Small Mammal Habitat Associations at Patch and Landscape Scales in Oregon

Karl J. Martin and William C. McComb

ABSTRACT. To investigate multiscale habitat associations, we examined patterns of capture rates of small mammals in thirty 250–300 ha landscapes in the central Oregon Coast Range. We compared capture rates of 14 species within ≥7 patch types to expected capture rates based on sampling effort. We used landscape level capture rates to test for associations with percent area (composition) and pattern indices at the landscape scale. Capture rates of 10 of 14 small mammal species were higher in conifer and/or mixed large sawtimber patch types. At the landscape scale, capture rates of 6 of 14 species of small mammals were positively associated with the area of patch types. The pattern of patches on the landscape may influence the distribution of 5 small mammal species in this region. We conclude that some small mammals may respond to landscape pattern and/or composition, while other small mammals may not respond to either landscape pattern or composition. Our results suggest that mature forest habitat, patch richness, pattern, and composition are key landscape features that should be considered in management plans, particularly when biodiversity of forest floor mammals is a management objective. For. Sci. 48(2):255–264.

Key Words: Biodiversity, forest, pattern, composition, richness.

Small mammals are integral components of forest ecosystems because they are predators, insectivores, and prey. Small mammals contribute to forest regeneration by dispersing seeds and mycorrhizal fungal spores (Ure and Maser 1982, Hayes et al. 1986). Changes in abundances of small mammals as a result of human alteration of habitat may alter some ecosystem processes and lead to changes in productivity, sustainability, and biodiversity (Peterson et al. 1998).

The primary anthropogenic alteration of forested ecosystems in the Pacific Northwest has been the conversion of old and mature forests to a variety of younger stands (Franklin and Forman 1987, Cohen et al. 1995). Over the past 50 yr, landscapes in the central Oregon Coast Range became increasingly dominated by younger patches of forest with lesser amounts of old and mature forest. Once relatively homogeneous landscapes became increasingly fragmented (Harris 1984, p. 25–43, Impara 1997). This change has been associated with adverse effects on some vertebrate populations (Forsman et al. 1977, 1984, Thomas et al. 1993, Gomez and Anthony 1996). There have been few studies in the Pacific Northwest that have evaluated the effects of fragmentation on small mammals, and most studies regarding habitat relationships and vertebrates have been either microhabitat or patch-level studies.

We compared the relative abundance of small mammals among 7 to 11 patch types. Our first goal was to determine if...
the distribution of small mammals differed among patch types in the central Oregon Coast Range and, more specifically, identify species associated with patches of mature forest. This information would prove useful in restoration of old-growth and late-seral forests (USDA Forest Service and USDI Bureau of Land Management 1994, Marcot and Thomas 1997).

Species may respond differently to similar habitat features at different scales, so once we determined associations between species and patch types, our second goal was to assess associations between capture rates and the composition and pattern of the selected patch type(s) on the landscapes sampled. We hypothesized that species may respond to different features at the patch- and landscape-scales. Composition is the proportion of selected patch types present on a landscape, while the pattern of patch types consists of several indices characterizing edge, core areas, patches, and shape of patches within the landscapes. For example, species associated with interior, mature forest with large core areas or low edge density would be associated with landscapes dominated by mature forest in a large contiguous configuration.

**Study Area**

We sampled landscapes in the Nestucca River, Lobster Creek, and Drift Creek basins in the central Oregon Coast Range (Figure 1) (McGarigal and McComb 1995). A stand replacement fire burned most of the study area in the mid-1800s, and the area was reforested through natural regeneration (Spies and Cline 1988, Impara 1997). Over the past 40 yr, forest managers have used 10 to 20 ha clearcuts interspersed with uncut forest areas of equal or larger size to improve slash disposal, forest regeneration, and development of access roads (Smith et al. 1996, p. 316–328; Franklin and Forman 1987). This has resulted in highly fragmented landscapes with bimodal age distributions of trees, <40 yr of age and 120–140 yr of age. Mature forests included isolated patches of old growth [multistory canopy, mean diameter at breast height (dbh) >81 cm, >200 yr old]. Land ownership is dominated by public agencies, including the USDA Forest Service, USDI Bureau of Land Management, and the Oregon Department of Forestry. A small portion of the total area sampled was in private ownership, primarily industrial forestland dominated by younger forest stands (<40 yr).

