NICHE DYNAMICS OF DEER MICE IN A FRAGMENTED, OLD-GROWTH-FOREST LANDSCAPE

MELISSA A. SONGER, MARK V. LOMOLINO, AND DAVID R. PERAULT

Department of Zoology and Oklahoma Biological Survey, University of Oklahoma, Norman, OK 73019

Peromyscus oreas and P. maniculatus were non-randomly distributed across macrohabitats (including continuous old-growth forests, old-growth corridors, old-growth fragments, and clearcuts) of the Olympic National Forest, Washington. At this landscape scale, population densities of P. oreas were significantly higher in old-growth sites, particularly continuous forest and corridors, while densities of P. maniculatus were highest in clearcuts. At a finer scale, niche breadths measured across local habitats (within each macrohabitat) were broadest in preferred macrohabitat of each species. The potential importance of interspecific interactions was reflected in an inverse correlation between densities of the two species across all sites, niche segregation at the landscape (between macrohabitat) and local scales, and by the relatively high densities of P. oreas in forest fragments that lacked P. maniculatus. Relative densities of the two species combined were nearly as high in corridors as they were in continuous old-growth, and were nearly double that found in fragments and clearcuts. Given the importance of these rodents as prey for other vertebrates, including the endangered northern spotted owl (Strix occidentalis caurina), maintaining stands of continuous old-growth and forested corridors should remain a priority for conserving diversity of native forest communities.

Key words: Peromyscus, deer mice, fragmentation, corridors, niche, old-growth, Olympic Peninsula

As Wilcox and Murphy (1985:879) wrote more than a decade ago, "... habitat fragmentation is the most serious threat to biological diversity and is the primary cause of the present extinction crisis." Habitat fragmentation threatens thousands of plants and animals now isolated on ever-shrinking islands of native habitat. The ecological effects of deforestation and other forms of fragmentation include those associated with habitat reduction, increased isolation, and increased edge effects (Harris, 1984; Saunders et al., 1991; Shafer, 1990). The effects of fragmentation may be especially severe for non-volant mammals in comparison to birds and other species with greater dispersal abilities (Laurance, 1989). For example, in the fragmented, tropical forests of Queensland, Australia, mammalian diversity decreases as fragments become smaller, older, more irregular in shape (i.e., more edge), and more isolated (Laurance, 1989, 1990, 1991). Distributions of individual species among fragments of these and other forests tend to be correlated with area and isolation of the fragment (e.g., Bronmark, 1985; Laurance, 1989, 1990; van Dorp and Opdam, 1987; Verboom and van Apeldoorn, 1990). Fragmentation can directly threaten many species through loss of habitat, food resources, and shelter, or indirectly by affecting populations of predators, parasites, competitors, and other symbiotes (Harris, 1984; Saunders et al., 1991). Thus, the effects of fragmentation and associated changes in the landscape may cascade through the community and result in the loss of species across many trophic levels.

Understanding how species respond to changes in these large-scale features is an important component of both landscape ecology and conservation biology (Lidick-
er, 1995). Given this, it may be fruitful, albeit more challenging, to adopt a broader view of the ecology of fragmentation, one that includes the effects of environmental features and interspecific interactions from local to landscape levels.

The fragmented landscape of the Olympic National Forest offers an excellent opportunity to study the effects of fragmentation on the structure of old-growth forest communities. This temperate rainforest was logged extensively between 1940 and 1980, leaving a patchwork of old-growth forest (Fig. 1). The Olympic National Forest consists primarily of mid-elevation, Douglas-fir (Pseudotsuga menziesii) forests encircling the unfragmented, higher elevation forests of Olympic National Park. Most of the area outside the National Park and National Forest is of low elevation and either cleared or dominated by second-growth forests. The Olympic National Forest itself is a complex mixture of patches of stands including clearcuts, young and old second-growth, and old-growth. In addition, a few corridors extend through this landscape along rivers and streams (Fig. 1).

