

SCIURIDS IN PACIFIC NORTHWEST MANAGED AND OLD-GROWTH FORESTS¹

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Abstract. An understanding of the factors governing sciurid abundance in the Pacific Northwest is essential for prescribing forest management practices for second-growth forests where recovery of Spotted Owl (*Strix occidentalis*) populations and enhancement of biodiversity are objectives. We compared results of companion studies of sciurids in western Washington and Oregon and examined patterns of abundance in relation to habitat elements on the Olympic Peninsula to elucidate governing factors and make recommendations for forest management. Regional contrasts show that *Glaucomys sabrinus* and *Tamias townsendii* in Douglas-fir forests in Oregon are 4 times more abundant than in western hemlock forests in Washington, and dietaries of *Glaucomys*, and the fungal communities that provide its food, are more diverse in Oregon than in Washington. *Glaucomys sabrinus* in old forests are 2 times more abundant than in young, managed forests without old-forest legacies (large live trees, large snags and large, decaying fallen trees): populations in young forests with old-forest legacies and with understory development may equal those in old Growth. On the Olympic Peninsula, *Glaucomys sabrinus* abundance can be predicted by density of large snags and abundance of ericaceous shrubs. At least seven large snags/ha and well-distributed patches of dense shrubs (cover within patches >24% and patches covering 40% of the total area) are necessary for high densities of *Glaucomys sabrinus*. Abundance of *Tamias townsendii* reflects size of dominant tree and well-developed understories. Abundance of *Tamiasciurus douglasii* seems to reflect territoriality in concordance with food supply and was greatest where *Glaucomys* and *Tamias* were low in abundance. Patterns of abundance of the sciurids in old- and managed forests suggests that silvicultural manipulation of vegetation and creative snag or den-tree management could be used in a management strategy to accelerate the development of Spotted Owl habitat in areas where old Growth is lacking.

Key words: biodiversity; ecosystem management; forest ecology; *Glaucomys*; managed forest: old growth; Pacific Northwest; squirrels: snags; *Strix occidentalis*; *Tamias*; *Tamiasciurus*.

INTRODUCTION

Three species of Sciuridae are common inhabitants of the coniferous forests of western Oregon and Washington: northern flying squirrel (*Glaucomys sabrinus*), Douglas' squirrel (*Tamiasciurus douglasii*), and Townsend's chipmunk (*Tamias townsendii*). The flying squirrel is of particular interest in applied ecology because it is the most important prey of the threatened Northern Spotted Owl (*Strix occidentalis caurina*) in Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) forests. But all three species are important prey for avian and terrestrial predators and all three are important in forest ecosystem processes because of their consumption of fungi and dispersal of fungal spores (Maser and Maser 1988). All three species have been found more abundant in old forests than in managed forests in at least parts of their ranges or during particular seasons (Volz 1986, Carey 1989, 1991, 1993a, Buchanan et al. 1990; Carey et al. 1992, Witt 1992, Rosenberg and Anthony 1993).

The features of old forests that may benefit these species are varied: large, decaying fallen trees: large, standing dead trees (snags); large live trees: and well-developed understories. Northern flying squirrels may be limited by the availability of den sites, particularly cavities

in trees (Carey 1991). Old forests may have > 10 times the number of large snags found in younger, managed forests (Carey et al. 1991b). These large snags are preferred by cavity-excavating birds (Carey et al. 1991b, Lundquist and Mariani 1991) whose cavities are used by flying squirrels (Wells-Gosling and Heaney 1984, Carey 1991).

Food, mushrooms, and the hypogeous sporocarps of mycorrhizal fungi may also be limiting to flying squirrels (Carey 1991, Carey et al. 1992, Rosenberg and Anthony 1992). The relationship between the abundance of fungi and stand age is unknown, although it is thought that coarse woody debris may be important to the diversity and abundance of fungi (J. M. Trappe, *personal communication*). The abundance and diversity of ericaceous shrubs can also influence the variety and abundance of mycorrhizal fungi by supporting ericoid species and ectomycorrhizae of Pinaceae as well (Smith 1993). Both the Townsend's chipmunk and the Douglas' squirrel are mycophagous; but they consume conifer seed and the seeds of other woody plants as well. A strong relationship exists among seed production, size of tree, and age of tree (see Carey [1991] for a review). Overhanging and vertical cover are determining factors in space use by Townsend's chipmunk (Harestad 1991) and could be important to foraging flying squirrels also. Den sites in the form of cavities are not thought to be limiting to Douglas' squirrels and Townsend's chipmunks (Carey 1991). Douglas' squirrels are territorial and

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TABLE 1. Fall population densities in 1986/1987 (mean \pm 2 SE) of three sciurids in old forests in western Oregon and Washington. $P = 0.05$.

Location	Dominant vegetation, THZ†	No. of old forest stands	No. of sampling periods	Population density (animals/ha)						Source
				Northern flying squirrel		Townsend's chipmunk		Douglas' squirrel		
				\bar{x}	2 SE	\bar{x}	2 SE	\bar{x}	2 SE	
Oregon: Southern Coast Ranges	PSME	9	20	1.9	0.4	1.9	0.2	0.2	0.0	Carey et al. 1992
Oregon: Central Western Cascades	PSME	5	10	2.3	0.4	4.5	1.0	*	*	Rosenberg and Anthony 1992, 1993
Washington: Western Olympic Peninsula	TSHE	6	14	0.5	0.4	0.4	0.4	<0.1	0.0	This study
Washington: North Cascades	TSHE	3	3	0.2	0.2	0.5	0.6	0.5	0.6	Carey 1993a

* No information on Douglas' squirrels was provided.

† *Tsuga heterophylla* Zone (THZ): PSME = Douglas-fir (*Pseudotsuga menziesii*) dominated; TSHE = western hemlock (*Tsuga heterophylla*) dominated.

may simply be limited by food and space (Smith 1968).

The importance of old forests to biodiversity and the loss of these forests to logging in some areas of the region has resulted in a need to manage second-growth forests to create old-forest-like characteristics, accelerate the development of habitat suitable for Spotted Owls, and provide habitat for other late-successional wildlife (Thomas et al. 1990, Carey and Johnson 1995). Old forests, however, vary markedly in character across the Pacific Northwest (Old-Growth Definition Task Group 1986) and in their capacity to support wildlife (Carey 1989, Carey et al. 1992, Carey and Johnson 1995). Thus, physiographic province-specific and species-specific information on the factors influencing animal abundance is necessary to formulate strategies for managing second-growth forests for old-forest values. Carey and Johnson (1995) provide such information for forest-floor small mammals on the Olympic Peninsula.

Here, I describe the sciurid populations on the Olympic Peninsula in the context of abundances across western Oregon and Washington. Then, using data from the Olympic Peninsula, I examine the relationships among three sciurids, managed- and old forests, and the elements of forest structure that are of putative importance to each species. Combining my results with the growing body of knowledge of forest ecology in the Pacific Northwest, I discuss implications for forest management.

METHODS

Regional comparisons

This study was one of four designed to examine the relationships among arboreal rodents, old forests, and managed forests to determine the ecological values of old forests and factors influencing Spotted Owls in *Tsuga heterophylla* Zone (THZ) forests of western Washington

and Oregon (Carey and Spies 1991). The THZ is the most extensive vegetation zone in western Washington and Oregon and the most important in terms of timber production (Franklin and Dyrness 1973). The zone extends south from British Columbia, west of the crest of the Cascade Range through five physiographic provinces in Washington (Olympic Peninsula, Northern Cascades, Southern Washington Cascades, Puget Trough, and Coast Ranges) and two in Oregon (Western Cascades and southern Coast Ranges). Near the Pacific Coast the THZ intergrades with the *Picea sitchensis* Zone; near the Cascade Crest, with the subalpine forest zones. In southwestern Oregon the THZ zone inter-grades with the Mixed-Conifer and Mixed-Evergreen Zones (Franklin and Dyrness 1973). The THZ is characterized by strong North-South temperature-moisture gradients along 4° of latitude, with a transition from western-hemlock-dominated forests in the North to Douglas-fir-dominated forests in the south. Franklin and Dyrness (1973) describe the climate, soils, and vegetation of these physiographic provinces.

