WINTER POPULATIONS OF DOUGLAS' SQUIRRELS IN DIFFERENT-AGED DOUGLAS-FIR FORESTS

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Abstract: We counted Douglas' squirrels (*Tamiasciurus douglasii*) along established transects in naturally regenerated old-growth and younger Douglas-fir (*Pseudotsuga menziesii*) forests in the Cascade Range of southern Washington State during 3 consecutive winters beginning in 1983–84. Squirrel populations were generally higher in old-growth forests and varied dramatically from year to year in synchrony with variations in the annual production of conifer cones. Old-growth forests appear to provide higher-quality habitat for Douglas' squirrels than younger forests due to greater and more reliable quantities of conifer seeds. Converting old-growth Douglas-fir forests to even-aged plantations of younger Douglas-fir would probably result in lower Douglas' squirrel populations. Alternative silvicultural strategies designed to provide increased levels of cone production over time may be an effective means of improving the habitat quality of young forests for Douglas' squirrels.

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In the Pacific Northwest, tree squirrels of the genus *Tamiasciurus* defend individual territories throughout the year that vary in size as an inverse function of the density of available food (Smith 1968, Sullivan and Sullivan 1982). Squirrels that survive the winter period of food scarcity either subsist upon conifer cones or dried fungi collected and cached the previous fall, or emigrate to other areas containing adequate food (Bailey 1936; Smith 1968, 1981).

In Douglas-fir-western hemlock (*Tsuga heterophylla*) forests of the Pacific Northwest, yearly cone production for Douglas-fir can range from absence to superabundance. Douglas-fir cone production generally follows a 2–7-year cycle between average to above-average cone crops (Allen and Owens 1972). Cone production records since 1909 from the west slope of the Cascade Range in Washington and Oregon, however, show that abundant cone crops occur in this region about once every 3 years (Anonymous 1909–89). Western hemlock cone production also generally follows a 3–4-year cycle but, unlike Douglas-fir, at least some seed is produced every year (Fowells 1965). Population densities of Douglas' squirrels fluctuate dramatically in response to seasonal or annual variation in food supply (Smith 1970, Sullivan and Sullivan 1982), with highest densities occurring every 3 or 4 years (Flyger and Gates 1982). During the years of Douglas-fir cone failure, particularly in a succession of low years, Douglas' squirrel populations decline as a result of a decrease in available food (Smith 1970).

In the Pacific Northwest, conversion of old-growth Douglas-fir forests to younger, even-aged plantations has raised concerns about the potential loss or degradation of this unique ecosystem, especially as wildlife habitat (Franklin et al. 1981, Meslow et al. 1981, Ruggiero and Carey 1984). Forest and wildlife managers are being asked to provide recommendations and guidelines for resource management decisions, yet information on the importance of old-growth forests to wildlife is limited.

The objectives of our study were to (1) compare winter populations of Douglas' squirrels in young and old-growth Douglas-fir forests, (2) monitor trends in Douglas' squirrel populations in these forests over successive years, and (3) relate patterns of variation in Douglas' squirrel populations to variation in habitat features.

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STUDY AREA

We studied 15 forest stands dominated by Douglas-fir and western hemlock in 2 geographic regions in the Cascade Range of southern Washington: 8 stands near the Columbia Gorge in the southern portion of the Gifford Pinchot National Forest and 7 stands in the northern Gifford Pinchot National Forest and in Mount Rainier National Park, approximately 100 km to the north. The study areas were located in the western hemlock zone and in lower elevations of the Pacific silver fir (*Abies amabilis*) zone as described by Franklin and Dyrness (1973). Both forest zones are characterized by a wet and mild maritime climate with heavy precipitation occurring mostly in winter.