Overstory vegetation was dominated by Douglas-fir (Pseudotsuga menziesii), with lesser amounts of western hemlock (Tsuga heterophylla), Sitka spruce (Picea sitchensis), western redcedar (Thuja plicata), red alder (Alnus rubra), and bigleaf maple (Acer macrophyllum). Understory vegetation was primarily composed of salmonberry (Rubus spectabilis), salal (Gaultheria shallon), vine maple (Acer circinatum), sword fern (Polystichum munitum), devil’s club (Oplopanax horridus), and thimbleberry (Rubus parviflorus). The central Oregon Coast Range has cool, dry summers and mild, wet winters receiving 170–300 cm of annual precipitation. Temperatures in the central Oregon Coast Range rarely rise above 27˚C or drop below 0˚C (Franklin and Dyrness 1973, Brown and Curtis 1985).

**Methods**

**Study Design**

We selected ten 250 to 300 ha landscapes in each of three basins (Lobster Creek, Drift Creek, Nestucca River) located in Benton, Tillamook, Yamhill, and Lincoln counties in the central Oregon Coast Range (n = 30 landscapes; Figure 1). Each landscape was traversed by a third- or fourth-order stream and was comprised of multiple patch types. Landscapes were selected based on the percentage of the landscape in mature forest (mean dbh >53 cm) condition (0, 20, 40, 60, 80 or 100%) and density of mature forest edges (i.e., high or low fragmentation level) (Figure 2). McGarigal and McComb (1995) previously used these sites to assess relationships between observations of avifauna and landscape patterns. Subbasins were used to

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**Figure 1.** Location of Drift Creek, Lobster Creek, and Nestucca River basins in the central Oregon Coast Range. Small mammals and amphibians were trapped in April–May 1995 and 1996 (adapted from Brooks 1997).

**Figure 2.** Schematic representation of study design replicated over the Nestucca River, Drift, and Lobster Creek basins in the central Oregon Coast Range. Small mammals and amphibians were trapped during April–May 1995 and 1996 (adapted from McGarigal 1993).
delineate landscapes because watersheds often are used as management units. Landscapes were v-shaped with surface water limited to the stream channel.

**Patch Delineations**

Vegetation mapping was based on a classification scheme used for wildlife habitat classification in western Oregon and Washington (Hall et al. 1985). Using a stereoscope we delineated patch types from aerial photos and then evaluated for consistency with field-based observations. Five nonforested and 22 forested patch types were identified. The nonforested patch types were brush fields, grass-forb dry hillsides, hardwood shrubby wetlands, herbaceous wetlands, and open water. Forested patch types were based on plant community (conifer, hardwood, mixed), seral condition (grass/forb, shrub, sapling, pole, small sawtimber, large sawtimber), and canopy closure (closed, open) for sapling and pole seral conditions (see Table 1 for definitions). Minimum patch size was 0.79 ha and ≥50 m at its narrowest width.

**Landscape Analyses**

We used a Geographic Information System (GIS) to reclassify previously digitized landscapes from multiple patch types into three new patch types based on patch selection for each species (>, <, or = to expected). Patch weights were based on the level of patch selection for each species. All patches in which a species was captured more frequently than expected based on trapping effort were considered one patch type and given a weight of 1.0. Similarly, patches where we could not detect a difference in capture rates were grouped together and given a weight of 0.5, and patches in which a species was captured less frequently than expected based on trapping effort were given a relative weight of 0.0. These relative weights were used to quantify edge contrast indices in FRAGSTATS (McGarigal and Marks 1995). We reclassified landscapes with FRAGSTATS to generate 29 indices (Table 2) representing patch characteristics, edge distances, shape indices, and core indices for each landscape (McGarigal and Marks 1995).

Since resource managers rarely manage landscapes based on individual species, we assessed potential factors influencing species richness at the landscape scale based on our single species analyses. Specifically, we assessed associations between species richness and the percentage of mature forest and patch richness on the landscape based on our patch scale results. These two factors appear to be of primary importance at the patch scale and were, therefore, logical variables to assess influences on species richness at the landscape scale.

**Small Mammal Trapping**

Within each landscape, line transects were located at 400 m intervals perpendicular to each stream with pitfall trapping stations (hereafter stations) located at 200 m intervals along each transect. The first transect was randomly located within each landscape, with subsequent transects located in reference to the first. This resulted in a 200 × 400 m grid pattern with 31–38 stations in each landscape. There was an average of 5.8 (range 1–11) stations per transect and an average of 6.1 (range 4–8) transects per landscape depending on the shape and size of the landscape. A total of 1,032 trapping stations were distributed across the 30 landscapes.

Pitfall trapping techniques were used in an effort to get a complete sample of forest floor vertebrates and assess habitat associations (Block et al. 1998). At each station, one pitfall trap was established in each cardinal direction 10 m from the center point of the grid station (four traps per station) (Bury and Corn 1987, McComb et al. 1991). Pitfall traps were constructed from two #10 cans taped together with the top and bottom removed from the top can and the top removed from the bottom can. A funnel was placed inside the top of the trap to prevent escapes. Two holes about 4 mm in diameter were drilled in the wall of the trap about 7.5 cm from the bottom to allow drainage. Traps were buried level or slightly below ground level.