This report focusses on a study conducted on the Olympic Peninsula and contrasts the findings there with previously reported studies in the North Cascades near Baker Lake, Washington (Carey 1993a), the center of the Western Cascades of Oregon (Rosenberg and Anthony 1992, 1993), and the transition forests of the Coast Ranges in southwestern Oregon (Carey et al. 1992). All four studies used the same sampling techniques (Carey et al. 1991a), except Rosenberg and Anthony (1992, 1993) differed in length of trapping period (8-21 nights vs. 6-8 nights in the other studies). Results from fall trapping with wire-box live traps in old forests are presented in a table (Table 1) to allow regional contrasts. Rosenberg and Anthony (1993) used a different type of trap in their summer sampling; those results are not included in the contrasts.

Fecal pellets were collected from flying squirrels captured in 2-wk trapping periods in four old and four

young stands in the southern Coast Ranges in 1986 and five old and four young stands on the western Olympic Peninsula in 1987. These samples were analyzed following the procedures of McIntire and Carey (1989) to produce a regional contrast in dietary diversity.

Olympic Peninsula study areas

A general description of the study areas was provided by Carey and Johnson (1995) for a companion study of forest-floor small mammals. We chose stands thought to be homogeneous, that appeared to have resulted from a single, catastrophic regenerative disturbance, and that were surrounded by forests of similar age and condition (to avoid edge effects). One stand, however, proved to be a heterogeneous matrix resulting from a major windstorm in 1921, with patches of dense 66-yr-old trees and 300-yr-old forest; and, before sampling was undertaken, two adjacent stands were clearcut. All were on the western half of the Peninsula, six (three old, one mixed-age, two managed) were in Clallam County near Forks and five (two old, three managed) were in Grays Harbor County near Hump Tulips. I sampled 9 stands in 1987, 11 in 1988, and 4 in 1989; 9 stands were sampled in two seasons, 2 in three seasons. Because captures varied among years, I used average values in my analyses.

The ages of stands were determined by counting rings on stumps of nearby felled trees, taking increment cores from trees, and reviewing Henderson et al.'s (1989) fire history and landowners' management records. The old stands were 250-400-yr-old and had not been logged. The managed stands were 44-67-yr-old and had been established after clear-cutting, and none had residual live trees. One stand had been seeded and thinned. The other young stands had been seeded artificially and naturally and had not been thinned, but varied in tree density.

Sampling procedures

I used the trapping procedures suggested by Carey et al. (1991a) that were used in the three companion studies: 16-ha, 10 X 10 grids with 40-m spacing, with two wire-box traps per station (one trap on the ground, one trap 1.5 m high in a tree). Traps were opened for four nights in each of two successive weeks in the fall after rains had commenced. This procedure is highly effective for flying squirrels and chipmunks, but less so for Douglas' squirrels because few are recaptured (Carey et al. 1991a). Because of lack of rain, trapping did not commence until 20 October and extended to 20 November in 1987. Trapping was conducted in October in 1988 and 1989, after fall rains had taken place. All animals captured were tagged with ear tags, weighed, and examined for reproductive condition and age. Fecal pellets were collected from the anus if the animal began to defecate. Fecal pellets were pooled by stands and examined for frequency of food items following McIntire and Carey (1989).

Each trap station was described with 55 variables, including species and diameter of the nearest dominant or codominant tree (details of sampling for stand description were reported by Carey and Johnson 1995). The number of snags (lightly to moderately decayed standing dead trees >2 m tall) in each of two size classes (10-50 cm in diameter at breast height [dbh] and ≥ 50 cm dbh) within 10.6 m were counted. The percentage covers of low woody vegetation (<2 m tall), tall shrubs and understory trees (≥ 2 m tall), dominant and codominant species in each stratum, and fallen trees (three decay classes) within 5.6 m were estimated visually.

Analytical procedures

I used a hierarchical approach: (1) comparing densities of the sciurids across the Pacific Northwest using published and unpublished 95% confidence intervals from this and other studies; (2) summarizing Olympic stand characteristics pertinent to squirrels and stage of forest development, (3) performing tests to determine if the squirrel populations differed between naturally originated, old (including mixed-age) and clear-cut originated, young, managed forest; (4) performing regression analyses using variables of putative importance to each species; and (5) comparing rankings of stands by age, an index to forest development, and to habitat quality for flying squirrels.

Stand character.—Habitat variables (stand means) were used by Carey and Johnson (1995) to describe the study stands in terms of age, site, and forest type and to contrast the structure of old-growth and managed stands. They found that understory vegetation was best described by the prevalence (percentage of total number of plots) with low-shrub cover >24% and understory cover (primarily *Acer circinatum*, *A. macrophyllum*, and coniferous trees) >24% because plots tended to have either sparse or heavy understory cover. Prevalence is a measure of consistency of occurrence of significant cover of vegetation in a stand. Prevalence differs from mean percentage cover in that the same mean cover value can be derived from markedly different distributions of cover (e.g., random, uniform, or clumped). Abundance of fallen trees was best described by the mean total cover of fallen trees. I use the Intransformed mean values for large snags; prevalence (with arcsine transformation) of ericaceous shrubs (primarily *Gaultheria shallon* and *Vaccinium* spp.); mean cover of fallen trees; and mean dbh of dominant and codominant trees as predictor variables in regression equations. In addition, a variable for origin of stands (clear-cutting vs. natural windstorm or fire) was created.

Capture data.—Densities of flying squirrels and chipmunks were estimated using the Chapman modification of the Lincoln-Petersen index (Menkens and Anderson 1988), and effective trapping area was calculated by the mean maximum distance individuals moved (Wilson and Anderson 1985). Carey et al. (1991a) recommended this method because it produced lower coefficients of variation for density estimates (and fewer extreme values) than more complex estimators.

Mann-Whitney rank-sums tests were used to compare densities in old and managed stands on the Olympic Peninsula. I calculated catch per unit effort (CPUE) indices (number of individuals captured per 100 trap-nights, corrected for sprung traps and total captures; Nelson and Clarke 1973) for each species. Indices based on CPUE often have smaller sampling errors than estimates of absolute abundance, especially when density estimators are applied to small numbers of captures, as in this study (Skalski and Robson 1992). Carey et al. (1991a) showed that values of this CPUE index for flying squirrels and chipmunks were highly correlated ($r = 0.92$ and 0.99 , respectively) with Chapman estimates of population size over a wide range (268 individuals) of population sizes in Oregon. Coefficients of variation for Chapman estimates were variable and sometimes high. Thus, I used CPUE indices for regressions. The Box-Cox procedure was used in regression analyses to determine the need for and utility of transforming measures of abundance; $\ln(\text{CPUE} + 1)$ or inverse-square transformations were combined with all-possible-subsets regression and regression by groups (Dixon 1990). Regression by groups was used to determine if there were significant differences in slopes of the regression curves between young and old forest. All-possible-subsets regression with Mallows' C_p (Dixon 1990) was used to determine which of the putative predictors of squirrel abundance should be included in the regression equations. To further avoid including spurious variables in the regression, only variables with coefficients significantly different from 0 ($P < 0.05$) were retained, and regressions were accepted only when normal probability plots of residuals did not suggest significant departures from normality. However, sample size (number of stands) was small; thus, evaluation of normality was restricted to detecting obvious departures.

Population characteristics.—Captures were too few to compare population characteristics other than densities using stand means. Therefore I combined data on individuals across stands and years to contrast populations in old and young stands: proportion female, proportion reproductive female (lactating or post-lactating), proportion young (juvenile or subadult), mean body mass of adults, and mean body mass of young squirrels. Alternative measures of population responses to stand conditions are important in evaluating habitat quality (Maguire 1973), for example, to address the possibility that high-density populations might represent ecological sinks. Even though data were too few to calculate stand means and confidence intervals, they were sufficient to calculate means for stand conditions (old vs. young) to support the hypothesis that differences in density represent differences in habitat quality.