Across the Olympic Peninsula <20% of the original old-growth forest is left (Morrison 1989; Norse, 1990). The declines of at least two officially threatened species, the northern spotted owl (Strix occidentalis caurina) and the marbled murrelet (Brachyramphus marmoratus), have been directly linked to the destruction and fragmentation of old-growth forests (Carey et al., 1992;
In addition, forests of the Pacific Northwest support one of the most diverse mammal faunas in the United States (Corn and Bury, 1991; Norse, 1990), with mammals comprising >25% of the vertebrate species in this area (>70 species of mammals on the Olympic Peninsula). Throughout the forested regions of Washington and Oregon the common deer mouse (Peromyscus maniculatus) occurs in relatively low numbers. However, the forest deer mouse (P. oreas) is abundant, especially in old-growth forests of the Olympic Peninsula (Carey and Johnson, 1995). The presence of these two species of Peromyscus on the Peninsula provides an excellent opportunity to study interactions of closely related species in a changing landscape.

The hypothesis that competition is a major force in determining distribution and abundance of species is a persistent theme in ecology (e.g., Connell, 1983; Dueser and Shugart, 1978; Grant, 1972; Heske et al., 1994; Schoenner, 1974, 1983; Scott and Dueser, 1992; Adler, 1985). Many studies, especially those of insular or otherwise isolated communities, have shown that species may shift their realized niches in the absence of putative predators or competitors (e.g., Crowell and Pimm, 1976; Lomolino, 1984; MacArthur et al., 1972; Munger and Brown, 1981; Schoener and Spiller, 1987). Because fragmentation results in insularization and loss of key competitors or predators, species occupying fragments also may exhibit niche shifts analogous to populations on real islands.

While many studies have focused on effects of area and isolation on the species composition of forest fragments (Burkey, 1989; Cutler, 1991; Malcolm, 1988; Quinn and Harrison, 1988; Simberloff and Abele, 1982), such changes may not account for all effects of fragmentation on a forest community. Habitat quality of the remaining forest patches, corridors, and the surrounding matrix may all influence the diversity of old-growth-forest mammals. Perhaps just as important, clearcutting may well result in range expansion of generalists and early successional species, such as P. maniculatus, at the expense of P. oreas and other species dependent on old-growth forests.

The purpose of this study is to test the hypothesis that mammals inhabiting old-growth forests are strongly influenced by both direct and indirect effects of fragmentation. Specifically, we focus on distributions and densities of deer mice and test the following predictions: 1) when viewed across the entire fragmented landscape (irrespective of habitat), densities of P. oreas and P. maniculatus should be inversely correlated; 2) across macrohabitats (continuous old-growth, corridors, fragments, or clearcuts), the two species should segregate their spatial niches, with P. oreas exhibiting higher densities in stands of old-growth while densities of P. maniculatus should be higher in clearcuts; 3) within macrohabitats, the two species should segregate their realized niches, with P. oreas exhibiting higher densities at sites with more closed canopies while densities of P. maniculatus should be higher at sites with open canopies and generally lower forest development; 4) when viewed across dominant macrohabitats of this landscape (here old-growth, corridors, forest fragments, and clearcuts), niche breadths should be higher for the habitat generalist, P. maniculatus, than for the old-growth specialist, P. oreas; 5) just as on true islands, P. oreas should exhibit ecological release in fragments lacking its putative competitor (P. maniculatus). In addition to testing these predictions, we also discuss the potential importance of old-growth corridors and the relevance of our findings with respect to conservation of old-growth mammals such as P. oreas and dependent, predatory species including spotted owls.