Stands were classified into 2 broad age classes. Northern sites consisted of 4 young stands (60–165 yr) and 3 old-growth stands (250–730 yr); southern sites consisted of 4 young stands (42–140 yr) and 4 old-growth stands (all 375 yr). Stand elevations ranged from 415 to 850 m. All stands resulted from natural regeneration following catastrophic fires; none underwent extensive silvicultural treatments. Old-growth stands typically contained large numbers of both Douglas-fir and western hemlock and, in wet sites, western redcedar (*Thuja plicata*); young stands were dominated by Douglas-fir (Spies In Press). In both age classes, other species such as red alder (*Alnus rubra*), vine maple (*Acer circinatum*), bigleaf maple (*A. macrophyllum*), Pacific silver fir, and western hemlock occurred in lesser amounts.

METHODS

Sampling Procedures.—Douglas' squirrels give territorial calls to advertise occupancy and in response to intrusion by conspecifics and other species (Smith 1968). We recorded both territorial calls and visual observations, and we used these data to estimate the relative abundance of squirrels in each stand. We attempted to count each individual only once. At the 8 southern stands, we counted Douglas' squirrels in each of 3 winters (mid-Dec to mid-Mar) from 1983 to 1986. At the 7 northern stands, data were collected in 2 winters from 1984 to 1986. We counted all squirrels encountered at or between census points along transects established to conduct variable circular plot (Reynolds et al. 1980) surveys of diurnal bird populations. Squirrels were also counted within 75 m of the transect line as we entered or departed each stand. During winter 1985–86, we also estimated distances to squirrels detected from sample points and used the computer program TRANSECT (Burnham et al. 1980) to calculate squirrel densities in each stand. Density estimates derived from program TRANSECT account for potential differences in squirrel detectability among stands and therefore provide a means to evaluate the reliability of our estimates of relative abundance from count data.

Four visits were made to each stand in 1983–84 and 1984–85, whereas in 1985–86, each stand was visited 8 times. Counts were conducted for 8 minutes at each of 12 points spaced 150 m apart along established transects. Transects were located at least 75 m within the boundaries of each stand. Mean survey duration (including movement between stations) was approximately 2.5 hours. All surveys were conducted between 0900 and 1600 hours, which is within the peak activity period reported for *Tamiasciurus* (Smith 1968). Most surveys were conducted in fair weather, but on occasion, a light drizzle or snow fell. Ambient temperatures during censuses ranged from −6 to 10 C.

Data Analysis.—Data collected at the same site in successive years are not independent. Consequently, we used a split-plot-in-time ANOVA to examine differences between seral stages and among years in each study area (Wilkinson 1988). Because our sample was stratified into northern and southern study areas and because cone production varies substantially between these regions (S. R. Martinson, USFS, pers. commun.), data for each area were analyzed separately. To stabilize variances, data from the southern stands were log-transformed before analysis.

To calculate density estimates from TRANSECT, we used a minimum of 30 detections to establish probability density functions [$f(0)$ values] for each stand. For stands in which Douglas' squirrel counts were <30, $f(0)$ values were calculated by pooling data within each age class. Fourier series models generally provided the best fit to the distance data, but we also used exponential polynomial models.

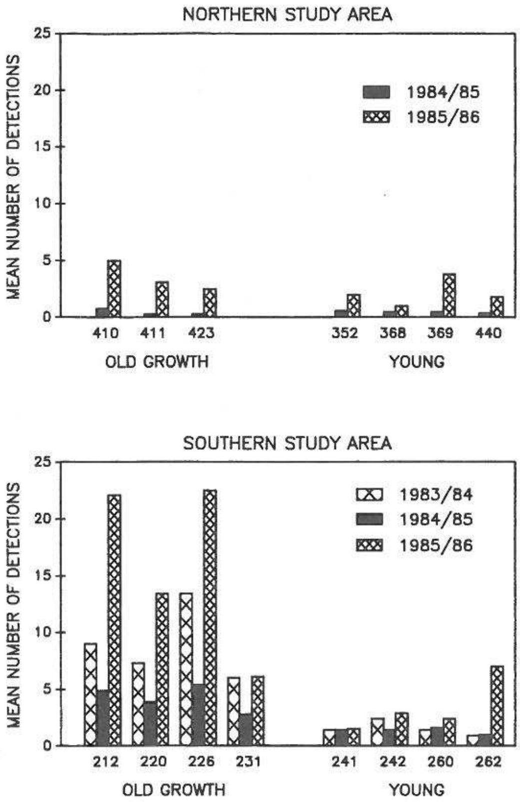

Fig. 1. Mean number of Douglas' squirrel detections in each study stand. Stand numbers are shown at the bottom of each set of histograms. Data for northern stands for 1984–86 are shown in the upper graph, and data for southern stands from 1983–86 are shown in the lower graph. Cone availability was highest in 1985–86 and lowest in 1984–85.