Comparison of ranks.—Maturing forest plant communities (stands) can be categorized based on their structure, composition, and history (e.g., old-growth vs. managed, young stands). Alternatively, these stands can be assigned to a phase of development-for

example, stem exclusion phase, understory reinitiation phase, or old growth (Oliver and Larson 1990). Numerous characteristics of developing stands are correlated with age. But while there is a commonality in development, the nature of individual stands can vary markedly, even within a climatic or vegetation zone and within a management regime (see papers in Ruggiero et al. [1991] for the Pacific Northwest). It is in these differences that keys to future management for old-growth restoration and biodiversity lie (Carey and Johnson 1995). I examined correlations among variables and differences among stands within the managed and old-forest categories to determine if the predictor variables for mammal abundance were reflecting the overall process of stand development or representing specific features of stands. To expand on this analysis, I developed three rankings for the 11 stands: age, forest development, and flying-squirrel habitat. First, stands were ranked by the age of overstory dominant trees. Next, as a simple index to forest development, I scored (-1, 0, +1) the stands relative to my sample means ($<0 - 1 \text{ SE}$, $=0 \pm 1 \text{ SE}$, $>0 + 1 \text{ SE}$) for characteristics definitive of old growth (Franklin et al. 1981, Old-Growth Definition Task Group 1986): (1) size of dominant trees, (2) abundance of large, standing dead trees, (3) abundance of fallen trees, and (4) layering of vegetation (shrub, tall understory, and canopy covers). These scores were summed for a ranking. Then, stands were ranked as flying-squirrel habitat by the abundance of flying squirrels as predicted by the best all-possible-subsets regression equation (which incorporated the abundance of large snags, ericaceous shrubs, and an interaction term). I used Kendall's coefficient of concordance (W) to determine if the three rankings differed significantly and Kendall's coefficient of rank correlation (τ) and its graphical representation (Sokal and Rohlf 1981) to illustrate that the predictors were not simply correlates of age or stand development.

RESULTS

Regional comparisons

Flying squirrels and Townsend's chipmunks were >4 times more abundant in the Douglas-fir-dominated old forests of central southern Oregon (44° north latitude) than in the western-hemlock-dominated old forests in Washington (47° – 49° N); Douglas' squirrels were most abundant in the northernmost old forests (Table 1).

Flying-squirrel diets in the Coast Ranges were more varied (had less emphasis on any single taxon) and rich (contained more taxa) than on the Olympic Peninsula (Table 2). In both old and managed stands, flying squirrels consumed >2 times more fungal taxa per stand, had >2 times more taxa appearing consistently across stands in the pellets, and had 5 times more taxa occurring with a mean frequency $>50\%$. Diets in old forests were more diverse than in young forests.

TABLE 2. Mean frequency of occurrence of fungal taxa and fungal diversity in northern flying squirrel diets in the southern Coast Ranges (CR), 1986, and on the Olympic Peninsula (OP), 1987.

	Old-growth forest		Young managed forest	
	CR	OP	CR	OP
No. of stands	4	5	4	4
Fungal taxa				
<i>Balsamia</i>	5.2	...	1.2	...
Boletaceae	...	36.0	...	18.2
<i>Chamomixia</i>	...	12.6	...	6.1
<i>Elaphomyces</i>	3.9	10.3	1.5	2.8
<i>Gautieria</i>	55.6	...	76.7	25.0
<i>Genea</i>	0.5	0.8	0.2	...
<i>Hydnotrya</i>	...	2.9
<i>Hymenogaster</i>	21.6	...	30.4	...
<i>Hysterangium</i>	13.8	19.6	70.4	27.5
<i>Leucogaster</i>	34.8	18.1	...	1.0
<i>Leucophleps</i>	83.6	...	30.7	...
<i>Martellia</i>	6.3
<i>Melanogaster</i>	85.0	...	77.3	23.2
<i>Octavianina</i>	5.8	40.8	10.2	5.6
<i>Picoa</i>	0.2
<i>Rhizopogon</i>	88.4	41.9	100.0	100.0
Russulaceae	62.7	...	74.5	...
<i>Thaxterogaster</i>	...	15.4
<i>Tuber</i>	0.1
Vascular plants	12.2	9.5	2.4	10.8
Number of fungal taxa				
Total	15	11	11	10
No./stand (mean \pm 2 SE)	12.5 \pm 0.5	5.6 \pm 1.1	9.2 \pm 0.5	4.2 \pm 0.5
Universal*	9	4	6	1
Freq. > 50%†	5	1	5	1

* Number of taxa occurring \geq 80% of stands.

† Number of taxa with a mean frequency >50%.

Olympic stand characteristics

The stands ranged in age from 44 to 400 yr. Average diameter at breast height (dbh) of canopy trees ($r = 0.89$), density of large snags ($r = 0.83$), abundance of coarse woody debris ($r = 0.72$), and development of tall understory vegetation ($r = 0.76$) increased with age. Canopy closure ($r = -0.84$) and total density of snags ($r = -0.74$) decreased with age. Means were significantly different between old and young stands for all but coarse woody debris (Table 3); coarse woody debris, large snags, and canopy closure were more variable among the old stands than among the young stands.

Rankings on age and forest development were positively correlated (Kendall's $\tau = 0.75$, $P < 0.01$). The abundance of ericaceous shrubs was not correlated with age and was highly variable (coefficient of variation [CV] = 0.96). Shrub abundance was negatively correlated ($r = -0.67$) with density of dead trees (indicators of the stem exclusion phase of stand development) and positively ($r = 0.75$) with tall understory vegetation (indicators of understory reinitiation phases well underway). Shrub, tall understory, and total understory abundances were not significantly correlated with canopy

closure: only tall understory was highly correlated with age ($r = 0.76$). Similarly, tall understory vegetation was highly correlated ($r = 0.69$) with density of large snags (these indicate canopy openings in old forest). No other stand element was as variable as shrub abundance, but the density of large snags (CV = 0.96) and prevalence of understory vegetation (CV = 0.84) were highly variable.

Only one stand diverged markedly from its rank on age to its rank on forest development (Fig. 1). This stand, 57 yr old, had the largest mean dbh, number of large snags, shrub abundance, midstory abundance, and coarse woody debris abundance of all the young stands and even surpassed all the old stands in shrub cover. The rankings based on weighted values of large snags and shrubs (regression-predicted numbers of flying squirrels), however, diverged markedly from the rankings on age and forest development ($\tau = 0.31$, $P > 0.10$). The rankings were significantly different (Kendall's $W = 0.57$, $\chi^2 = 17.03$, $P < 0.01$). Three stands differed markedly in the rankings. The 57-yr-old stand increased in ranking from 10 on age to 5 on forest development and I on flying squirrel habitat. The 400-yr-old stand of Kitka spruce (*Picea sitchensis*) and western hemlock had the largest mean dbh, understory cover, and amount of coarse

TABLE 3. Characteristics of five young stands originating after clear-cutting and six old stands originating after natural disturbances on the western Olympic Peninsula, 1987–1989.

Characteristic	Old		Young		Student's <i>t</i>	Levene's <i>P</i> *
	\bar{X}	SE	\bar{X}	SE		
dbh (cm)†	67	7	40	4	3.02	0.01
Fallen trees (%)‡	12	3	7	1	1.44	0.21§
Large snags/ha	23	3	2	1	6.13	0.00§
Total no. of snags/ha¶	66	15	123	30	-1.81	0.10
Low shrubs (%)#	39	10	30	17	0.45	0.66
Understory (%)**	28	6	11	6	1.95	0.08
Canopy (%)††	61	7	89	4	-3.24	0.01§

* Norusis 1993.

† Diameter at breast height, i.e., at 1.5 m.

‡ Fallen tree percentage cover.

§ Variances significantly different between old and young, Levene's *P* < 0.05; *t* test based on separate variances. Levene's *P* homogeneity-of-variance test is less dependent on assumptions of normality than most tests and thus particularly useful with ANOVA. It is obtained by computing, for each case, the absolute difference from the cell mean and performing a one-way ANOVA on the difference.

|| Large snags >50 cm dbh.

¶ Total snags >10 cm dbh.

% of plots with >24% cover of ericaceous shrubs.

** % of plots with >24% cover of vegetation >2-m tall in the understory.

†† % of plots with closure >64%.

woody debris of any stand—but the lowest number of large snags of any old stand, and was the only stand dominated by spruce and hemlock. This stand ranked first on age and forest development but 10 on flying squirrel habitat. The 100-yr old, mixed-age stand decreased from 6 on age to 8 on forest development (because of scant shrub and understory layers), but increased to 2 on flying squirrel habitat. Other stands changed only 1-2 places in rank.