Traps were opened for 31 days at the Drift Creek sites during April–May 1995 and 31 days at the Nestucca River and Lobster Creek sites during April–May 1996. Small mammals were bagged, frozen, and identified in the laboratory. Small mammals were disseminated to museums at the University of Minnesota, University of Massachusetts, Oregon State University, and the University of Alaska–Fairbanks. The Institutional Animal Care and Use Committee at Oregon State University reviewed and approved our methodology before collection of animals.

**Statistical Analyses**

Vertebrate capture rates were compared among the 13 most abundant patch types (Table 1) depending on the total number of captures for each species (species with >100 captures were compared across 11 patch types and species

### Table 1. Definition of patch types delineated across 30 landscapes in the central Oregon Coast Range and used in comparisons of small mammal capture rates. Pitfall trapping was conducted for 31 days in April–May 1995 and 1996.

<table>
<thead>
<tr>
<th>Patch type</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conifer, large sawtimber</td>
<td>&gt;70% conifer composition, &gt;20% cover, &gt;53.3 cm mean dbh</td>
</tr>
<tr>
<td>Mixed, large sawtimber</td>
<td>&lt;70% conifer or hardwood composition, &gt;20% cover, &gt;53.3 cm mean dbh</td>
</tr>
<tr>
<td>Hardwood, large sawtimber</td>
<td>&gt;70% hardwood composition, &gt;20% cover, &gt;53.3 cm mean dbh</td>
</tr>
<tr>
<td>Conifer, closed pole</td>
<td>&gt;70% conifer composition, 70–100% crown cover, &gt;3 m mean ht, 10.2–30.5 cm mean dbh</td>
</tr>
<tr>
<td>Conifer, open pole</td>
<td>&gt;70% conifer composition, 20–70% crown cover, &gt;3 m mean ht, 10.2–30.5 cm mean dbh</td>
</tr>
<tr>
<td>Mixed, closed pole</td>
<td>&lt;70% conifer or hardwood composition, 70–100% crown cover, &gt;3 m mean ht, 10.2–30.5 cm mean dbh</td>
</tr>
<tr>
<td>Mixed, open pole</td>
<td>&lt;70% conifer or hardwood composition, 20–70% crown cover, &gt;3 m mean ht, 10.2–30.5 cm mean dbh</td>
</tr>
<tr>
<td>Conifer, open sapling</td>
<td>&gt;70% conifer composition, 20–70% crown cover, &gt;3 m mean ht, 2.5–10.2 cm mean dbh</td>
</tr>
<tr>
<td>Mixed, open sapling</td>
<td>&lt;70% conifer or hardwood composition, 20–70% crown cover, &gt;3 m mean ht, 2.5–10.2 cm mean dbh</td>
</tr>
<tr>
<td>Conifer, open sapling/pol e</td>
<td>&gt;70% conifer composition, 20–70% crown cover, &gt;3 m mean ht, 2.5–30.5 cm mean dbh</td>
</tr>
<tr>
<td>Mixed, open sapling/pole</td>
<td>&lt;70% conifer or hardwood composition, 20–70% crown cover, &gt;3 m mean ht, 2.5–30.5 cm mean dbh</td>
</tr>
<tr>
<td>Brush and shrub sites</td>
<td>&lt;20% in trees, &lt;3 m mean ht, &lt;2.5 cm mean dbh, &gt;40% crown cover in shrubs or brush</td>
</tr>
<tr>
<td>Mixed, grass-forb</td>
<td>&lt;20% conifer or hardwood composition, &lt;3 m mean ht, &lt;2.5 cm mean dbh, &gt;40% crown cover any ht</td>
</tr>
</tbody>
</table>
with <100 captures were compared across 7 patch types). GIS was used to classify stations into either single or multiple patch types based on the percent composition of each patch type within a 50 m radius (0.79 ha) surrounding each station. Patch types consisting of <25% of a station’s total patch composition (<0.20 ha) were eliminated and reclassified to the dominant patch type(s) comprising the 50 m radius surrounding the station (n = 251 stations).

Selection or avoidance of a patch type was defined based on a comparison of capture rates of individuals in each patch type to what would be expected at random. Simultaneous confidence intervals based on multinomial probabilities were used to facilitate these comparisons (Bailey 1980, Cherry 1996). We used 95% confidence intervals around the expected use value (no. of stations in a particular patch type / total no. of captures of the same species in all patches) for each patch type. If a species’ actual use (no. of captures for a species in a particular patch type / total no. of captures of the same species in all patches) was greater than the upper confidence interval then we concluded that the species “selected” that patch type. If a species’ actual use was more than the lower confidence interval and less than the upper confidence interval then we could not determine selection or avoidance of that patch type. If a species’ actual use was less than the lower confidence interval then the species “avoided” that particular patch type.