RESULTS

Counts and Density Estimates.—In old-growth stands, mean counts of squirrels were higher in the southern study area than in the northern study area (Fig. 1). In winter 1984–85, counts in old-growth stands were 9.4 times higher in the south than in the north, whereas in winter 1985–86 they were 5.2 times higher. Strong regional differences in mean squirrel counts in young stands, however, were not evident; counts were relatively low in both study areas (Fig. 1). In 1984–85, mean squirrel counts in young stands were 2.6 times higher in the southern study area than in the northern stands, whereas in 1985–86, they were only 1.5 times higher.

Mean squirrel counts were significantly different both between age classes and among years in the southern study area (Table 1). Although mean counts in the northern study area were also significantly different between years, they did not differ significantly between age classes. In all stands sampled, mean squirrel counts were highest in the winter of 1985–86 (Fig. 1).

Table 1. Split-plot ANOVA for mean squirrel counts in western Washington during winters from 1984 to 1986.

Source	df	SS	MS	*F*	*P*
Northern study area					
Age class	1	1.56	1.56	1.68	0.251
Error	5	4.65	0.93		
Yr	1	19.07	19.07	30.38	0.003
Error	5	3.14	0.63		
Age class × yr	1	1.72	1.72	2.74	0.159
Error	5	3.14	0.63		
Southern study area					
Age class	1	13.46	13.46	46.94	0.000
Error	6	1.72	0.29		
Yr	2	4.16	2.08	13.36	0.001
Error	12	1.87	0.16		
Age class × yr	2	0.45	0.22	1.43	0.277
Error	12	1.87	0.16		

Mean density estimates in both age classes were 5 times higher in the southern study area than in the northern study area (Table 2). In both study areas, mean densities of squirrels were 3 times higher in old-growth than in younger forests. Results derived from both surveys and density estimates indicate that Douglas' squirrels were more abundant in old-growth stands than in younger forests during winter. Only in the southern study area, however, were counts significantly higher in old growth (Table 1). Patterns of variation among density estimates are similar to those found in the count data, except for the much lower abundance values in old-growth stands in the northern study area derived from count data (Fig. 1, Table 2). Because these density estimates account for potential differences in squirrel detectability among stands (Reynolds et al. 1980), environmental or behavioral factors may have impaired our ability to detect squirrels in old-growth stands in the northern study area.

Correlations with Cone Crops.—In the southern Washington Cascade Range, Douglas-fir and western hemlock cone production was described as "very good" in 1982 and 1985, but "very poor" and "extremely poor" in 1983 and 1984, respectively (Anonymous 1982–85). An-

Table 2. Density estimates (*n*/40 ha) of Douglas' squirrels in Douglas-fir forests during winter 1985–86 in western Washington.

	Stands							
	Old-growth				Younger			
Study area	Stand no.	Total count	Density	*f*(0)[a]	Stand no.	Total count	Density	*f*(0)
Northern	410	39	10.9	0.669	352	14	2.1	0.355
	411	17	6.0	0.846	368	8	1.2	0.355
	423	16	5.6	0.846	369	22	3.3	0.355
					440	11	3.5	0.764
Southern	212	126	57.5	1.105	241	11	3.5	0.764
	220	64	24.7	0.925	242	18	5.7	0.764
	226	127	49.4	0.933	260	16	7.6	1.145
	231	33	16.1	1.173	262	44	30.4	1.657

[a] Probability density function.

nual variations in our squirrel counts were closely synchronized with these qualitative differences in cone production (Fig. 1). Squirrel populations were moderate in the winter of 1983–84, following a year of very poor cone production that was preceded by a very good year. Low abundances of squirrels in winter 1984–85 followed 2 successive years of very poor cone production. Cone production improved dramatically in 1985 and was followed by high abundances of squirrels in the winter of 1985–86. Because we measured squirrel populations both after a very good cone year and after 2 successively low years, it is likely that we measured much of the range of variation in numbers that these populations exhibit.