MATERIALS AND METHODS

Description of research area.—Studies were conducted in the Hood Canal District of Olympic National Forest (Fig. 1; Songer, 1996). The
dominant species of tree in this area are Douglas firs (P. menziesii), sitka spruce (Picea sitchensis), western red cedars (Thuja plicata), western hemlocks (Tsuga heterophylla), mountain hemlocks (Tsuga mertensiana), and white firs (Abies concolor). Continuous old-growth forest, as defined by the Old-growth Definition Task Group (1986) for the Pacific Northwest, constitute areas >50 km², with ≥8 trees/0.4 ha older than 200 years or >15 cm dbh, and with a deep multilayered canopy having at least four conifer snags of 15 m long.

Trapping surveys and habitat analyses.—Field studies were conducted June–August, 1994 and 1995. Live-trapping was carried out within each of four macrohabitats; continuous old-growth forest, old-growth fragments, old-growth corridors, and clearcuts. Areas that met the above definition of old-growth were considered continuous old-growth forest. Fragments were defined as old-growth forests completely surrounded by clearcuts and second-growth, and ranged from 0.1 to 2.0 km², at least 3 km in length, and connected to continuous old-growth. Clearcuts were defined as areas cut within the past 25 years.

During each trapping session, traps were set at five sites in continuous old-growth. Forest fragments also were trapped during most sessions. Three to five sites were set up within each fragment, covering the extent of all but the largest fragments. Two trap sites were set up within corridors and paired with two trap sites in adjacent clearcuts. Corridor and adjacent clearcut sites were always monitored during the same session. To promote independence of samples, all trap sites were spaced 75 m apart and recaptures were excluded from all statistical analyses. Trap sites also were situated ≥75 m from the nearest forest edge. During the study, trapping was conducted at a total of 35 sites in old-growth, 71 in fragments, 22 in corridors, and 22 in adjacent clearcuts.

At each site, four Sherman traps were set within 5 m of the center of the site in a variety of microhabitats and baited with peanut butter and oats. The traps were locked open for 5 days before each trapping session, then rebaited, unlocked, and checked daily for the next 7 days. Three trapping sessions were conducted during 1994 and four during 1995. Each small mammal caught was sexed, weighed, aged, measured for length, and assessed for reproductive status. The animals were then marked by toe-clipping and released.

At each trap site, 22 habitat characteristics were recorded during the trapping session (Table 1). Two 10-m ropes, knotted at 1-m intervals, were placed along the cardinal directions crossing at 90° angles at the center of the site. Under each knot the presence of dominant habitat components was recorded including litter, rock, fern, moss, herbaceous plant, shrub, stump, log, or tree. Also, the number and size of trees, logs, and stumps were counted within a 10-m radius of the plot center. Categories included snags and trees, stumps, and logs that were <20 cm dbh, 20-40 cm dbh, and >40 cm dbh. Canopy closure was measured by use of a spherical densiometer. A clinometer was used to estimate slope and canopy height. The distance from the site to the nearest edge of the macrohabitat also was recorded.