We combined conifer shrub, hardwood shrub, brush fields, and mixed shrub patch types to form a new patch type called brush-shrub. Patch types covering <15 total stations (conifer closed sapling, conifer small sawtimber, grass-forb dry hillsides, hardwood closed pole, hardwood closed sawling, hardwood open pole, hardwood open sawling, hardwood small sawtimber, hardwood-shrubby wetlands, herbaceous wetlands, mixed closed sawling, mixed small sawtimber, and open water) and all stations composed of two or more patch types were eliminated to meet sample size assumptions (Cherry 1996). This reduced the number of trapping stations in the analyses to 820 and the number of patch types to 11 for species with >100 total captures.
Species were divided into two categories: those with >100 total captures (n = 9 species) and species with 20–100 total captures (n = 5 species). For species with >100 captures we compared patch use among 11 different patch types. To meet the 95% confidence interval requirements (Cherry 1996) for species with 20–100 captures, we combined conifer open pole and conifer open sapling into a new patch type called conifer open sapling/pole. Similarly, we combined mixed open pole and mixed open sapling to form mixed open sapling/pole. Lastly, we eliminated brush-shrub and hardwood large sawtimber patch types because the expected number of captures was too low to assess “selection” accurately (Cherry 1996). After combining and dropping patch types to meet sample size assumptions, we compared patch use among 7 patch types encompassing 769 stations for species with 20–100 captures. Species with <20 captures (n = 6 species) were not used in these analyses.

We used linear regression to test for associations between composition of selected patch types on the landscape (independent variable) and capture rates for each species (dependent variable). Forward stepwise regression was used to assess associations between capture rates of mature forest associates and the dichotomous fragmentation classification (Figure 2), which was based on mature forest edge density within each landscape.

Many of the landscape pattern indices generated using FRAGSTATS are highly correlated; hence, we used correlation analyses to reduce the number of variables within subgroups of pattern statistics. Subgroups were divided by patch, edge, shape, and core indices and a correlation coefficient ≥0.7 between variables within each subgroup was considered significant. This reduced the number of pattern indices to 8, with 2 indices from each of the subgroups (Table 2).

Forward stepwise regression was used to assess associations with fragmentation indices generated from FRAGSTATS independent of composition effects (percentage of landscape in various patch types) by first forcing the area of selected patch types into the model as an independent variable. To reduce spurious correlations we used P-values ≤0.05 and partial $R^2$ statistics ≤0.10 to assess significant association between pattern indices and capture rates for each species. If the selected patch types for a species comprised <15% of a landscape, then the landscape was not used in the pattern analysis. Species detected in <10 landscapes were not used in the pattern analyses.

Patch richness was calculated for each landscape by summing the number of patch types comprising ≥1% (2.5–3.0 ha) of the landscape. Species richness was the number of species captured in each landscape at a rate ≥5% of their total captures across all landscapes sampled. Forward regression was used to assess the association between species richness and patch richness, percentage area of the landscapes in mature forest habitat, and the interaction of these two terms (patch richness × percent area mature forest).

Results

We captured 16,892 small mammals of 20 species in 127,900 trap nights. Fourteen species of small mammals had >20 captures. Each species was associated with 1–4 patch types (Table 3). Ten species were associated with one of the large sawtimber patch types sampled (Table 3).

At the landscape scale, capture rates were related to composition and pattern in one of four ways (Table 4). Some species (27%) were not associated with landscape composition or pattern, while other species (27%) were associated with percent composition of selected patch types on the landscape and not associated with the landscape pattern. Some species (27%) were associated with landscape pattern, but were not associated with the composition of selected patch types on the landscape. Lastly, some species (19%) were associated with percent composition and pattern of selected patch types at the landscape scale.

Species-Specific Responses

Red-tree voles (Arborimus longicaudus) selected conifer large sawtimber patch types, but at the landscape scale they were not associated with the percent composition of conifer large sawtimber. However, landscape pattern analyses revealed that red tree voles were associated with landscapes that had decreasing patch densities (i.e., fewer individual patches) of conifer large sawtimber.

Pacific shrews (Sorex pacificus) selected mixed large sawtimber, hardwood large sawtimber, mixed closed pole, and brush-shrub patch types. Vagrant shrews (Sorex vagrans) were associated with mixed large sawtimber, hardwood large sawtimber, brush-shrub, and mixed grass-forb patch types. Pacific jumping mice (Zapus trinotatus) were associated with mixed large sawtimber, hardwood large sawtimber, brush-shrub, and mixed grass-forb patch types. At the landscape scale, Pacific shrews, vagrant shrews, and Pacific jumping mice were associated with the percent composition of selected patch types; however, the pattern indices of these patch types were not correlated with the capture rates of these species.

