northern latitudes in Washington is characterized by replacement of taxa within genera, increasing species richness, and increasing abundances of shrew-moles, vagrant shrews, and creeping voles (Carey and Johnson 1995). Among the species I investigated, shrew-moles and vagrant shrews

were associated with the microclimates within a stand in a manner that is similar to the pattern of their associations with the regional moisture-temperature gradient; I found that shrew-moles were associated with cool microsites and vagrant shrews with moist microsites. In contrast, creeping voles were associated positively with warm microsites within stands, an association that is completely opposite of the pattern predicted from their association with the regional moisture-temperature gradient. In addition, I found associations of deer mice with dry microclimates at both microsite and stand scales and associations of western red-backed voles with dry and cool microclimates at the stand scale. The association of deer mice with dry microclimate was consistent with their habitat association with xeric habitats in southern Alberta (Morris 1996), and Aubry et al. (1991) also reported a negative association of western red-backed voles with increasing moisture in western Oregon. Furthermore, the consistent habitat association of western red-backed voles to upland areas rather than riparian areas (Doyle 1990, McComb et al. 1993, Gomez and Anthony 1998) may be explained by their preference toward the drier microclimates occurring in upland sites.

Downed Wood

At both microsite and stand scales, abundance of downed wood had less influence on the habitat associations of vertebrates than did microclimate, stand structure, and species composition of plant community. Effects of downed wood abundance on habitat association were particularly weak for small mammals at the stand scale, and none of small mammal species showed the association with downed

wood at this scale. Even western red-backed voles, a species most commonly described their association with downed wood (Doyle 1987, Hayes and Cross 1987, Tallmon and Mills 1994), did not show a strong association with downed wood at both microsite and stand scales. Among those species that showed association with downed wood, only rough-skinned newts were consistently associated with downed wood at both spatial scales. Other species, such as shrew-moles, were associated with downed wood only at the microsite scale. This finding is in contrast to the previous studies that described positive associations of shrew-moles with downed wood at the stand scale across the ecoregions of the Pacific Northwest (Aubry 1991, Carey and Johnson 1995). In the current study, abundance of shrew-moles was associated positively with the red alder/herb community at the stand scale along the compositional gradient of plant community but was not associated with the downed wood gradient.

Although vertebrate species are generally associated with downed wood to varying degrees depending on their life-history requirements (Harmon et al. 1986), their associations might not be evident when the other ecological factors, such as food resources, has an overriding influence on the distribution of species (Mills 1995). The coarse wood in my stands was a legacy from the previous stands and was at medium to advanced stages of decay; therefore, the quality of wood was probably not a factor responsible for the lack of vertebrate association with downed wood. In the case of western red-backed voles, gradients of plant community composition and moisture seem to have overriding influences on their habitat association. The abundance and

distribution of hypogeous mycorrhizal fungi might have influenced the observed habitat associations of western red-backed voles (Mills 1995). It is also possible that the variability of downed wood abundance among stands or within stands might not be significant enough for vertebrate species to select habitats based on the abundance of downed wood at each spatial scale. Considering the extensive fire history and salvage operation following the fire in my study sites, the abundance and distribution of coarse wood might have been relatively uniform among the stands and also across the landscape in the north Oregon Coast Range; however, this variability might have been greater at smaller spatial scale reflecting the complexity in local topography and microclimate. Consequently, many rodent species that perceive habitat at larger spatial scales, such as deer mice and western red-backed voles, did not show strong association with distribution of downed wood within stands. In contrast, species with limited abilities to explore habitat at large spatial scale, such as shrew-moles, might have showed strong association with downed wood at the microsite scale. In any case, it is probably difficult to generalize the association of vertebrates to downed wood from a study conducted at one spatial scale due to the process of downed wood accumulation and decay as well as vertebrate responses operating at multiple spatial scales.