DISCUSSION

Regional variation in cone production apparently accounts for the much higher number of Douglas' squirrels found in the southern study area. The southern stands occur in the highest cone-producing region within the Gifford Pinchot National Forest (S. R. Martinson, pers. commun.). In addition, there is a localized area of superabundant cone production adjacent to stand 262 (young), which may explain the relatively high numbers of squirrels detected in this stand during the winter of 1985–86.

Because Douglas' squirrel populations are limited by food supply and, in particular, by the availability of conifer seeds in winter (Smith 1968, 1970), the higher squirrel abundances we observed are probably due to greater and more reliable quantities of conifer seeds in old growth than in younger forests. Manuwal and Huff (1987), who worked in the same stands we sampled, reported that in winter, seedeating birds were also much more abundant in old growth than in younger forests.

Maximum seed production in Douglas-fir occurs between 200 and 300 years of age (Fowells 1965), after the stand has attained old-growth characteristics (Franklin et al. 1981). In addition, open-grown Douglas-fir trees receiving sunlight from all directions produce about 10 times as much seed as trees in a closed stand (Fowells 1965). Old-growth Douglas-fir forests are characterized by a multilayered canopy that often contains gaps resulting from the death of senescent individuals. Typically, a stand is 200–250 years old before it begins to develop this structural diversity (Franklin et al. 1981). Consequently, the structure of old-growth stands results in greater amounts of foliage receiving direct sunlight than in younger stands with a more uniform canopy, possibly resulting in higher levels of cone production in old-growth forests. Old-growth stands also typically contain higher proportions of western hemlock than younger stands (Franklin et al. 1981, Spies In Press). Because hemlock produces at least some cones every year, old-growth stands may also provide more conifer seed resources than young stands, especially during years of total cone failure for Douglas-fir (Manuwal and Huff 1987).

At least in some areas, old-growth Douglas-fir forests support significantly higher numbers of Douglas' squirrels than do younger forests. Squirrel populations also differed significantly from year to year in both study areas in synchrony with the annual production of conifer cones. Ecological, structural, and physiological differences between old-growth and younger stands strongly suggest that the higher squirrel populations we observed in old-growth stands result from higher levels of Douglas-fir and western hemlock seed production in old-growth forests. Because Douglas' squirrel populations fluctuate from year to year in response to changing environmental conditions (Smith 1981), local extinctions may occur in low-quality habitats during a succession of poor cone crops. Residual squirrel populations in old-growth forests may serve as a source from which unoccupied territories can be recolonized.

MANAGEMENT IMPLICATIONS

The younger stands we sampled had regenerated following catastrophic wildfires, and they contain vegetative and structural features characteristic of old-growth forests, such as residual old-growth trees, large logs, and snags (Spies and Franklin 1988). These features, which may contribute to increased levels of cone production or available cache sites, do not typically occur in intensively managed forests (Spies and Cline 1988). Forest management practices that replace multilayered, old-growth Douglas-fir forests containing a high proportion of western hemlock with younger, even-aged, Douglas-fir plantations would be expected to adversely affect Douglas' squirrel populations.

Alternative silvicultural strategies designed to provide a broad spectrum of ecological values in managed forests (Franklin 1989) may have implications for the management of Douglas' squirrels. For example, retaining green trees to ensure the continued production of cones, planting mixed species to provide alternate seed sources during years of Douglas-fir cone failure, and harvesting that results in multilayered or irregular canopies would all be expected to improve the habitat quality of managed forests for Douglas' squirrels.

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