Manunal populations

A total of 312 individual sciurids were captured 751 times in the 11 stands: 168 Townsend's chipmunks, 99 northern flying squirrels, and 45 Douglas' squirrels. Flying squirrels were more abundant in naturally originating old forests than in young, managed stands (*P* = 0.07 for density), but the abundances of Townsend's chipmunks and Douglas' squirrels did not differ between old and managed stands, *P*s > 0.50 (Table 4). Within-

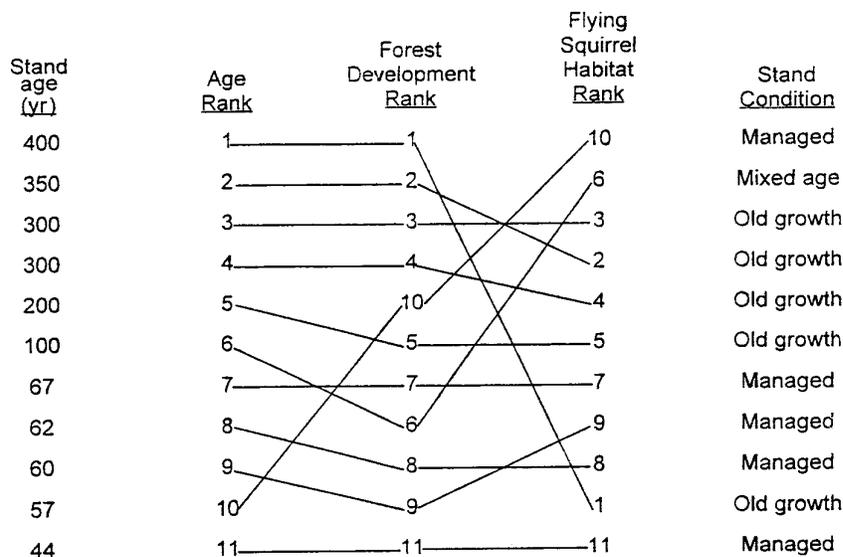


FIG. 1. Graphical representation of Kendall's coefficient of rank correlation for 11 forest stands on the western Olympic Peninsula, Washington; 1988. Stands are numbered by their rank on age, then ordered by their ranks on forest development and northern flying-squirrel habitat. Lines connect the individual stands, and the numbers of intersections indicate departures from perfect correlation and were used in statistical computations.

TABLE 4. Biological characteristics of populations of three sciurids in five young and six old forests on the Olympic Peninsula, Washington; 1987-1989.

Species	Stand type	Animals captured				Body mass (g)				Population density (no./ha)		
		Total no. of individuals	Composition (%)*			Adult		Young		\bar{x}	SE	Levene's P^\dagger
			F	RF	Y	\bar{x}	SE	\bar{x}	SE			
Flying squirrel	Old	71	55	31	25	136	4	84	7	0.5	0.2	0.07
	Young	28	50	29	46	128	5	102	5	0.2	0.1	
Townsend's chipmunk	Old	136	43	12	37	73	1	68	1	0.4	0.2	0.58
	Young	32	44	19	69	77	2	67	1	0.2	0.1	
Douglas' squirrel	Old	28	46	7	50	161	6	133	7	0.01	0	0.57
	Young	17	47	18	38	169	10	130	5	0.01	0	

* Percentage of individuals that were female (F), reproductive female (RF), and young (Y).

† Norusis 1993.

stand, mean maximum distances moved (MMDM) by flying squirrels were 56-156 m (mean \pm 1 SE = 102 \pm 21 m) in young stands and 83-90 m (87 \pm 2 m) in old forests. Stand-mean MMDM for chipmunks was 38-160 m (averaging 106 \pm 17 m) in young stands and 40-114 m (83 \pm 10 m) in old forests.

The greatest stand means for young forests (in both primary trapping years) for both flying squirrels and chipmunks were in the 57-yr-old managed stand. Overall catch per unit effort (CPUE) varied three-fold among years, but rank order of abundance of stands did not appear different among years. Mean flying squirrel CPUE ranged from 0.07 to 0.99 in old stands and from 0.0 to 0.83 in managed stands. Chipmunk CPUE ranged from 0.0 to 1.98 in old forests and from 0.0 to 0.64 in young stands. Douglas' squirrels were few but consistent (CV = 0.27 compared to 1.05 for flying squirrels and 1.41 for Townsend's chipmunk). The average number of individual Douglas' squirrels caught in individual stands was 1.5-2.5 squirrels in old forests and 1.0-2.5 squirrels in managed stands. The species did not differ between old and young stands in proportion female, proportion reproductive female, proportion young, adult body mass, or young body mass (Table 4).

TABLE 5. Contributions of ericaceous shrubs, large snags, and stand origin to explaining variance in northern flying squirrel abundance on the Olympic Peninsula, Washington; 1987-1989.

Number of stands*	Contribution to R^2 (%)			Regression		
	Shrubs	Snags	Origin†	R^2	F	P
10	26	25	16	83	10.3	0.010
11‡	16	67	48	85	6.5	0.003

* 10 stands: 5 young, 5 old growth; 11 stands: 5 young, 1 mixed age, 5 old growth.

† 16 naturally originated by fire or wind vs. 48 originated by clear-cutting.

‡ Regressions using one variable produced slopes (and R^2) of: 0.26 (41) for shrubs; 0.34 (42) for snags.

Habitat relationships

Northern flying squirrels reached high (for the Olympic Peninsula) abundance (CPUE > 0.4) only where there were >5 large snags/ha and where, with one exception (the mixed-age stand), prevalence of ericaceous shrub cover was \geq 40%. Flying squirrels were very low in abundance in the 400-yr-old spruce-hemlock stand (CPUE = 0.07), despite the presence of large snags (15 snags/ha) and ericaceous shrubs (prevalence = 66%). Flying squirrels were absent from one stand with 0.3 large snags/ha but were present in two stands with 0.9 snags/ha and 1.4 snags/ha. Large snags were 11 times more abundant in old stands than in young stands, and large snag densities were 0.3-35 snags/ha. Three of five young stands were in the stem exclusion phase of forest development (147-206 small snags/ha, 0-34% of stations with significant understory vegetation); these stands had low flying squirrel CPUE (0.0-0.07).

These three young stands also had low (0.0-0.15) CPUE for Townsend's chipmunk, and one had the lowest abundance of Douglas' squirrels (0.07 CPUE). Chipmunks were rare to absent in stands with the prevalence of ericaceous shrubs <40%, including the mixed-age stand and one old stand. Chipmunks were most abundant in the oldest stand with the largest trees and most coarse woody debris (the 400-yr-old spruce-hemlock stand) where flying squirrels were at their lowest abundance among the old forests.

Three variables provided the best regression equation for predicting the numbers of flying squirrels (Table 5): prevalence of ericaceous shrubs, abundance of large snags, and stand origin. These variables had good predictive power for the 11 stands and a reduced set of 5 young and 5 old-growth stands (Table 5). Only mean dbh proved to be a good predictor for Townsend's chipmunk ($R^2 = 0.61$; $F = 14.1$, $df = 2, 8$; $P = 0.006$). No significant predictors were found for Douglas' squirrels.

DISCUSSION

Limitations on interpretations

The Olympic Peninsula is characterized by sharp climatic gradients, two major stand-replacing processes (wind and fire), and the full variety of processes that influence development of any forest stand. A sample size of 11 stands is certainly not adequate to address all the variability in stand structure and mammal populations that exist even just within the Western Hemlock Zone on the peninsula. In addition, I studied sciurid populations only in the fall. Fall is probably not the limiting season for sciurids (Carey 1991). The importance of habitat elements and mammalian response to them certainly varies seasonally and annually. Populations on the peninsula were low and variable, including variability among years. I studied most stands for only 2 yr. Finally, my approach was retrospective and exploratory. Such an approach cannot demonstrate cause and effect. On the other hand, the effort applied in this study was concerted (>35 000 trap-nights and 1400 vegetation plots) and study stands were large (16 ha) compared to most small-mammal studies. And comparative data existed from three other areas. The study stands were well distributed across the western peninsula and across the range of variation to be found in closed-canopy Western Hemlock Zone stands. Relationships emerging from the analyses should prove to be robust for the western peninsula.