Stand Structure

Stand structure is commonly identified as a factor underlying habitat associations of forest-floor vertebrates at microsite (e.g., Dueser and Shugart 1978,

1979; Morrison and Anthony 1989) and at stand scales (e.g., Carey and Johnson 1995). However, stand structure often is somewhat confounded with other ecological factors, such as local and regional climate (Carey and Johnson 1995). I found greater direct influence of stand structure on habitat association of vertebrates at the microsite scale probably because the gradient of microclimate at the microsite scale was small relative to that at the stand scale. At this scale, the gradients of near-ground understory structure had a greater influence on the association of vertebrates than did the gradient of vertical understory structure. Vertical structural diversity is an important factor affecting habitat association of birds (MacArthur 1958, MacArthur and MacArthur 1961, MacArthur 1964) and some small mammals (Rosenzweig and Winakur 1969); however, at least at the microsite scale, it did not seem to influence habitat association of forest-floor vertebrates in my study sites. The lack of habitat association with vertical understory structure at a microsite scale was previously described for microtine rodents, including western red-backed voles and creeping voles, in the western Oregon Cascade Range (Doyle 1987). Similarly, I did not find associations of rodents with the gradient of vertical understory structure at the microsite scale.

The trend of habitat association between the gradients of near-ground and vertical structure was reversed at the stand scale. At the stand scale, the influence of vertical understory structure was greater than that of near-ground understory structure; however, the gradients of microclimate are also strong and seem to produce confounding effects on habitat association of vertebrates. Therefore, associations of

deer mice and coast moles with mixture of tall and low shrubs probably is closely related to their association with drier habitat, whereas the association of vagrant shrews to herb dominant stand may be related to the moisture of the stand.

Nonetheless, associations of deer mice and Trowbridge's shrews with shrubby habitats at the stand scale are in agreement with findings of Carey and Johnson (1995).

Because forest-floor vertebrates generally lack the ability to use vertical structure directly, their association with vertically complex habitat may simply be an indirect influence of other related ecological factors, such as availability of food resources, predator avoidance, suitable microclimate, and other environmental conditions.

Generalists vs. Specialists, Patterns of Association at Multiple-Spatial Scales

Among the 4 species of mammal I investigated, Trowbridge' shrews and western red-backed voles failed to follow the patterns of habitat association predicted for habitat generalists and specialists. Therefore, the habitat association rules based on the generalist-specialist dichotomy do not always apply for small mammals in managed Douglas-fir dominated forests of the Oregon Coast Range. Instead, there seems to be a dichotomy between rodents and shrews in selecting habitats at multiple spatial scales. I found that 4 shrews (vagrant, Baird's, Pacific, and Trowbridge's shrews) were generally consistent in their habitat association at the microsite and stand scales, whereas 3 rodents (western red-backed voles, deer mice, and Pacific jumping mice) were inconsistent in their habitat associated at the microsite and stand scales (Table 9 and 10). For example, vagrant shrews and Baird's shrews were consistently

associated with plant community characterized by red alder trees in the overstory and ferns and oxalis in the herb-dominated understory at both spatial scales (Tables 12, 15, and 18). Furthermore, Pacific shrews were associated with herbaceous understories dominated by oxalis and sword fern, whereas Trowbridge's shrews were associated with shrub-dominated understories. Among rodents, western red-backed voles and deer mice were associated with cool-dry mixed conifer stands; however, at the microsite scale, western red-backed voles were associated with Douglas-fir dominated plant communities and deer mice did not show associations with tree species composition or plant community composition (Tables 13, 16, and 19). Habitat associations of Pacific jumping mice were also inconsistent at the microsite and stand scales; at the microsite scale, jumping mice were associated with red alder communities with understory dominated by herbs, whereas at the stand scale, they were positively associated with increasing moisture.

This rodent-shrew dichotomy may be a result of differences in the abilities of rodents and shrews to recognize habitats at multiple spatial scales. For example, large-bodied rodents with relatively large home ranges may be able to explore habitats at both large and small spatial scales (Morris 1992, Stapp 1997), whereas small-bodied shrews may only explore habitats at a small spatial scale. Organisms can perceive landscape at a certain range of spatial scales, and the smallest and the largest scales at which they perceive landscape are referred as grain and extent (Kotliar and Wiens 1990). Johnson (1980) first introduced the idea of hierarchical selection of habitat by organisms at multiple spatial scales; however, only a handful of studies to date

