EFFECTS OF NEW FOREST MANAGEMENT STRATEGIES ON SQUIRREL POPULATIONS

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Abstract. Two strategies for managing forests for multiple values have achieved prominence in debates in the Pacific Northwest: (1) legacy retention with passive management and long rotations, and (2) intensive management for timber with commercial thinnings and long rotations. Northern flying squirrels *(Glaucomys sabrinus),* Townsend's chipmunks (*Tamias townsendii*), and Douglas' squirrels (*Tamiasciurus douglasii*) were studied retrospectively in Douglas-fir (*Pseudotsuga menziesii*) forests managed under the alternative strategies in the Puget Trough of Washington. Flying squirrels were twice as abundant under legacy retention as under intensive management for timber, almost as abundant as in old-growth western hemlock (*Tsuga heterophylla*) forests on the Olympic Peninsula of Washington, but <50% as abundant as in old-growth Douglas-fir forests in western Oregon. Chipmunks were four times as abundant under intensive timber management, as under legacy retention, but less abundant than in old-growth forests. Abundance of Douglas' squirrels did not differ between strategies. Neither strategy produced the increased abundance of all three species that is an emergent property of late-seral forests. A third strategy holds promise: active, intentional ecosystem management that incorporates legacy retention, variable-density thinning, and management for decadence.

Key words: biodiversity; Douglas-fir; ecosystem management; forest ecology; forest management; Glaucomys sabrinus; *managed forest; Pacific Northwest; silviculture; squirrels;* Tamias townsendii; Tamiasciurus douglasii; *thinning; old growth restoration.*

INTRODUCTION

Two types of forest management have been prevalent in the Pacific Northwest (Kohm and Franklin 1997, Parminter 1998) and elsewhere: extensive and intensive (Swedish National Board of Forestry 1990, Plochman 1992, Hart 1995, Savill et al. 1997, Perry 1998). In the Pacific Northwest, merchantable forests were clear-cut, new forests were regenerated naturally or were planted, and new stands were left to grow without further intervention until harvest, generally at 40-50 yr on industrial land and 50-70 yr on public land. The extent of preparation of the site for a new stand, and the extent to which components of the previous stand (live trees, standing dead trees, fallen decaying trees, and other vegetative and fungal components) were retained after harvest, varied greatly from stand to stand and across the Pacific Northwest. With intensive management, merchantable stands were clear-cut; sites were burned to reduce debris and expose mineral soil; new stands were regenerated naturally or by planting; vegetation that competed with trees was controlled manually or chemically; sometimes precommercial thinnings were used to reduce stem density and promote rapid growth; sometimes commercial thinnings were used to obtain an early financial return, maintain growth, and reduce mortality due to self-thinning; and stands were bar

vested again through clear-cutting at an age (e.g., 4090 yr) commensurate with the landholder's marketing strategy. With both approaches, however, extensive clear-cutting had negative environmental consequences, alienated much of the public, and failed to capitalize on the productive capacity of the land (Curtis and Carey 1996, DeBell et al. 1997).

With increased worldwide concern for managing ecosystems to conserve biodiversity (Reid and Miller 1989, Hunter 1990, Swedish National Board of Forestry 1990, Plochman 1992, Goodland 1995, Perry 1998), several variations on traditional timber management have been suggested for lands managed jointly for economic and environmental values. Two approaches are commonly suggested in forest management literature and habitat conservation plans in the Pacific Northwest. Extensive management for high canopy closure and long rotations (>90 yr) after retention of standing live trees, standing dead trees, and fallen trees at harvest, singly and in patches, has been suggested as one pathway to maintaining or restoring natural biodiversity in second-growth forests; I refer to this approach as legacy retention (Hopwood 1991, Franklin 1993, Franklin et al. 1997). Repeated intermediate harvests (e.g., thinnings) are not recommended in legacy retention scenarios (Hopwood 1991). Some plans assume late-seral forest will develop automatically from reserved second-growth stands, with or without legacies (e.g., Forest Ecosystem Management Assessment Team 1993).