### Table 1.—Habitat characteristics used in principal-components analysis.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>CANC</td>
<td>Canopy closure (measured with spherical densiometer)</td>
</tr>
<tr>
<td>EDGE</td>
<td>Distance to nearest edge (forest or clearcut)</td>
</tr>
<tr>
<td>SLOPE</td>
<td>Percentage of slope (measured with a clinometer)</td>
</tr>
<tr>
<td>SNAG</td>
<td>Number of snags present within 10-m radius</td>
</tr>
<tr>
<td>T20, T2040, T40</td>
<td>Number of trees with a dbh of &lt;20 cm, 20–40 cm, and &gt;40 cm, respectively, within a 10-m radius</td>
</tr>
<tr>
<td>L20, L2040, L40</td>
<td>Number of logs with a dbh of &lt;20 cm, 20–40 cm, and &gt;40 cm, respectively, within a 10-m radius</td>
</tr>
<tr>
<td>S20, S2040, S40</td>
<td>Number of stumps with a dbh of &lt;20 cm, 20–40 cm, and &gt;40 cm, respectively, within a 10-m radius</td>
</tr>
<tr>
<td>MOSS</td>
<td>Frequency of moss at 22 points in plot</td>
</tr>
<tr>
<td>FERN</td>
<td>Frequency of ferns at 22 points in plot</td>
</tr>
<tr>
<td>GRASS</td>
<td>Frequency of grass at 22 points in plot</td>
</tr>
<tr>
<td>ROCK</td>
<td>Frequency of rock at 22 points in plot</td>
</tr>
<tr>
<td>SHRUB</td>
<td>Frequency of shrub at 22 points in plot</td>
</tr>
<tr>
<td>HERB</td>
<td>Frequency of herb at 22 points in plot</td>
</tr>
<tr>
<td>LITTER</td>
<td>Frequency of litter at 22 points in plot</td>
</tr>
<tr>
<td>TLOG</td>
<td>Frequency of a log or tree at 22 points in plot</td>
</tr>
<tr>
<td>SOIL</td>
<td>Frequency of exposed soil at 22 points in plot</td>
</tr>
</tbody>
</table>
**Statistical analyses.**—Relative densities for each species were calculated by dividing the number of individual mice captured (excluding recaptures) by the number of functional trapnights. Functional trapnights were calculated by subtracting from the total potential number of trapnights, 1.0 for traps that were not functional, subtracting 0.5 for traps that were disturbed, missing bait, or containing a recaptured individual (Songer, 1996).

To examine habitat selection across macrohabitats, we compared relative densities (individuals per functional trapnight) for each species within macrohabitat categories (continuous old-growth, corridors, fragments, and clearcuts) to the proportion of trapping effort within that macrohabitat. Here we define habitat selection as a significant difference between use and availability of resource (Ludwig and Reynolds, 1988). We used goodness-of-fit tests to compare the number of individuals captured in each habitat to the number expected. The expected number of individuals was calculated by multiplying total number of individuals caught for a species by the proportion of functional trapnights in a particular macrohabitat. A significant chi-square value would indicate that the species was not randomly distributed among macrohabitats. We then tested the null hypothesis that the two species of *Peromyscus* were selecting the same type of macrohabitat (Old-Growth Definition Task Group, 1986). Factor 2 explained 12.9% of the variation and was a measure of large trees and coarse woody debris in the understory, loading strongly on TLOG, T40, and S20. Combined, the factor scores explained 32.3% of variation among old-growth sites. The sites were then classified into one of three new habitat categories using KMEANS cluster analysis (SYSTAT, Inc., 1992).

For the corridor sites, GRASS and MOSS variables were removed because there was no grass or moss found in the corridor sites. Factor 1 explained 25.0% of the variation and was a measure of forest structure, loading strongly on CANC, SNAG, L40, T2040, SHRUB, SOIL, T40, LITTER, S20, and HERB. Factor 2 explained 15.7% of the variation and was a measure of openness of the understory, loading strongly on L20, TLOG, S2040, and LITTER. Together the factor scores explained 40.6% of the variation among corridor sites. The sites were then classified into one of three new habitat categories using KMEANS cluster analysis.

For the fragments, the MOSS variable was removed because there was no moss found in the fragment sites. Factor 1 explained 14.9% of the variation and was a measure of forest structure, loading strongly on CANC, SOIL, L40, T2040, and S40. Factor 2 explained 13.1% of the variation and was largely a measure of coarse woody debris in the understory, loading strongly on S20, S2040, L2040, L20, and T2040. Together the factor scores explained 28.0% of the variation. The fragments were divided into four new habitat categories using KMEANS cluster analysis.

For clearcuts, the variables T40, T2040, and MOSS were eliminated because they were not found in the clearcut sites. Factor 1 explained 21.9% of the variation and was a measure of coarse woody debris and distance to the edge, loading strongly on L2040, L20, EDGE, TLOG, SOIL, S40, and S20. Factor 2 explained 15.3% of the variation and was a measure of openness of the understory, loading strongly on T20, SLOPE, LITTER, and L40. Together the factor scores explained 37.2% of the variation. Clearcut sites were then classified into one of three new habitat categories using KMEANS cluster analysis.