described habitat selection of organisms at multiple spatial scales (e.g., Orians and Wittenberger 1991, Morris 1992). Orians and Wittenberger (1991) reported that female yellow-headed blackbirds selected foraging habitat at a larger spatial scale based on the availability food resources, subsequently they select nesting habitat based on vegetation density at a smaller spatial scale. Among small mammals, Morris (1992) reported that deer mice explore habitats at a smaller spatial scale for foraging and at a larger spatial scale for dispersal. Additional studies suggested that population densities for many rodent species in Temperate Zone of Ontario (Morris 1987) and in Chihuahuan Desert of New Mexico (Jorgensen and Demarais 1999) were more closely related to the patterns at a macrohabitat scale, the scale larger than a size of home range of a species, than that at a microhabitat scale. However, there are exceptions, such as northern grasshopper mice (*Onychomys leucogaster*), whose population density was more closely associated with microhabitat characteristics of mounds and burrows rather than macrohabitat characteristics of shrubs and soil types (Stapp 1997). I am not aware of any studies that investigated habitat associations of shrews or other insectivores at multiple spatial scales.

Although to which degree micro- and macro habitat characteristics influence population density of vertebrates in the current study is unknown, I hypothesized possible scenarios of habitat associations at multiple spatial scales based on my observations and previous studies. At the stand scale I found associations of western red-backed voles and deer mice with mixed conifer overstories comprised of Douglas-fir and western hemlock and with shrub understories comprised of vine maple, salal,

and shade-tolerant conifer seedlings. This description of habitat characteristics at the stand level captures aspects of the late successional habitats that are typically described as prime habitat for western red-backed voles (Rosenberg et al. 1994). At the microsite level, however, habitat association of these species were more general, and I could not detect associations of western red-backed voles and deer mice with mixed conifer overstory or associations of deer mice with overall plant community composition at the microsite scale (Table 10). Therefore, I infer that the population densities of western red-backed voles and deer mice in young managed Douglas-fir dominant forests can be explained better by overall characteristics at the stand scale than by availability of suitable habitat patches within stands. In contrast, I infer that population densities of Pacific jumping mouse can be explained better by availability of suitable habitat patches within stands than by overall habitat characteristics at the stand scale. Only at the microsite scale, I could detect associations of Pacific jumping mice with red alder/herb communities, (Table 10) and habitats with herb-dominant understories are generally considered to be typical habitat for this species (Borrecco et al. 1979). The stand scale association of Pacific jumping mice with moist stands may also indicate that this species uses moist macrohabitat for their dispersal or for other life-history functions.

Small-bodied shrews probably perceive landscape at a smaller size of grain and extent than large-bodied rodents; the grain and extent of shrews may not exceed the size of a forest stand. Therefore, for those 3 shrew species that were consistent in habitat association at the stand and microsite scales (Baird's shrews, Trowbridge's

shrews, and vagrant shrews), I conclude that their population densities or abundances are closely related to availability of suitable habitat patches within a stand rather than overall habitat characteristics at the stand scale.

Population densities of Pacific shrews may be also closely related to the availability of suitable habitat patches of red alder/herb communities within stands; however, based on the stand-scale association of this species with herb understory comprised of sword fern and oxalis, I also hypothesize that this species may require wide distribution of herbaceous vegetation throughout the stand for their dispersal or other life history functions.

Unlike other insectivores, habitat associations of shrew-moles were inconsistent at the 2 spatial scales. Despite their relatively small body size, shrew-moles may have the ability to explore habitat at different spatial scales. At the stand scale, shrew-moles were associated with stands with increasing red alder density and covers of sword fern and oxalis in the understory; however, they were associated with cool microclimate and coarse downed wood at the microsite scale. It is not clear whether the population density of this species is closely associated with habitat characteristics measured at the stand scale or those measured at the microsite scale.

CONCLUSIONS

Habitat associations of generalist and specialist species at multiple spatial scales did not consistently follow the patterns predicted from their theoretical foraging strategies. Instead, there seem to be differences in habitat selection at multiple spatial scales between rodents and insectivores, particularly shrews.