Marsh shrews (Sorex benderi) selected mixed large sawtimber and hardwood large sawtimber patch types, fog shrews (Sorex sonomae) selected mixed large sawtimber and conifer open pole patch types, and Trowbridge’s shrews (Sorex trowbridgii) selected mixed large sawtimber patch types. At the landscape scale, marsh shrews, fog shrews, and Trowbridge’s shrews were not associated with the percent composition of selected patch types or the pattern of the selected patch types.

White-footed voles (Arborimus albipes) selected mixed closed pole and mixed open sapling patch types, and at the landscape level were not associated with the percent composition of these patch types. However, white-footed voles were associated with landscapes that contained decreasing levels of core area of the selected patch types.

Deer mice (Peromyscus maniculatus) selected mixed open pole, brush-shrub, and mixed grass-forb patch types and were associated with the percent composition of these patch types at the landscape level. Deer mice also were associated with landscapes with increasing levels of edge density (density of edges between selected, unselected, and neutral patch types).

Shrew moles (Neurotrichus gibbsii) selected conifer large sawtimber and conifer open sapling patch types, but were not
include 5 of the 11 original patch types and 2 new patch types resulting from the combination of the open and pole stands in both conifer and mixed stands. Actual capture rates are either less than expected (\(<\) ), greater than expected (\(>\) ), or equal to expected (\(\equiv\) ) capture rates.

### Table 3. Observed capture rates (# of captures by patch type/total # of captures) of small mammals vs. expected capture rates (# of traps by patch type/total # of traps in all patch types) in the central Oregon Coast Range during April–May 1995 and 1996. Species with > 100 total captures are compared across 11 patch types and species with < 100 captures are compared across 7 patch types. The 7 patch types include 5 of the 11 original patch types and 2 new patch types resulting from the combination of the open and pole stands in both conifer and mixed stands.

<table>
<thead>
<tr>
<th>Species</th>
<th>California red-backed vole (780)*</th>
<th>Shrew-mole (223)</th>
<th>Deer mouse (552)</th>
<th>Creeping vole (82)</th>
<th>White-footed vole (85)</th>
<th>Red tree vole (42)</th>
<th>Coast mole (71)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conifer, large sawtimber (216)</td>
<td>((0.02/0.35)) ((0.20/0.21))</td>
<td>((0.13/0.31))</td>
<td>((0.05/0.21))</td>
<td>((0.13/0.21))</td>
<td>(\equiv(0.41/0.21))</td>
<td>((0.26/0.21))</td>
<td></td>
</tr>
<tr>
<td>Mixed, large sawtimber (180)</td>
<td>((0.17/0.23)) ((0.14/0.17))</td>
<td>((0.16/0.17))</td>
<td>((0.17/0.17))</td>
<td>((0.17/0.17))</td>
<td>((0.07/0.17))</td>
<td>((0.07/0.17))</td>
<td></td>
</tr>
<tr>
<td>Hardwood, large sawtimber (24)</td>
<td>((0.03/0.02)) ((0.02/0.02))</td>
<td>((0.03/0.02))</td>
<td>((0.02/0.02))</td>
<td>((0.02/0.02))</td>
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<tr>
<td>Conifer, closed pole (156)</td>
<td>((0.15/0.15)) ((0.10/0.15))</td>
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<td>((0.03/0.15))</td>
<td>((0.07/0.15))</td>
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<td>((0.12/0.15))</td>
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</tr>
<tr>
<td>Conifer, open pole (49)</td>
<td>((0.06/0.05)) ((0.04/0.05))</td>
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<td>((0.05/0.05))</td>
<td>((0.04/0.05))</td>
<td>((0.09/0.05))</td>
<td>((0.00/0.05))</td>
<td></td>
</tr>
<tr>
<td>Mixed, closed pole (54)</td>
<td>((0.02/0.05)) ((0.06/0.05))</td>
<td>((0.05/0.05))</td>
<td>((0.04/0.05))</td>
<td>((0.09/0.05))</td>
<td>((0.00/0.05))</td>
<td>((0.28/0.05))</td>
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</tr>
<tr>
<td>Mixed, open pole (31)</td>
<td>((0.03/0.03)) ((0.04/0.03))</td>
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<td>((0.04/0.05))</td>
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</tr>
<tr>
<td>Conifer, open sapling (33)</td>
<td>((0.06/0.03)) ((0.03/0.03))</td>
<td>((0.05/0.03))</td>
<td>((0.02/0.02))</td>
<td>(\equiv(0.02/0.02))</td>
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<tr>
<td>Mixed, open sapling (20)</td>
<td>((0.03/0.02)) ((0.04/0.02))</td>
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<td>((0.02/0.02))</td>
<td>((0.02/0.02))</td>
<td></td>
</tr>
</tbody>
</table>

* Number of trapping stations.
† Number of individuals captured.
†† Results in bold are considered significant ($P \leq 0.05$).
§ Sample size is too small to analyze pattern indices.