To calculate niche breadth for each species of *Peromyscus* across or within macrohabitat cate-
Fig. 2.—Relative densities of *Peromyscus oreas* and *P. maniculatus* were inversely correlated across trap sites ($r_s =$ Spearman rank correlation $= -0.21, P < 0.05$). Relative densities were calculated by dividing the number of individuals captured by the number of functional trapnights. Trap sites lacking both species were excluded from this figure and from tests of interspecific correlations. The MGLH procedure of SYSTAT (1992) identified seven outliers or points with undue influence (triangles) that were excluded from statistical analysis.

**RESULTS**

We recorded a total of 1,414 captures of 980 individual small mammals during the study. Sixty percent of newly caught individuals were *Peromyscus*. Species captured in order of abundance were *P. oreas* (50.2%), *Clethrionomys gapperi* (24.6%), *Tamias townsendi* (8.8%), and *P. maniculatus* (5.8%). The remaining species combined made up 11% of the captures, with no single species accounting for >2% of total captures. These included *Sorex monticolus*, *S. trowbridgei*, *Mustela erminea*, *Zapus trinotatus*, *Spilogale putorius*, *Glaucomys sabrinus*, *Neotoma cinerea*, *Tamiasciurus douglasi*, *Microtus longicaudus*, and *Mustela frenata*. Overall, *P. oreas* represented 89% of newly caught *Peromyscus* individuals.
Population densities and distributions among macrohabitats.—Relative densities of *P. oreas* and *P. maniculatus* were inversely correlated when viewed across all sites combined ($r_{\text{Spearman}} = -0.21, P < 0.05$; Fig. 2). This result stems in large part from niche segregation of these species at the landscape level. That is, *P. oreas* and *P. maniculatus* exhibited significant segregation of their spatial niches across macrohabitats (old growth, corridors, fragments, and clearcuts; Fig. 3). Goodness-of-fit tests showed significant macrohabitat selection for both species ($P < 0.001, \chi^2 = 64.76$ and 55.57 for *P. oreas* and *P. maniculatus*, respectively, $d.f. = 3$). A test of independence showed that the two species were selecting different types of macrohabitats ($P < 0.001, G = 68.50, d.f. = 3$). As predicted, *P. oreas* showed a strong preference for old-growth and had its lowest density in the clearcuts (Fig. 3). Densities of *P. oreas* also were relatively high in corridors, intermediate in fragments, and lowest in clearcuts. In contrast, relative densities of *P. maniculatus* were highest in clearcuts, but low in all other macrohabitats. Counter to our predictions, however, *P. oreas* exhibited the broadest niche breadth across macrohabitats ($NB = 0.84$ and 0.66 for *P. oreas* and *P. maniculatus*, respectively).

Habitat selection at the local scale.—Patterns of habitat selection and niche segregation at the local scale differed markedly among macrohabitats (Fig. 4). For example, *P. oreas* failed to exhibit significant habitat selection within old-growth and corridor stands ($NB = 0.918$ and 0.99, $\chi^2 = 5.34$ and 0.08, respectively; $d.f. = 2, P \gg 0.05$). In contrast, this species exhibited relatively narrow niche breadths in fragments and clearcuts, with its highest density occurring in fragment sites with more open canopies (ca. 35% canopy cover) and relatively few
snags, large logs, or trees, and in clearcut sites located closest to old-growth forests (cluster a in Fig. 4D; NB = 0.63 and 0.65, χ² = 116.52 and 17.03, respectively; d.f. = 2, P < 0.001).