In managed Douglas-fir-dominant forests in the stem-exclusion stage, a gradient of plant community composition that changes from a red alder-mixed overstory with understory dominated by herbaceous species (such as sword fern and oxalis) to a exclusively conifer overstory with understory dominated by shrub species (such as salal, Oregongrape, and vine maple) had a stronger influence on vertebrate associations than did gradients in stand structure or abundance of downed wood. This influence was consistent at both the microsite and stand scales. More species, particularly insectivores, were associated with red alder/herb community than with conifer/shrub community. Therefore, conservation and management of red alder patches in Douglas-fir-dominant forests have the potential to play a role in maintaining biodiversity across the landscape of the Oregon Coast Range.

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CHAPTER 4: CONCLUSIONS

Thinning did not have substantial detrimental effects on any of the species I investigated and had positive effects on several, particularly those species that are typically associated with early seral habitats, including the creeping vole, Pacific jumping mouse, and deer mouse. In the long term, thinning of stands in the stem-exclusion stage of stand development also has the potential to improve habitat quality for the western red-backed vole, a species generally considered to be a late-seral or interior-forest associate (Rosenberg et al. 1994, Mills 1995). Thinning may have potential negative effects on abundance of western red-backed salamander in the long term. However, my analysis and a previous study (Gomez and Anthony 1996) of habitat association indicated that western red-backed salamanders are more closely associated with moist red-alder/herb communities than with dry conifer/shrub communities in the Oregon Coast Range. Therefore, thinning of conifers while preserving hardwood patches within a stand may protect suitable habitat for red-backed salamanders as well as other species associated with hardwood patches. At least in the short term, the effects of thinning on abundance of vertebrates appear to be independent of thinning intensity within the range of densities examined in this study; however, reproductive responses of some small mammals, such as creeping voles and deer mice, to thinning may be influenced by thinning intensities. We still lack information on the long-term effects of heavy thinning on abundance and reproduction of forest-floor vertebrates. Therefore, this point should be addressed in future study.

In managed Douglas-fir-dominant forests in the stem-exclusion stage, a gradient of plant community composition that changes from red alder overstory with understory dominated by herb species to conifer overstory with understory dominated by shrub species (Red alder/Herb—Conifer/Shrub gradient) had a stronger influence on vertebrate association than did in stand structure or abundance of downed wood; this influence was consistent at both the microsite and stand scales. At the stand scale, a gradient of tree species composition, the Red alder—Mixed conifer gradient, alone could explain habitat associations of the same species that were associated with Red alder/Herb—Conifer/Shrub gradient. This information may be useful in predicting vertebrate community composition without intensive field habitat sampling of understory vegetation; composition of overstory tree species within a stand could be determined easily from aerial photos or satellite imagery in many cases. The influence of the moisture gradient also considerably overlapped with the Red alder/Herb—Conifer/Shrub gradient at the stand scale but not at the microsite scale. More species, particularly insectivores, were associated with red alder/herb community than with conifer/shrub community at microsite scale. Therefore, conservation and management of patches of red alder in forests dominated by Douglas-fir may play an important role in maintaining biodiversity across the landscape of the Oregon Coast Range.

Habitat associations of known generalist and specialist species at multiple spatial scales did not completely follow the patterns of association predicted from their theoretical foraging strategies. Instead, there seems to be differences in habitat selection at multiple spatial scales between rodents and shrews.

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APPENDICES

APPENDIX 1

Mean numbers of captures per 100 trap nights (TN), 95% confidence intervals, and *P*-values from 2 orthogonal contrasts with repeated measures ANOVA comparing abundance of forest-floor vertebrates between control (C) and thinned (T) stands before and after experimental thinning of 35-45 year old Douglas-fir forests, northern Oregon Coast Range, 1994-1996. The contrast "Pre vs. Post" tested the null hypothesis of no difference in change in number of captures per 100 TN before and after treatment between thinned and control stands. The contrast "95 vs.96" tested the null hypothesis of no difference in changes in number of captures per 100 TN from 1995 to 1996 between control and thinned stands.