Regional comparisons

Forest development.—Patterns in forest development are similar across western Oregon and Washington, but there are notable differences (Spies and Franklin 1991) that could influence sciurids. Many of these differences are compositional: shade-tolerant trees such as western hemlock, Pacific silver fir (*Abies amabilis*), and western redcedar (*Thuja occidentalis*) increase from south to north; evergreen shrubs and broadleaf evergreen trees are more prevalent in the south, deciduous shrubs and lichens in the north. Fire disturbance histories decrease from south to north; concomitantly, humus, litter, and coarse woody debris increase. Rooting in mineral soil is predominant in the south, and rooting in decaying wood is most common in the north. Abundance and diversity of ectomycorrhizal hypogeous fungi appear to be substantially lower in the northern western-hemlock-dominated forests than in the southern Douglas-fir forests and greatest in the mixed-conifer forests of southwestern Oregon (J. Trappe and D. Luoma, *personal communication*).

Fungi and mammal dietaries.—Hypogeous fungi compose the bulk of the diet of the northern flying squirrels, the only exclusively mycophagous (consuming epigeous fungi, hypogeous fungi, and lichens) sciurid in the Pacific states (Gunther et al. 1983, Maser and Maser 1988, Hall 1991). North (1993) sampled hypogeous sporocarp populations in the North Cascades and on the western Olympic Peninsula (including the stands I sampled for sciurids) and compared his results with

Luoma's (1991) from the vicinity of the stands sampled by Rosenberg and Anthony (1992, 1993) in the Western Cascades in Oregon. North (1993) found that sporocarp diversity was similar between the North Cascades and Olympic Peninsula, but species richness in the northern forests was only 59% that in the central Western Cascades. Maser et al. (1985) found that flying squirrels consumed 16 species of hypogeous fungi with 3 species predominant in the dietaries of populations in old forests in the Western Cascades—values similar to mine for the southern Coast Ranges in Oregon (Table 2). Additionally, North (1993) found species evenness was substantially less in the north, with one species, *Elaphomyces granulatus*, composing 92% of the biomass in old growth: this species was rare in young stands.

North's (1993) results agree well with my diet data (Table 2): on the Olympic Peninsula, only one species occurred with a mean frequency >50%, whereas in the southern Coast Ranges, five species were consistently in the diets. Reduced species diversity of hypogeous sporocarps (North 1993) and marked seasonal and annual variation in species production of sporocarps (Luoma 1991) suggests there is a real difference between the northern and southern forests in amount of food available to mycophagists over time. Maser et al. (1986) and Hall (1991) found that flying squirrels are mycophagous year-round, with diet composition reflecting seasonal availability of fungal genera.

Carey and Johnson (1995) found an increased emphasis on insectivory and granivory and reduced emphasis on mycophagy in forest-floor mammal communities on the Olympic Peninsula compared to the Western Cascades and Coast Ranges in Oregon. The differences I report here in abundances of flying squirrels might well reflect the differences in species diversity of ectomycorrhizal fungi. Townsend's chipmunk is much less dependent on fungi than the flying squirrel (Gunther et al. 1983, McIntire and Carey 1989). It consumes a wider variety of foods (Sutton 1993), but still seems food limited (Sullivan et al. 1983).

Abundance of sciurids.—Flying squirrels were similar in abundance among the old forests in Oregon and among the old forests in Washington. But abundances in old forests in Oregon were 4 times those in old forests in Washington. Townsend's chipmunk, however, was more than twice as abundant in old forest in the Western Cascades as elsewhere (Table 1). Doyle (1985) also found densities of Townsend's chipmunks to be high (relative to flying squirrels) in the Western Cascades. Among 70 trapping samples in 19 stands over 5 yr in the southern Coast Ranges, I found Townsend's chipmunk densities to exceed 2.5 animals/ha only once (3.3 chipmunks/ha, *unpublished data*). The chipmunks in the Western Cascades old forests also had smaller movements, with mean maximum distances moved (MMDM) = 76 ± 5 m (mean \pm 1 SE) (Rosenberg and Anthony 1993) vs. 93 ± 5 m in the southern Coast Ranges old forests (Carey et al. 1991a). While some of the differences in chipmunk (and flying squirrel)

densities between the Western Cascades and southern Coast Ranges of Oregon could be due to differences in the length of the trapping period (Rosenberg and Anthony [1993] sample "more open" populations) and type of estimator used, the difference is large and appears real. It appears that the central Western Cascades old forests with large, old Douglas-fir and western hemlock, well-developed understories that include a variety of fruit and seed-producing shrubs and trees, and diverse fungal communities provides the optimal environment for Townsend's chipmunk because of the diversity of food types, especially in conifer seed and fungi. The southern Coast Ranges transition forests often are lacking in western hemlock, a consistent and prolific producer of seeds (see Carey [1991] for a review). The highest chipmunk density on the Olympic Peninsula (1.3 animals/ha compared to a mean of 0.4 animals/ha in old growth) was in the 400-yr-old spruce-hemlock stand with an understory of conifers, bigleaf maple, vine maple, and huckleberries.

Douglas' squirrel abundance varies markedly among years in response to conifer seed abundance (Smith 1970). Carey (1989) also found marked annual variation in spring Douglas' squirrel abundance measured by point counts. As in this study, Anthony et al. (1987) and Carey (1989) found no differences in Douglas' squirrel abundance among young, mature, and old-growth forests. Carey (1989) reported differences in abundance among the southern Coast Ranges, Western Cascades, and Southern Washington Cascades but, because the areas were sampled in different years, could not draw firm conclusions. Abundances were lowest in the Western Cascades (where Doyle [1985] and Rosenberg and Anthony [1993] found exceptionally high abundances of Townsend's chipmunks). Buchanan et al. (1990) found marked annual variation in winter abundances of Douglas' squirrels in the Southern Washington Cascades, but concluded that the squirrels were generally more abundant in old forests than in young forests. They concluded the greater abundance of western hemlock in old forests (compared to young stands) and the age of the old trees produced a more reliable seed source than did young stands. Sullivan and Sullivan (1982) manipulated food supply in western hemlock-Douglas-fir forests in British Columbia and concluded that food was limiting to Douglas' squirrels and that the squirrels used territorial behavior to achieve a spacing in concordance with food supply.

It appears from all available evidence (1) that Douglas' squirrels are tied to conifer seed crops despite extensive use of fungi (Maser and Maser 1988), (2) that in unmanipulated stands their abundance reflects territorial behavior adapted to protect food resources, and (3) that marked annual variation could obscure relationships with habitat variables. Northern flying squirrels are not territorial (Wells-Gosling and Heaney 1984; A. B. Carey, *personal observation*). Townsend's chipmunks show some territoriality and marked inter-specific aggression (Sutton 1993), but can achieve exceptionally high

densities (Doyle 1985, Rosenbero and Anthony 1993).

In the scramble for food resources, the Douglas' squirrel may be at a competitive disadvantage faced with both a nocturnal mycophagist (the flying squirrel) and a diurnal seed and fungal specialist (Townsend's chipmunk). Carey (1991) and Carey et al. (1991a) reported that they could not find large caches of cones typical of the genus *Tamiasciurus* despite extensive searches, and suggested the presence of the seed-eating Townsend's chipmunk could interfere with central-place storage of food. I found the greatest catch-per-unit effort of Douglas' squirrels in the North Cascades where flying squirrel and chipmunk populations were low (Table 1).

Population structure and movements.—Density is not the only measure of population response to habitat variability (Maguire 1973). Van Horne (1983) questioned the utility of density as an indicator of habitat quality, referencing concepts of population sources and dispersal sinks. Season also may influence populations (Fretwell 1972). Among the biological characteristics of the populations that I examined on the Olympic Peninsula (Table 4), I found only density of flying squirrels to be significantly different between young and old stands. Two behavioral characteristics also differed, with flying squirrels moving less and consuming a more diverse diet in old forests. Densities were greater, diets more diverse, and movements less in old forests than in young forests in the southern Coast Ranges also (Carey et al. 1991a, 1992: this study). Densities and movement relationships did not differ between spring and fall in the southern Coast Ranges (Carey et al. 1991 a, 1992). Rosenberg and Anthony (1992) found no differences in flying-squirrel demographics or distances moved between young and old forests in the Western Cascades, except sex ratios were skewed toward females in young forests.