Just as *P. oreas* exhibited its broadest niche breadth within its preferred macrohabitats (i.e., old-growth and corridors), *P. maniculatus* exhibited its broadest niche in clearcuts (NB of *P. maniculatus* = 0.89 in clearcuts versus 0.53, 0.54, and 0.54 in fragments, corridors, and old-growth, respectively). Sample sizes were too small to justify statistical tests in all but clearcut sites. Here, however, *P. maniculatus* exhibited highly significant selectivity for clearcut sites with few snags, large logs or trees, as well as sites with a relatively steep slope, a high coverage of small to medium-sized logs and a limited amount of litter. Tests of independence, which again could only be conducted for sites in clearcuts, indicated significant niche segregation between *P. oreas* and *P. maniculatus* in clearcuts (G = 8.92, d.f. = 2, P < 0.025).

**Discussion**

The results of these studies generally are consistent with the hypothesis that mammals inhabiting old-growth forests may be strongly influenced by both direct and indirect effects of fragmentation. The results also confirm the strong association of *P. oreas* with old-growth forests and *P. maniculatus* with clearcuts. Thus, these species exhibit highly significant niche segregation, primarily at the landscape level (i.e., across macrohabitats). As may be typical of most landscapes, the source for one species may serve as a sink for others. Indeed, niche segregation appears to be so strong that these species may have only limited opportunity to compete in syntopy. It is possible that competition may, however, contribute to the relatively low densities of *P. oreas* in clearcuts and fragments. The limited, natural experiment conducted in fragments suggests that *P. maniculatus* may be inversely related to densities of *P. oreas*, but manipulative field experiments are required to rigorously test any causal explanation for this pattern.

Interestingly, *P. oreas* exhibited a much broader niche breadth than *P. maniculatus* when measured across all macrohabitats, while both species exhibited relatively broad niches within their principal habitats (*P. oreas* in continuous old-growth and corridors, *P. maniculatus* in clearcuts). Relatively broad niches in these macrohabitats may stem from high densities and a tendency for individuals to spill over into otherwise suboptimal, local habitats. While sur-
FIG. 4.—Patterns of habitat selection and niche segregation for *Peromyscus oeras* and *P. maniculatus* within four macrohabitats. The variable forest structure increases with canopy closure and with the occurrence of snags, moss, large trees, or logs (Figs. 4A, B, and C). The abscissa in Fig. 4-D is a direct measure of distance from nearest forest and exposed soil, medium- to large-sized logs and large, and cut stumps (thus, sites included in clearcut cluster a were situated closest to old-growth forests). Niche breadth (NB) within each macrohabitat was calculated from a modified electivity measure (Feinsinger et al., 1981). Niche breadth of each species was highest in their principal habitat (continuous old-growth and corridors for *P. oeras*, and clearcuts for *P. maniculatus*).
prising and counter to our prediction, these results serve to emphasize the scalar nature of ecology. Patterns in niche breadths, habitat affinities, and densities of these species differ among macrohabitats and across spatial scales.

Viewed at the landscape scale, however, these distributional and niche dynamics are not surprising. In fact, they are equivalent to those of two subspecies of *P. maniculatus* in response to clearing of eastern forests of North America during the 19th century. During this earlier period of deforestation, *P. m. bairdi* expanded its range eastward in concert with expansion of its grassland habitats (Baker, 1968; Brown and Gibson, 1983; Harris, 1952; Hooper, 1942; Wecker, 1963, 1964). In contrast, *P. m. gracilis* contracted its range during this period as its principal habitat, mature mesic forests, was reduced. In the case of old-growth rainforests of the Pacific Northwest, however, deforestation is more recent, more rapid (Fig. 1), and has more serious implications for loss of biodiversity.