		Pre-treatment ^a		Post-treatment ^b		<i>P</i> -values	
		\bar{x}	95% CI	\bar{x}	95% CI	Pre vs. Post	95 vs.96
Small Mammals							
Total mammal	C	12.47	8.82-17.63	10.56	8.27-13.49	0.965	0.591
	T	11.95	9.35-15.26	10.23	8.60-12.16		
Baird's shrew	C	0.83	0.40-1.38	0.47	0.19-0.81	0.166	0.874
	T	0.64	0.34-1.00	0.68	0.43-0.97		
Marsh shrew	C	0.23	0.11-0.36	0.23	0.14-0.32	0.868	0.326
	T	0.18	0.09-0.27	0.19	0.12-0.25		
Pacific shrew	C	1.51	0.98-2.05	1.58	1.19-1.98	0.413	0.563
	T	1.76	1.37-2.16	1.52	1.22-1.83		
Trowbridge's shrew	C	7.95	5.60-10.31	7.02	5.77-8.27	0.913	0.665
	T	7.17	5.49-8.86	6.07	5.16-6.99		
Vagrant shrew	C	0.35	0.00-0.69	0.31	0.00-0.61	0.979	0.774
	T	0.49	0.18-0.80	0.44	0.16-0.73		
Shrew-mole	C	0.32	0.05-0.59	0.43	0.18-0.68	0.124	0.375
	T	0.35	0.12-0.57	0.20	-0.00-0.41		

APPENDIX 1 (Continued).

Coast mole	C	0.07	0.02-0.12	0.08	0.04-0.11	0.574	0.903
	T	0.04	0.00-0.07	0.02	0.00-0.05		
Western red-backed vole	C	0.34	-0.02-0.84	0.34	-0.01-0.81	0.072	0.094
	T	0.54	0.17-1.01	0.23	-0.05-0.59		
White footed-vole	C	0.07	0.02-0.13	0.02	-0.03-0.06	0.048	0.764
	T	0.05	0.01-0.09	0.06	0.03-0.09		
Creeping vole	C	0.24	0.08-0.42	0.15	-0.01-0.34	0.058	0.268
	T	0.13	0.03-0.25	0.26	0.13-0.40		
Deer mouse	C	0.46	0.04-0.88	0.35	0.07-0.63	0.031	0.935
	T	0.54	0.22-0.85	0.83	0.61-1.05		
Pacific jumping mouse	C	0.13	0.03-0.24	0.19	0.02-0.39	0.897	0.098
	T	0.10	0.03-0.17	0.17	0.04-0.30		
Amphibians							
Total amphibian	C	0.43	0.19-0.96	0.43	0.19-0.93	0.093	0.026
	T	0.35	0.20-0.62	0.24	0.13-0.41		
Ensatina	C	0.09	0.01-0.19	0.10	0.02-0.19	0.836	0.019
	T	0.08	0.01-0.14	0.09	0.03-0.16		
Western red-backed salamander	C	0.15	0.04-0.27	0.12	0.03-0.22	0.798	0.135
	T	0.09	0.01-0.17	0.05	-0.02-0.11		

^a Mean and 95% CI for 1994.

^b Mean and 95% CI for 1995 and 1996 combined.

APPENDIX 2: Interpretation of Ordination Axes

Microclimate

Two gradients of microclimatic factors, temperature and moisture, were identified at both the microsite and the stand scales. At the microsite scale within stands, the first axis was a temperature gradient that was correlated positively with cover of cool-site indicators, including queen cup beedlily ($r = 0.258$), big huckleberry ($r = 0.467$), and dogwood bunchberry ($r = 0.246$), and it was correlated negatively with cover of warm-site indicators, including baldhip rose ($r = -0.476$), trailing blackberry ($r = -0.396$), dwarf Oregon grape ($r = -0.254$), red huckleberry ($r = -0.267$), and salmonberry ($r = -0.117$). The second axis was a moisture gradient and was correlated positively with cover of dry-site indicators, including dwarf Oregon grape ($r = 0.852$) and baldhip rose ($r = 0.364$), and was correlated negatively with cover of moist-site indicators including devil's club ($r = -0.139$), salmonberry ($r = -0.412$), lady fern ($r = -0.333$), stream violet ($r = -0.314$), and deer fern ($r = -0.218$).

Similarly, at the stand scale, the first axis was a moisture gradient and was correlated positively with the cover of a dry site indicator species, Oregon grape ($r = 0.382$), whereas it was correlated negatively with cover of 2 moisture indicators, salmonberry ($r = -0.673$) and devil's club ($r = -0.30$). The second axis was a temperature gradient and was correlated positively with cover of 2 cool-site indicator species, mountain huckleberry ($r = -0.801$) and bunchberry ($r = -0.721$).