Rosenberg and Anthony (1993) did find Townsend's chipmunk populations in the fall to be more dense and less variable and movements to be shorter in old forests than in young stands. They reported similar results for the summer. On the Olympic Peninsula, chipmunk populations were highly variable among stands and among years (with no statistically significant differences between old and young stands), but movements were less in old forest than in young forest. Chipmunks in the southern Coast Ranges were more abundant (1.9 ± 0.1 animals/ha [mean \pm 1SE]) in the fall in old forest than in young forest (1.0 ± 0.1 animals/ha, A. B. Carey, *unpublished data*); movements were more variable in young than in old stands but means did not differ (93 ± 14 m vs. 93 ± 5 m, respectively [means \pm 1 SE], Carey et al. 1991a). Results were similar in the spring. Among the various studies I found no evidence to indicate that density was a misleading indicator of environmental quality, whereas population size could be related to habitat variables of ascribable biological importance to the sciurids.

Measures of movement (including home range), when combined with demographic information, dietaries and food availability, measures of habitat characteristics

and habitat selection, and landscape structure can provide considerable insight into the ecology of species, as Carey et al. (1992) showed for the Northern Spotted Owl. In small-mammal studies the mean of the maximum distance moved (MMDM) between subsequent recaptures of individuals within a trapping period (1-14 d) is often used as a surrogate for home range size and to determine the effective area sampled by a trapping grid (White et al. 1982). As such, it is an integral part of the estimate of density, and thus not independent of density.

Estimates of MMDM, like any estimator of movement (including home range), are sensitive to (and generally increase with) number of animals caught, number of recaptures per animal, and length of sampling (trapping) period. Witt (1992) provides such data for flying squirrels in the southern Coast Ranges. Samples from low-density populations are necessarily characterized by few individuals caught, and often by few total captures; thus MMDM may underestimate distances moved. Similarly, estimates of MMDM calculated from populations where probability of recaptures are low may underestimate distances moved. Underestimates of distances moved produce overestimates of density. Overestimation is most severe (1) with small trapping grids; (2) with long, narrow trapping grids; (3) with long trapping periods when bait serves as an attractant or when animals shift den sites; and (4) where the study area may attract animals from nearby areas of different character. For example, Rosenberg and Anthony (1992, 1993) warned that, because of low recapture rates for flying squirrels, their estimates could be biased for several of these reasons. Similarly, in my studies of low-density populations on the Olympic Peninsula and North Cascades, estimates could be biased (negatively for movements and positively for density).

What MMDM measures may vary with species. Townsend's chipmunks travel on the ground (Carey 1991), and MMDM may reflect well overall distances moved within trapping periods (although trapping itself inhibits movement). Flying squirrels, however, travel through trees (Carey 1991), and MMDM may represent only movements during foraging on the ground, as Witt (1992) suggests. As Mowrey and Zasada (1984), Carey (1991), and Witt (1992) report, flying squirrels routinely change den sites, and can move large distances through tree tops in a night. Changes in den sites may or may not be accompanied by changes in foraging sites. In the fall, flying squirrels change den sites about every 2 wk, with about 25% changing nests in any 1 wk (A. B. Carey, *personal observation*). Thus, the longer the trapping period, the more individual squirrels may be trapped—and without an apparent change in MMDM. This information suggests caution must be used in interpreting MMDM: estimates are likely to be underestimates, and estimates from low-density populations are likely to be more underestimated than estimates from high-density populations.

Estimates of MMDM of flying squirrels in old forests were remarkably consistent (84-89 m) and not

significantly different among the Olympic Peninsula, Western Cascades, and southern Coast Ranges. In Western Cascades young stands where densities were not significantly different from densities in old forests, MMDM was the same (87 m). But in the southern Coast Ranges and on the Olympic Peninsula, where densities were lower than in old forests, movements were larger (102-108 m), not smaller as would be expected due to sample size. These results suggest the squirrels had to forage over larger areas where large snags or fungi were scarce. If MMDM reflect foraging movements, then the data fail to support a hypothesis of fungal diversity determining foraging area—MMDM in old growth should differ among geographic areas. But in the southern Coast Ranges, I found 4 of 5 1 seasonal populations of flying squirrels in 11 old-growth stands to be 3.0-3.7 squirrels/ha (Carey et al. 1992), the highest densities reported in the Pacific Northwest; MMDM were 60-76 m, substantially lower than the average MMDM in old forests. These data are supportive of food availability determining foraging area. On the Olympic Peninsula, I found the highest flying-squirrel density in a 57-yr-old stand that also had the highest prevalence of ericaceous shrubs. This stand had the highest MMDM I have observed for both flying squirrels (156 m) and Townsend's chipmunk (160 m), suggesting it attracted sciurids from the adjacent second-growth stands. If MMDM reflect distances from den sites to foraging areas (with areas being searched for fungi constant), then there is broad (across geographic area) agreement with a hypothesis that movement reflects large snag abundance. The data suggest, however, that foraging patch size may vary with food abundance, that number of patches used could vary, and that overall distances traveled by flying squirrels may vary with both availability of den sites and quality of foraging patches. Telemetry studies of flying squirrels will be necessary to obtain a fuller understanding of density and movements in flying squirrel populations (Rosenberg and Anthony 1992).

Habitat elements

Many of the aspects of forest development I report here are similar to those reported by Carey et al. (1991b) for the southern Coast Ranges and by Spies and Franklin (1991) for the Southern Washington Cascades, Western Cascades, and southern Coast Ranges. Abundances of snags and percentage covers of shrubs were highly variable in these data sets.

Snags.—Spies and Franklin (1991) surveyed large snags in naturally regenerated forests in the Southern Washington Cascades, the Western Cascades, and the southern Coast Ranges. They found 24 ± 2 snags/ha (0 ± 1 SE) in old forests and 25 ± 4 snags/ha in young, naturally originated stands (about 50% were well decayed). The degree to which large snags are retained in young, clear-cut-originated, managed stands is highly variable. Whereas snag densities in old forests in the

sciurid study areas were similar (17-23 snags/ha) to those reported by Spies and Franklin (1991), densities were lower and more variable in the young, managed stands: 7 ± 5 snags/ha (range: 1-26 snags/ha) in the Oregon Cascades (Rosenberg and Anthony 1993); 5 ± 2 snags/ha (range: 1-14 snags/ha) in 8 stands in the southern Coast Ranges (A. B. Carey, *unpublished data*); and 2 ± 1 snags/ha (range: 0-5 snags/ha) in Olympic Peninsula stands (Table 3). Rosenberg and Anthony (1993) noted that residual old-growth components (large coarse woody debris, snags, and live trees) in their second-growth stands may have obscured differences in animal abundances that might more generally exist between old forests and managed stands. Similar findings were reported in other studies of vertebrate communities in the Pacific Northwest (see papers in Ruggiero et al. [1991]).

Large snags with cavities (including excavations by Picidae) provide den sites for northern flying squirrels in the Pacific Northwest. But these flying squirrels also use other structures for den sites: cavities in both coniferous and deciduous live trees, cavities in suppressed and decaying pioneer species such as red alder (*Alnus rubra*), hollow branches of fallen trees, crevices in large stumps, stick nests of other species, and lichen and twig nests they construct (Wells-Gosling and Heaney 1984, Carey 1991; A. B. Carey, *personal observation*). Non-cavity nests, except for witches brooms (Mowrey and Zasada 1984), may be less secure and less thermally beneficial than cavities (Carey 1983, Wells-Gosling and Heaney 1984). Individual flying squirrels use multiple den sites, and most den sites are used simultaneously by several adult squirrels, except for maternal den sites. Multiple occupancy by adults and use of low, fragile structures by pregnant females in young, managed stands suggests that maternal den sites, in particular, may be lacking where large snags are few (A. B. Carey, T. M. Wilson, C. C. Maguire, and B. L. Biswell, *unpublished manuscript*).