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### Table 4. Associations between capture rates of 14 small mammal species and the composition and pattern of patch types selected by each species. Small mammals were captured in the central Oregon Coast Range during April–May 1995 and 1996.

<table>
<thead>
<tr>
<th>Species</th>
<th>Landscape composition*</th>
<th>Landscape pattern†</th>
<th>Area-weighted mean patch fractal dimension</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calif. red-backed vole</td>
<td>6.18 0.02 +0.18 20</td>
<td>12.59 0.003 –0.40</td>
<td>Contrast weighted edge density</td>
</tr>
<tr>
<td>Shrew-mole</td>
<td>0.04 0.85 0.001 18</td>
<td>7.10 0.02 –0.32</td>
<td>Edge density</td>
</tr>
<tr>
<td>Deer mouse</td>
<td>8.50 0.01 +0.23 10</td>
<td>133.60 &lt;0.001 +0.32</td>
<td>Core area density</td>
</tr>
<tr>
<td>White-footed vole</td>
<td>1.81 0.19 0.06 20</td>
<td>4.20 0.06 –0.18</td>
<td>Patch density</td>
</tr>
<tr>
<td>Red tree vole</td>
<td>1.60 0.22 0.05 17</td>
<td>4.81 0.05 –0.19</td>
<td></td>
</tr>
<tr>
<td>Coast mole</td>
<td>2.25 0.15 0.07 6†</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pocket gopher</td>
<td>1.95 0.17 0.06 4†</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Creeping vole</td>
<td>19.91 &lt;0.001 +0.42 4†</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Marsh shrew</td>
<td>2.18 0.15 0.07 17</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pacific shrew</td>
<td>5.76 0.02 +0.17 26</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fog shrew</td>
<td>0.26 0.61 0.01 21</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trowbridge’s shrew</td>
<td>0.91 0.35 0.03 16</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vagrant shrew</td>
<td>11.25 0.002 +0.29 20</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pacific jumping mouse</td>
<td>7.89 0.01 –0.22 20</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Area of selected patch types across all 30 landscapes sampled.
† Pattern variables with a significant relationship ($P \leq 0.05$).

associated with the percent composition of these patch types at the landscape level. However, shrew moles did prefer landscapes with decreasing levels of contrast weighted edge densities (density of weighted edges between selected, unselected, and neutral patch types).

California red-backed voles (Clethrionomys californicus) were associated with conifer large sawtimber and conifer open sapling patch types. At the landscape scale, California red-backed voles were associated with the percent composition of selected patch types and landscape patterns with...
decreasing levels of area weighted mean patch fractal dimension (i.e., patches which minimize edge-to-area ratios).

Coast moles (Scapanus orarius) were associated with conifer large sawtimber and mixed closed pole patch types, but were not associated with the percent composition of these patch types on the landscape. Creeping voles (Microtus oregoni) and pocket gophers (Thomomys mazama) were associated with the mixed grass-forb patch type and creeping voles were associated with the percent composition of this patch type on the landscape; however, pocket gophers were not associated with percent composition on the landscape. Path types selected by coast moles, creeping voles, and pocket gophers were not distributed across enough of the landscapes sampled to allow us to assess patterns. None of the small mammals sampled selected the two mature forest patch types (conifer large sawtimber and mixed large sawtimber) precluding us from assessing associations with the dichotomous landscape classification of high and low fragmentation levels (Figure 2).

**Patch Associations**

By breaking patch types down by seral class we found that 37.8% (14/37) of potential species/patch associations resulted in selection of one of the large sawtimber patch types. Similarly, 39.1% (9/23) of potential species/patch associations resulted in selection of one of the early seral patch types (i.e., brush-shrub and mixed grass-forb). In contrast, only 10.4% (8/77) of potential species/patch associations resulted in selection of one of the sapling and pole patch types.

**Species Richness**

We selected patch richness and the percent of mature forest as the two variables most likely to influence species richness based on our results at the species level. Patch richness and percent mature forest on the landscape were weakly correlated with species richness ($P > 0.22$). However, the interaction term of patch richness and percent mature forest was highly correlated with species richness ($F = 7.8, P = 0.009$, $R^2 = 0.47$), indicating that mature forest and patch richness together are important components for species richness of small mammals.