Downed wood

The gradients of downed wood were primarily related to abundance of downed wood in different size classes rather than to abundance in different decay classes at both the microsite and the stand scales. At the microsite scale within stands, 3 axes were identified as gradients of downed wood abundance. The first axis was a gradient of small wood abundance that was correlated negatively with the length of small wood in each decay classes (decay 1, $r = -0.629$; decay 2-3, $r = -0.517$; decay 4-5, $r = -0.269$) and all decay classes combined ($r = -0.799$). Additionally, this gradient was highly correlated with the cumulative length of downed wood in all size and decay classes combined ($r = -0.739$). The second axis was a gradient of large wood abundance that was correlated negatively with lengths of large wood in each decay class (decay 2-3, $r = -0.792$; decay 4-5, $r = -0.290$) and all decay classes combined ($r = -0.792$). The second axis was also correlated positively with lengths of small wood in 2 decay classes (decay 1, $r = 0.236$; decay 2-3, $r = 0.346$) and all decay classes combined ($r = 0.426$); therefore, as the abundance of large wood increased, the abundance of small wood decreased along this axis. The third axis was mainly a gradient of abundance in medium wood and was correlated positively with lengths of medium wood in 2 decay classes (decay 2-3, $r = 0.512$; decay 4-5, $r = 0.784$) and all decay classes combined ($r = 0.775$).

At the stand scale, 2 axes of downed wood abundance were identified. The first axis was a gradient for abundance in both medium and large wood and was correlated positively with the length of medium ($r = 0.909$) and large wood ($r =$

0.811). Furthermore, it was correlated positively with the cumulative length of downed wood in all size classes combined ($r = 0.938$). The second axis, on the other hand, was a gradient of abundance in small wood and correlated positively with the length of small wood ($r = 0.938$).

Tree Species Composition

The gradients of tree species composition were characterized by changes in tree species composition from single-species communities comprised of Douglas-fir to multi-species communities comprised of mixture of Douglas-fir trees and increasing densities of red alder, western hemlock, or noble fir trees.

At the microsite scale, 3 ordination axes were identified; however, only the first 2 of the 3 axes represented compositional gradients. The first axis was a gradient from tree-species compositions dominated by Douglas-fir to those dominated by red alder was correlated positively with stem densities of Douglas-fir in the 3 largest DBH classes (20-30 cm, $r = 0.225$; 30-40 cm, $r = 0.443$; 40-50 cm, $r = 0.370$) and correlated negatively with stem densities of red alder in all DBH classes (0-10 cm, $r = -0.564$; 10-20 cm, $r = -0.753$; 20-30 cm, $r = -0.808$; 30-40 cm, $r = -0.694$). The second axis was a compositional gradient with increasing densities of western hemlock trees and correlated positively with stem densities of western hemlock in all DBH classes (0-10 cm, $r = 0.734$; 10-20 cm, $r = 0.687$; 20-30 cm, $r = 0.605$; 30-40 cm, $r = 0.473$). Furthermore, it was also correlated positively with densities of shade tolerant conifer seedlings, including western hemlock ($r = 0.734$), noble fir ($r = 0.590$) and western

redcedar ($r = 0.424$). The third axis was a gradient of increasing density of Douglas-fir trees in large DBH classes and was correlated negatively with densities of Douglas-fir trees in the 2 largest DBH classes (40-50 cm, $r = -0.319$; 50-60 cm, $r = -0.707$). The regeneration of Douglas-fir seedlings also increased ($r = -0.408$) as the density of large Douglas-fir trees increased along the third axis.

At the stand scale, 2 ordination axes were identified. The first axis was a gradient of compositional change at the stand scale from overall tree species compositions dominated by Douglas-fir trees to those with increasing densities of western hemlock trees and was correlated positively with densities of western hemlock trees > 10 cm in DBH ($r = 0.521$) that was correlated negatively with densities of Douglas-fir trees in > 10 cm in DBH ($r = -0.637$). The second axis was a gradient of compositional change in Douglas fir dominant stands from species compositions with increasing red alder trees in one direction to those with increasing western hemlock trees in the other direction. This axis was correlated negatively with densities of western hemlock in 2 DBH classes (0-10cm, $r = -0.941$; 10-70 cm, $r = -0.967$), while it was correlated positively with densities of red alder in 2 DBH classes (0-10 cm, $r = 0.635$; 10-70 cm, $r = 0.828$).