Shrub abundance.—The rate at which young, managed stands pass through the stem exclusion and understory reinitiation stages is highly variable. Rosenberg and Anthony (1992, 1993) reported silvicultural treatments to their young stands (light burning, planting, fertilizing, and precommercial thinning) that may have promoted understory development, while retaining the old-growth legacies. The stands in my study areas that had been silviculturally treated (seeded or planted with Douglas-fir and thinned, or grown in an open condition) and retained large snags (but fewer than in the Western Cascades) had higher flying-squirrel densities than the clear-cuts that developed into dense, young stands of western hemlock. Mixed-age stands that contained old-growth components and a second age class of 66-100-yr old trees, in my Olympic Peninsula study areas and in southern Coast Ranges, had flying-squirrel densities of the same magnitude as undisturbed old forests.

Effects on sciurids.—Rosenberg and Anthony (1992) found no difference between young and old stands in flying-squirrel abundance. In contrast, on the Olympic Peninsula and in the southern Coast Ranges there were twice as many flying squirrels in old forests as in young stands (Carey et al. 1992). Whereas I found presence of large snags and prevalence of shrubs to be good predictors of flying-squirrel abundance, they found no relationship between large snag abundance and abundance of flying squirrels—but only one of their stands had <3 large snags/ha; they did not report the landscape context of their stands. They found only one significant correlation with a habitat variable (deciduous shrub cover) in 1 yr and suggested the result was spurious. All but one of their young stands had mean shrub covers >12%, which is equivalent to a prevalence of >40% for shrub covers >24%.

Comparative rankings on age, forest development, and flying-squirrel habitat and significant regression analyses suggest that large snags and ericaceous shrubs are associated with flying-squirrel abundance. Species composition of trees and shrubs may be important also, but can be demonstrated only by induction. Regionally, flying-squirrel abundance varied with forest type, with western-hemlock-dominated forests having fewer flying squirrels than Douglas-fir-dominated forests. Relatively high abundances of flying squirrels occurred where there were >5 snags/ha in Washington and >7 snags/ha in Oregon. On the Olympic Peninsula, lowest densities were found in young western-hemlock-dominated stands and in the old Sitka spruce-western hemlock stand. Densities in young Douglas-fir-dominated stands with salal (*Gaultheria shallon*) exceeded those in young hemlock stands. Hard-leaved ericaceous shrubs, such as salal, are most common in southern Douglas-fir forests; deciduous shrubs, such as huckleberries (*Vaccinium* spp.) are more abundant in northern western-hemlock forests. Densities of flying squirrels in old forests with Douglas-fir as a component exceeded those in the Sitka spruce-western hemlock stand.

I found that chipmunk numbers increased with size of dominant tree and were only abundant where prevalence of shrubs was >40%. While size of dominant tree can be related to seed production, it is indistinguishable from stage of forest development in many areas (Carey et al. 1991b, Spies and Franklin 1991; this study). Old forests are characterized by large trees, diverse tree species, well-developed understories (that include seed- and berry-producing shrubs and trees), abundant coarse woody debris, and, apparently, diverse fungal communities (Table 2). All are sources of food and cover for Townsend's chipmunk. Doyle (1990) also found that the abundance of Townsend's chipmunk increased with understory development, particularly evergreen shrubs. Rosenberg and Anthony (1993) found abundance of large snags in old forests (but not young stands) to be a good predictor of chipmunk abundance, but, in the absence

of apparent biological value to chipmunks, suggested large snags could be a surrogate for other features of the forest. I found large snags in old forests to be highly correlated with tall understory development which provides food and cover. However, on the Olympic Peninsula, tall understory cover was not a good predictor of the abundance of either Townsend's chipmunks or flying squirrels.

Implications for forest management

The regional comparisons I report here add further substantiation to the relationship between prey biomass and amount of old forest used by Spotted Owls as reported by Carey et al. (1992). The North Cascades data support the finding of low densities of the primary prey (flying squirrels) of the Spotted Owl in Washington where the amounts of old forests used are large. Rosenberg and Anthony's (1992) results support the findings of high flying-squirrel abundance in Oregon where amounts of old forest used are moderate. Amount of old forest used by Spotted Owls is lowest where high flying-squirrel populations and high woodrat populations (*Neotoma* spp.) occur in the Mixed-Conifer and Mixed-Evergreen Zones of southern Oregon and northern California (Carey et al. 1992).

The regional analysis of densities, dietaries, and fungal abundance strengthens the functional links among forest type, fungi, flying-squirrel abundance, and Spotted Owl use of old forests in the Pacific Northwest hypothesized by Carey et al. (1992). The contrasts of flying-squirrel abundances relative to snag abundances and ericaceous shrubs across the region and the demonstration that these habitat elements function somewhat independently of forest age suggest potential for silvicultural manipulations that could help accelerate the development of Spotted Owl habitat and help to restore old-growth conditions in areas where old forests are lacking. The high densities of flying squirrels in Rosenberg and Anthony's (1992) stands that had old-growth legacies and silvicultural treatments that stimulate understory production, in particular, demonstrate this potential. The high flying-squirrel densities in the 57-yr-old Douglas-fir-salal stand and the wind-created, mixed-age stand, both with remnant snags, suggests such improvement is possible in Washington. Similarly, mixed-aged stands with high flying-squirrel densities suggest the same potential in the southern Coast Ranges of Oregon. Spotted Owls do forage in young forest; where they forage in young forest, there is a high vertical diversity of vegetation, including an abundance of shrubs (Carey et al. 1992).

I suggest that thinnings can be used to promote understory development and that direct habitat improvements, particularly creating cavities in live trees (Carey and Sanderson 1981, Carey and Gill 1983), can be used to create long-lived den sites for flying squirrels and, eventually, for other cavity-

using wildlife. Manipulation of vegetation and provision of cavities in live trees that could result in increased flying-squirrel densities could have synergistic effects by the squirrels' dissemination of fungal spores that could promote fungal abundance and diversity and the growth of woody plants. This suggestion has been framed as a testable hypothesis, and I have implemented a complete randomized-block experiment to test this hypothesis. A video tape of the cavity-creating process and an accompanying summary and rationale for the experimental treatments is available upon request (Carey 1993b).

Carey and Johnson (1995) discuss thoroughly strategies for conservation of coarse woody debris, woody plant species diversity, and promotion of understory abundance to enhance biodiversity, emphasizing forest-floor small mammals. Their strategies would be of benefit to flying squirrels, Townsend's chipmunks, and Douglas' squirrels, the fungi consumed by these sciurids, and the terrestrial and avian predators of the squirrels. Here, I add a recommendation for retaining all large (>50 cm dbh) snags up to 20 snags/ha in the forest and providing new snags by creating cavities in trees where large snags are <5 snags/ha in Washington and <7 snags/ha in Oregon and the objective is to accelerate development of Spotted Owl habitat or restore old-growth conditions. I do not suggest that managed stands can duplicate all the functions and benefits of old-growth forests, only that ecosystem management can do much to conserve biodiversity.

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LITERATURE CITED

- Anthony, R. G., E. D. Forsman, G. A. Green, G. Witmer and S. K. Nelson. 1987. Small mammal populations in riparian zones of different-aged coniferous forests. *Murrelet* **68**:94-102.
- Buchanan, J. B., R. W. Lindquist, and K. B. Aubry. 1990. Winter populations of Douglas' squirrels in different-aged Douglas-fir forests. *Journal of Wildlife Management* **54**: 577-581.