**Discussion**

**Patch Associations**

The term “patch” has been defined as an area that has homogeneous environmental conditions (Morrison et al. 1992, p. 42) or alternatively, an area that differs in appearance from its surroundings (Forman and Godron 1986, p. 83–84). Previous research in the Pacific Northwest has focused on comparison of animal abundance between two or three distinct patch types (usually old-growth or mature forest and younger patch types; Bury 1983, Carey and Johnson 1995, Meiselman and Doyle 1996). California red-backed voles, red tree voles, and Trowbridge’s shrews are generally more abundant in old-growth and mature forests than in other forest types (Corn and Bury 1991, Gillesberg and Carey 1991, Thomas et al. 1993, Rosenberg et al. 1994, Mills 1995, Meiselman and Doyle 1996). In contrast, deer mice and creeping voles have been captured more frequently in younger than older forest stands (Sullivan and Krebs 1981, Van Horne 1981, Corn and Bury 1991, Songer et al. 1997).

Red tree voles selected only conifer large sawtimber patches, consistent with previous studies in the Pacific Northwest (Gillesberg and Carey 1991, Thomas et al. 1993, Meiselman and Doyle 1996). California red-backed voles, a species associated with down woody debris and older coniferous forests (Rosenberg et al. 1994, Tallmon and Mills 1994, Mills 1995) selected conifer large sawtimber and conifer open sapling patch types. Conifer large sawtimber and conifer open sapling are patch types on opposite ends of the successional sere. In contrast with earlier studies of California red-backed voles, these two patch types may not be associated with the highest levels of down woody debris in the central Oregon Coast Range (Spies et al. 1988). Both patch types may, however, be above a minimum threshold volume of down woody debris, making them suitable for California red-backed voles.

Trowbridge’s shrews selected mixed large sawtimber patch types, consistent with previous research (George 1989, Gomez 1992), though abundances were high in all patch types as observed throughout the range of this species (Carey and Johnson 1995). Shrew moles, vagrant shrews, marsh shrews, Pacific shrews, fog shrews, and creeping voles selected mixed large sawtimber patch types along with a variety of other patch types depending on the species. Although these species selected a variety of patch types, they all selected mixed large sawtimber patch types. Selection of conifer and mixed open sapling/pole patches by white-footed voles could be associated with high levels of deciduous shrub cover in these relatively open stands. This is in agreement with earlier habitat studies in the central Oregon Coast Range (Gomez 1992), but contradicts Brown (1985) and earlier dietary analyses for this species (Voth et al. 1983). Pocket gophers selected open patch types, which are younger forests associated with increased shrub cover. This is consistent with results from western Washington, where food caches collected from pocket gopher burrows were dominated by thistle (Cirsium spp.) and Scotch broom (Cytisus scoparius) (Witmer et al. 1996), early successional species associated with open forest areas. Deer mice, a disturbance-associated species (Sullivan and Krebs 1981, Van Horne 1981, Brown 1985, Wolff 1989), selected early successional patch types (mixed grass-forb, brush-shrub, mixed open pole) consistent with findings in the Olympic Peninsula of Washington (Songer et al. 1997). However, deer mice were habitat generalists captured frequently in all habitat types.

Numbers of species selecting for a particular habitat type were higher in the late successional mature forest habitats and the early successional brush-shrub and mixed grass-forb habitat types. This is probably associated with increased levels of understory vegetation within these more open stand types, which provides shelter and foraging opportunities for small mammals.

**Landscape Associations**

Fragmentation and composition of landscapes have varied temporally and spatially during the evolution of small mammals in western Oregon and elsewhere. Small mammals may be associated with landscape composition and pattern, composition alone, pattern alone, or neither pattern nor composition. We propose that many species have a multiscale, habitat selection process that allows different species to adapt to different land-
scape conditions, in addition to habitat selection at finer scales. Natural and human caused disturbances have modified landscapes both spatially and temporally throughout the development of these forested ecosystems (Spies and Turner 1999), and we speculate that mammals may respond differently to changes in pattern and composition at the landscape scale.

Red tree voles, California red-backed voles, and shrew moles were associated with unfragmented landscapes. However, deer mice and white-footed voles were associated with fragmented landscapes. Red tree voles were a habitat specialist selecting only conifer large sawtimber patch types and landscapes that minimize fragmentation of mature conifer forests (i.e., most abundant in contiguous mature conifer forest). Deer mice and white-footed voles were most abundant in early seral patch types and landscapes with a fragmented pattern; hence, we would characterize them as disturbance-associated species.

Marsh shrews, Pacific shrews, Trowbridge’s shrews, vagrant shrews, and Pacific jumping mice were not associated with landscape pattern. These species may be responding to patch and microhabitat characteristics rather than landscape scale patterns.