Stand Structure

The gradients of stand structure represented changes in at least 2 fundamental structural components of habitat: changes in understory structure near-ground and changes in vertical complexity of understory structure. At the microsite scale, 3 ordination axes were identified. The first axis was a gradient of vertical structural change in the understory from structurally simple microsites dominated by herbs to more complex microhabitats dominated by a mixture of low- and tall-shrubs that was correlated negatively with total herb cover ($r = -0.593$) and correlated positively with cover of low ($r = 0.738$) and tall shrubs ($r = 0.864$). The second axis was a gradient of near-ground understory structure from microsites with ground cover dominated by herbs to microsites with ground cover dominated by a mixture of low-shrub and moss and was correlated negatively with total herb cover ($r = -0.752$) and correlated positively with cover of low shrubs ($r = 0.494$) and moss ($r = 0.330$). The third axis was a gradient of increasing moss cover accompanied by increasing tall-shrub cover and was correlated negatively with moss cover ($r = -0.796$) and with tall shrub cover ($r = -0.350$).

Similarly, at the stand scale, the first axis was a gradient of vertical structural change of understory from stands with simple understory structure dominated by herb to stands with more complex understory structure comprised of mixture of low-shrubs and tall shrubs and was correlated negatively with herb cover ($r = -0.92$) and correlated positively with cover of low ($r = 0.863$) and tall shrubs ($r = 0.885$).

Additionally, overstory vegetation cover was correlated negatively with the first axis ($r = -0.529$), indicating that herbaceous vegetation was generally associated with closed canopy forests whereas a complex mixture of low- and tall-shrubs was associated with open-canopy forests. The second axis was a gradient of near-ground understory structure from stands with understory dominated by herb cover to stands with understory dominated by mixture of low shrub and moss covers and this axis was correlated positively with herb cover ($r = 0.347$) and correlated negatively with moss ($r = -0.704$) and low shrub ($r = -0.771$) cover.

Understory Composition

The gradients in understory composition represented changes in species composition of shrubs and herbs among microsites within stands and among the stands. Three ordination axes were identified at the microsite scale. The first axis was a gradient in understory composition that changes from upland shrub communities that characterize warm and dry-upland microsites to mixed shrub-herb communities that characterize moist microsites. This axis was correlated positively with covers of 5 shrub species (salal, $r = 0.658$; Oregon grape, $r = 0.478$; vine maple, $r = 0.396$; bald-hip rose, $r = 0.413$; ocean spray, $r = 0.329$) and correlated negatively with covers of 2 shrub species (mountain huckleberry, $r = -0.369$; salmonberry, $r = -0.302$) and of 3 herbaceous species (oxalis, $r = -0.697$; Siberian miner's lettuce, $r = -0.332$; and false-lily of the valley, $r = -0.314$). The second axis was a gradient in understory

composition that changes from boreal shrub communities to temperate herb communities and was correlated positively with cover of sword fern ($r = 0.552$), Siberian miner's lettuce ($r = 0.482$), oxalis ($r = 0.457$), hedge nettle ($r = 0.427$), and thimbleberry ($r = 0.357$) and correlated negatively with cover of mountain huckleberry ($r = -0.565$), twin flower ($r = -0.502$), salal ($r = -0.483$), dwarf Oregon grape ($r = -0.491$), and bunchberry ($r = -0.408$). The third axis was a gradient of increase in cover of vine maple ($r = -0.719$) in one direction and increase in cover of bracken fern ($r = 0.331$), red huckleberry ($r = 0.316$), and trailing blackberry ($r = 0.301$) in the other direction.