- Carey, A. B. 1983. Cavities in trees in hardwood forests. Pages 167-184 in Snag habitat management: proceedings of a symposium. USDA Forest Service General Technical Report **RM-99**.
- _____. 1989. Wildlife associated with old-growth forests of the Pacific Northwest. *Natural Areas Journal* **9**:151-162.
- _____. 1991. The biology of arboreal rodents in Douglas-fir forests. USDA Forest Service General Technical Report **PNW-GTR-276**.
- _____. 1993a. Prey ecology and Northern Spotted Owl diet. *Journal of Raptor Research* **27**:53-54.
- _____. 1993b. Creating cavities in trees—one facet of ecosystem management. Don Gedney Video Productions. Accompanying circular: Experimental manipulation of managed stands to provide habitat for Spotted Owls and to enhance plant and animal diversity. USDA Forest Service Pacific Northwest Research Station, Olympia, Washington, USA.
- Carey, A. B., B. L. Biswell, and J. W. Witt. 1991a. Methods for measuring populations of arboreal rodents. USDA Forest Service General Technical Report **PNW-GTR-273**.
- Carey, A. B., and J. D. Gill. 1983. Direct habitat improvements—some recent advances. Pages 80-87 in Snag habitat management: proceedings of a symposium. USDA Forest Service General Technical Report **RM-99**.
- Carey, A. B., M. M. Hardt, S. P. Horton, and B. L. Biswell. 1991b. Spring bird communities in the Oregon Coast Ranges. Pages 123-144 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service General Technical Report **PNW-GTR-285**.
- Carey, A. B., S. P. Horton, and B. L. Biswell. 1992. Northern Spotted Owls: influence of prey base and landscape character. *Ecological Monographs* **62**:223-250.
- Carey, A. B., and M. L. Johnson. 1995. Small mammals in managed, naturally young, and old-growth forests. *Ecological Applications* **5**:336-352.
- Carey, A. B., and H. R. Sanderson. 1981. Routing to accelerate tree-cavity formation. *Wildlife Society Bulletin* **9**: 14-21.
- Carey, A. B., and T. A. Spies. 1991. Sampling design of the old-growth forest wildlife habitat program. Pages 9-16 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service General Technical Report **PNW-285**.
- Dixon, W. J. 1990. BMDP statistical software manual. University of California Press, Berkeley, California, USA.
- Doyle, A. T. 1985. Small mammal micro- and macrohabitat selection in streamside ecosystems. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- _____. 1990. Use of riparian and upland habitats by small mammals. *Journal of Mammalogy* **71**:14-23.
- Franklin, J. F., K. Cromack, Jr., W. Denison, A. McKee, C. Maser, J. Sedell, F. Swanson, and G. Juday. 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA Forest Service General Technical Report **PNW-118**.
- Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service General Technical Report **PNW-8**.
- Fretwell, S. D. 1972. Populations in a seasonal environment. *Monographs in Population Biology* **5**:1-217.
- Gunther, P. M., B. S. Horn, and G. D. Babb. 1983. Small mammal populations and food selection in relation to timber harvest practices in the western Cascade Mountains. *Northwest Science* **57**:32-44.
- Hall, D. S. 1991. Diet of the northern flying squirrel at Sagehen Creek, California. *Journal of Mammalogy* **72**:615-617.
- Harestad, A. S. 1991. Spatial behavior of Townsend's chipmunks and habitat structure. *Acta Theriologica* **36**:247254.
- Henderson, J. A., D. H. Peter, R. D. Leshner, and D. C. Shaw. 1989. Forested plant associations of the Olympic National Forest. USDA Forest Service Pacific Northwest Region Technical Paper **R6-ECOL 001-88**.
- Lundquist, R. W., and J. M. Mariani. 1991. Nesting habitat and abundance of snag-dependent birds in the southern Washington Cascade Range. Pages 221-240 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service General Technical Report **PNW-285**.
- Luoma, D. L. 1991. Annual changes in seasonal production of hypogeous sporocarps in Oregon Douglas-fir forests. Pages 83-89 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service General Technical Report **PNW-285**.
- Maguire, B., Jr. 1973. Niche response structure and the analytical potentials of its relationship to the habitat. *American Naturalist* **107**:213-246.
- Maser, C., and Z. Maser. 1988. Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. *Great Basin Naturalist* **48**:358-369.
- Maser, C., Z. Maser, J. W. Witt, and G. Hunt. 1986. The northern flying squirrel: a mycophagist in southwestern Oregon. *Canadian Journal of Zoology* **64**:2086-2089.
- Maser, Z., C. Maser, and J. M. Trappe. 1985. Food habits of the northern flying squirrel (*Glaucomys rabinus*) in Oregon. *Canadian Journal of Zoology* **63**:1084-1088.
- McIntire, P. W., and A. B. Carey. 1989. A microhistological technique for analysis of food habits of mycophagous rodents. USDA Forest Service Research Paper **PNW-RP-404**.
- Menkens, G. E., Jr., and S. H. Anderson. 1988. Estimation of small-mammal population size. *Ecology* **69**:1952-1959.
- Mowrey, R. A., and J. C. Zasada. 1984. Den tree use and movements of northern flying squirrels in interior Alaska and implications for forest management. Pages 35 1-356 in W. R. Meehan, T. R. Merrell, and T. A. Hanley, editors. Fish and wildlife relationships in old-growth forests: proceedings of a symposium. American Institute of Fishery Research Biologists, Moorhead City, North Carolina, USA.
- Nelson, L., Jr., and F. W. Clarke. 1973. Correction for sprung traps in catch/effort calculations of trapping

- results. *Journal of Mammalogy* **54**:295-298.
- North, M. P. 1993. Stand structure and truffle abundance associated with Northern Spotted Owl habitat. Dissertation. University of Washington, Seattle. Washington, USA.
- Norusis, M. J. 1993. SPSS for Windows. Base system user's guide. Release 6.0. SPSS. Inc., Chicago, Illinois, USA.
- Old-growth Definition Task Group. 1986. Interim definitions for old-growth Douglas-fir and mixed-conifer forests in the Pacific Northwest and California. USDA Forest Service Research Note **PNW-447**.
- Oliver, C. D., and B. C. Larson. 1990. Forest stand dynamics. McGraw-Hill, New York, New York, USA.
- Rosenberg, D. K., and R. G. Anthony. 1992. Characteristics of northern flying squirrel populations in young second and old-growth forests in western Oregon. *Canadian Journal of Zoology* **70**:161-166.
- Rosenberg, D. K., and R. G. Anthony. 1993. Differences in Townsend's chipmunk populations between second- and old-growth forests in western Oregon. *Journal of Wildlife Management* **57**:365-373.
- Ruggiero, L. F., K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. 1991. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service General Technical Report **PNW-285**.
- Skalski, J. R., and D. S. Robson. 1992. Techniques for wildlife investigations: design and analysis of capture data. Academic Press. San Diego, California, USA.
- Smith, C. C. 1968. The adaptive nature of social organization in the genus of three squirrels *Tamiasciurus*. *Ecological Monographs* **38**:31-63.
- _____. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. *Ecological Monographs* **40**:349-374.
- Smith, J. E. 1993. Occurrence of ectomycorrhizae on ericaceous and conifer seedlings grown in soils from the Oregon Coast Range. Thesis. Oregon State University, Corvallis, Oregon, USA.
- Sokal, R. R., and F. J. Rohlf. 1981. Biometry: the principles and practice of statistics in biological research. Second edition. W. H. Freeman, San Francisco. California, USA.
- Spies, T. A., and J. F. Franklin. 1991. The structure of natural young, mature, and old-growth forests in Oregon and Washington. Pages 91-109 in L. R. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service General Technical Report **PNW-285**.
- Sullivan, T. P., and D. S. Sullivan. 1982. Population dynamics and regulation of the Douglas squirrel (*Tamiasciurus douglasii*) with supplemental food. *Oecologia* **53**:264-270.
- Sullivan, T. P., D. S. Sullivan, and C. J. Krebs. 1983. Demographic response of a chipmunk (*Eutamias townsendii*) population with supplemental food. *Journal of Animal Ecology* **52**:743-755.
- Sutton, D. A. 1993. *Tamias townsendii*. *Mammalian Species* **435**:1-6.
- Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, and J. Verner. 1990. A conservation strategy for the Northern Spotted Owl. Report of the interagency committee to address the conservation strategy of the Northern Spotted Owl. USDA Forest Service, Portland, Oregon. USA.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* **47**:893-901.
- Volz, K. 1986. Habitat requirements of northern flying squirrels in west-central Oregon. Thesis. Washington State University. Pullman, Washington. USA.
- Wells-Gosling, N., and L. R. Heaney. 1984. *Glaucomys sabrinus*. *Mammalian Species* **229**:1-8.
- White, G. C., D. R. Anderson, K. P. Burnham, D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Publication LA-8787-NERP. Los Alamos National Laboratory. Los Alamos. New Mexico. USA.
- Wilson, K. R., and D. R. Anderson. 1985. Evaluation of two density estimators of small mammal population size. *Journal of Mammalogy* **66**:13-21.
- Witt, J. W. 1992. Home range and density estimates for the northern flying squirrel. *Glaucomys sabrinus*, in western Oregon. *Journal of Mammalogy* **73**:921-929.