Species Richness

The intermediate disturbance hypothesis (IDH) has been suggested as a mechanism for increased species richness in a variety of systems including tropical rain forests and coral reef communities (Connell 1978, Huston 1979, Collins et al. 1995, Wootton 1998). This theory predicts that diversity will be greatest when a community is in a transition state or receives intermediate disturbance. We propose that IDH may also be applicable to associations between species richness and the overall composition of a landscape. The IDH suggests that landscapes with a moderate level of disturbance and, hence, heterogeneity of patch types, should have higher species richness per unit area of landscape than drastically disturbed or undisturbed landscapes.

Our results support the IDH at the landscape scale, with species richness being positively correlated with landscapes that have both mature forest patches and a variety of younger patch types. These intermediate landscapes are neither 100% mature forest cover nor 100% early successional stages, but rather a combination of both early- and late-successional conditions. Spies and Turner (1999), in their discussion of natural disturbance regimes, conclude that landscapes were often composed of multiple patch types, because most disturbances do not impact entire landscapes. Specifically, they refer to a “tail” in the forest age-class distribution that extends into the older age classes. We conclude that IDH may be a useful concept to explain species richness of terrestrial vertebrates at the landscape scale. IDH may also be a useful tool for resource managers concerned with maximizing biodiversity at regional scales. Wimberly et al. (2000) modeled temporal and spatial patterns of forest fires in the Oregon Coast Range and reported 0-100% variability in the historic distribution of old-growth forest cover over relatively small areas (40,000 ha). We conclude that local management actions should be tailored to contribute to regional goals that represent IDH conditions if species richness is a primary management objective.

Study Design

Since this is a retrospective study, the results are indicative of general trends and do not represent cause and effect relationships. However, our sample sizes were large, and we sampled multiple stands, patch types, landscapes, and basins. Sampling was conducted in the spring of the year to avoid estimates of abundances associated with reproduction and dispersal of juveniles during summer and autumn. Because we sampled sites only during a single spring season, results may differ in other seasons or among different years. This was a correlative study, however, and we are confident our data represent an accurate assessment of spring habitat use by small mammals in the central Oregon Coast Range.

Conclusions

Mixed large sawtimber and conifer large sawtimber patch types were selected by more forest floor vertebrate species than all other patch types combined. However, certain species, such as white-footed voles, did not select either of these patch types. The majority of species sampled were associated with either landscape composition, pattern, or both composition and pattern. We conclude that providing landscapes that represent a full range of vegetation patterns and composition over a region may be the best way to influence species richness. It has been the homogenization of landscapes in composition and structure that likely has led some species to low abundances (e.g., late seral interior species, dead wood associates with early seral conditions). However, contiguous areas of mature forest may be critical for several species of small mammals and should be given special consideration by ecosystem managers in western Oregon.

The variety of species-specific habitat associations we found at the patch and landscape scales provide support for the idea that ecosystem management cannot function without empirically based species-specific information from a variety of scales (Goldstein 1999). Species appear to be associated with a variety of ecosystem processes at patch and landscape scales providing support for the idea of multiple “target” species when designing ecosystem management alternatives. In order to identify these “target species,” we must investigate habitat associations at multiple scales, landscape patterns, and vegetative conditions. For example, red tree voles are associated with mature conifer patch types, but are negatively affected by increasing patch densities at the landscape scale. We conclude that multiple species and scales need to be considered during ecosystem management planning, but the allocation of seral stages onto a gradient of patch sizes over space and time presents the real challenge to resource managers.

Our results suggest that species select habitat at multiple scales, which is consistent with Johnson (1980). However, in addition to scales discussed by Johnson (1980), we found landscape scale characteristics seem to influence capture rates of several small mammals. This agrees with Merriam’s (1995) hypothesis that mammals may have evolved to adapt to fragmentation “because continuous habitat is functionally
patchy.” An example would be the deer mouse, which may have evolved to be positively impacted by fragmentation of landscapes. In contrast, other species we sampled, such as the Trowbridge’s shrew, do not appear to be affected by changes in the landscape features we sampled. An alternative explanation of our results is that species select habitat at one scale, but multiple scales are most useful in describing their relative abundance across a landscape. The scale at which habitat selection occurs is a difficult question and cannot be answered by our study. We did find that for some species, a multiple scale approach may be useful for management.

Future research should focus on manipulative studies at the patch and landscape scales. These studies could involve manipulating overstory cover, patch age, coarse woody debris, and tree composition at the patch and landscape scales with various strategies used in timber management. Investigating the metapopulation dynamics of these species would also be important to further refine understanding and management of these ecosystems.

**Literature Cited**


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