**Implications for conserving biodiversity of old-growth forests.**—Although corridors typically are considered old-growth habitats, they differ in a number of important features which, in turn, affect community structure. In comparison to continuous old-growth, corridors are narrower and are connected to continuous old-growth forest, have a higher ratio of edge to interior habitat, and are more susceptible to wind damage and other edge effects. Habitat analysis in our study showed an absence of moss in corridors, while it was common component of continuous old-growth sites. Despite these differences, densities of *P. oreas* in corridors were nearly equal to those in continuous old-growth, and much higher than those in fragments (0.20, 0.19, and 0.11, respectively). Apparently, connectivity and dispersal may compensate for the subtle differences in habitat quality of corridors and continuous old-growth.
In contrast, fragments, which differ both in habitat quality and in their isolation from corridors and continuous old-growth, harbor substantially lower populations of *P. oreas*. Habitat quality of fragments seems less suitable for this forest mammal. In addition, because they are isolated by clearcuts, populations inhabiting fragments are less likely to be supplemented, or rescued, by emigration from source populations (sensu Brown and Kodric-Brown, 1977). Thus, we predict that fragments farther from corridors or continuous old-growth will support lower densities of *P. oreas* and other forest mammals. Additional studies presently are underway to test this and related predictions on the role of riparian corridors in this fragmented landscape.

Finally, we consider the relevance of observed patterns in densities and distributions of deer mice for conservation of other animals occupying old-growth forests, especially predators. Old-growth is the principal habitat of the endangered northern spotted owl. About 20% of fecal pellets of owls collected in the Olympic Peninsula contain remains of *P. maniculatus* and *P. oreas* (Carey et al., 1992; Forsman et al., 1991). Unfortunately, it is sometimes assumed that clearcuts support more individuals of *Peromyscus* than do forested habitats (Algren, 1966; Corn and Bury, 1991; Gashwiler, 1959, 1970; Martell and Radvanyi 1977; Sullivan, 1979; Tevis, 1956). Other studies have reported similar densities and demographic characteristics of populations of *Peromyscus* between old-growth and recently logged areas in British Columbia (Petticrew and Sadleir, 1974; Sullivan, 1979). However, *P. oreas* did not occur in these regions.

Our research in the Olympic National Forest revealed that the combined density of these key prey species was highest in continuous old-growth forest and old-growth corridors (Figure 3). In fact, densities of *Peromyscus* in the continuous old-growth were nearly twice as high as densities in the clearcuts (0.20 and 0.11, respectively). Not only are densities of deer mice higher, but we suspect that availability of these and other prey also may be higher in forested habitats. As an arboreal species, *P. oreas* also is likely to be a more accessible prey for the spotted owl than *P. maniculatus*, which typically restricts its movements to the lowest stratum of the forest. Moreover, the northern flying squirrel (*Glaucomys sabrinus*), which makes up the greatest percentage of biomass in the diet of the northern spotted owl (Forsman et al., 1991), spends most of its time in the trees.

In summary, deforestation and fragmentation of old-growth forests of the Olympic Peninsula clearly have had a strong impact on distributions, densities, and niche dynamics of deer mice. Admittedly, we have much to learn as this is just the first product of our community wide studies on this complex system. It seems quite clear, however, that as this landscape becomes more fragmented, the combined densities of these key prey species will continue to decline, setting the stage for cascading effects and continued decline of old-growth-forest communities in general.

**ACKNOWLEDGMENTS**

We thank T. A. Franklin, A. Leikam, P. Leimgruber, M. Rene, and B. Rosewell for their assistance in collecting field data. G. A. Smith, T. A. Franklin, and two anonymous reviewers provided valuable comments on an earlier version of this manuscript. M. L. Johnson, N. Czaplewski, J. Lowry, and C. C. Vaughn aided with valuable comments throughout the project. GIS data were provided by W. Wettengel of the United States Department of Agriculture, Olympic National Forest. E. Milliman assisted with logistical support from Olympic National Forest. Field housing was furnished by T. Neilson at the Satsop Wells Environmental Learning Lodge of the Grays Harbor Conservation District. Funding for this project was provided by a National Science Foundation grant (DEB-9322699) to M. V. Lomolino.

**LITERATURE CITED**