Three ordination axes that represent gradients in understory composition were also identified at the stand scale. Among the 3, the first axis was a gradient in understory composition that changes from herb communities dominated by oxalis, sword fern, and bracken fern to shrub communities dominated by vine maple, mountain huckleberry, western hemlock seedling, and salal. This axis was correlated positively with cover of oxalis ($r = 0.614$), sword fern ($r = 0.769$), and bracken fern ($r = 0.603$) and correlated negatively with cover of vine maple ($r = -0.686$), mountain huckleberry ($r = -0.542$), western hemlock seedling ($r = -0.685$), and salal ($r = -0.494$). The second axis was a gradient of compositional change from mixed tall shrub and herb communities dominated by mountain huckleberry, red huckleberry, and oxalis to mixed tall- and low-shrub communities dominated by salal, vine maple, and western hemlock seedling. This axis was correlated positively with cover of mountain huckleberry ($r = 0.719$), red huckleberry ($r = 0.510$), oxalis ($r = 0.731$) and correlated

negatively with cover of vine maple ($r = -0.740$), western hemlock seedling ($r = -0.425$), and salal ($r = -0.438$). The third axis was a gradient of compositional change from herb communities dominated by sword fern and oxalis to mixed low- and tall-shrub communities dominated by Oregon grape, salal, vine maple, and western hemlock seedling; it was correlated negatively with cover of sword fern ($r = -0.771$) and oxalis ($r = -0.817$) and correlated positively with cover of Oregon grape ($r = 0.710$), salal ($r = 0.937$), vine maple ($r = 0.541$), and western hemlock seedling ($r = 0.645$).

Plant Community Composition

The gradients in plant community composition represented changes in species composition of plants of all forms, including trees, tall and low-shrubs, and herbs, among microsites and among stands. Three ordination axes were identified at the microsite scale. The first axis was a gradient in species composition of understory plants that changes from communities dominated by herbaceous species to communities dominated by shrub species. This axis was correlated negatively with covers of 3 herbaceous species; oxalis ($r = -0.482$), Smith fairlybell ($r = -0.330$), and sword fern ($r = -0.302$); and correlated positively with covers of 4 shrub species; salal ($r = 0.634$), Dwarf Oregon grape ($r = 0.561$), red huckleberry ($r = 0.473$), mountain huckleberry ($r = 0.382$), and bunchberry ($r = 0.306$). The second axis was a gradient in plant species composition that changes from communities of mixed conifer overstory with mixed herb-shrub understory to communities of red alder overstory

with shrub understory. This axis was correlated negatively with cover of noble fir ($r = -0.585$), western hemlock ($r = -0.465$), mountain huckleberry ($r = -0.609$), twin flower ($r = -0.556$), vanilla leaf ($r = -0.363$), bunchberry ($r = -0.356$), three-leaved anemone ($r = -0.309$), and sweet cicely ($r = -0.304$) and correlated positively with cover of thimbleberry ($r = 0.426$) and red alder ($r = 0.337$). The third axis was a gradient of plant species composition that changes from communities of red alder with herb-dominated understory to communities of Douglas-fir with shrub dominated understory. This axis was correlated negatively with cover of red alder ($r = -0.776$), oxalis ($r = -0.628$), sword fern ($r = -0.521$), sweet-scented bedstraw ($r = -0.418$), and hedge nettle ($r = -0.417$) and correlated positively with cover of Douglas-fir ($r = 0.342$), salal ($r = 0.506$), vine maple ($r = 0.483$), dwarf Oregon grape ($r = 0.364$), and western hemlock seedling ($r = 0.347$).

Two axes were identified at the stand scale. The first axis was a gradient of community composition that changes from communities of herbs dominated by sword fern and oxalis to communities of shrubs dominated by salal and Oregon grape. This axis was correlated positively with covers of sword fern ($r = 0.682$) and oxalis ($r = 0.580$) and correlated negatively with covers of salal ($r = -0.868$) and Oregon grape ($r = -0.832$). Increasing western hemlock canopy was also negatively associated with this axis ($r = -0.466$) thereby indicating that it was positively associated with increasing salal and oxalis. The second axis is a gradient of community composition that changes from communities of red alder with understory dominated by herb to communities of mixed conifer with increasing western hemlock overstory and with

understory dominated by mixture of tall and low shrubs. This axis was correlated negatively with red alder overstory ($r = -0.840$), sword fern ($r = -0.843$) and oxalis ($r = -0.924$) and was correlated positively with western hemlock overstory ($r = 0.744$), vine maple ($r = 0.853$), salal ($r = 0.749$), and western hemlock seedling ($r = 0.836$).