Another commonly suggested approach is intensive management that includes (but is not limited to) multiple commercial thinnings and long rotations to produce forests with developed understories that are hypothesized to function as late-seral, natural forest. This approach, emphasizing growing large trees through long rotations, has been called "high-quality forestry" (Weigand et al. 1993), but is more appropriately labeled management for high-quality timber (Perry 1998); hereafter, I refer to this strategy as management with thinnings. Because active management of second-growth forests on long rotations in the Pacific Northwest is a relatively recent phenomenon, and because early clear-cutting left behind highly variable stand conditions, few studies have attempted to evaluate empirically (retrospectively or prospectively) management strategies for second-growth forests. Prospective experimental studies would require >100 yr to evaluate a strategy. Most studies of the environmental effects of forest management have focused on the short-term (<5 yr) effects of particular silvicultural practices, such as clear-cutting or other harvest methods (Hooven and Black 1976, LaMothe 1980, Hayes et al. 1995, Waters and Zabel 1995, Von Treba et al. 1998); herbicide application (Slagsvold 1977, Cole et al. 1998, Easton and Martin 1998, Sullivan et al. 1998); intermediate partial harvests, such as thinning (Conroy et al. 1982, Carey et al. 1996b, Hagar et al. 1996); or more general broad-scale comparisons of old growth and second growth (e.g., Carey 1995, Carey and Johnson 1995, Bobiec 1998). Simulations of alternative management strategies based on broad-scale data, suggest ecologically significant differences among alternative strategies (e.g., Carey et al. 1996a, 1999b, Pausas et al. 1997). While heuristic, simulations are merely examinations of the simulators' assumptions and inferences drawn from correlative retrospective studies (e.g., Carey 1998b).

Many second-growth forests on both private and public lands in the Pacific Northwest are just now reaching a merchantable age. Decisions are being made on their disposition and future management, with many assumptions and implications for conservation of species associated with late-seral forests, especially the Northern Spotted Owl (*Strix occidentalis caurina*) (Thomas et al. 1990, Forest Ecosystem Management Assessment Team 1993, Carey 1998a, b). These decisions are often made in an adversarial context within which inferences drawn from retrospective comparisons of natural and variously managed forests are discounted, both because the studies are broad-scale retrospectives, and because the management evaluated is not representative of current management practices (*personal observation*). Thus, there is an urgent need for (1) retrospective examination of second-growth stands representative of commonly recommended forest management strategies (Thomas et al. 1993), and (2) determination of the potential of alternative strategies for promoting late-seral forest conditions (Thomas et al. 1990,

Forest Ecosystem Management Assessment Team 1993).

Ideally, such an examination would be in the form of the response of a key species or species group. Forest squirrels have been found particularly responsive to forest environmental conditions (e.g., Carey 1995, Scheibe and Robins 1998, Taulman et al. 1998, Wauters and Dhondt 1998). In the Pacific Northwest, the northern flying squirrel (*Glaucomys sabrinas*), Townsend's chipmunk (*Tamias townsendii*), and Douglas' squirrel (*Tamiasciurus douglasii*) constitute a group of species whose abundance and reproduction is responsive to environmental variability and differences in management history (Carey 1995, 1998b, 1999). This group's abundance is a good measure of (1) carrying capacity of Douglas-fir forests for predators including owls, raptors, and mustelids (Carey et al. 1992, Carey and Peeler 1995, Carey 1998b); (2) reproductive activity of ectomycorrhizal fungi, trees, and shrubs (Smith 1970, Carey et al. 1992, 1996b, 1999a, Sutton 1993); and (3) capacity for dissemination of fungal spores and propagules of lichens and mosses (Maser et al. 1978, Hayward and Rosentreter 1994, Carey 1995, 1996, 1998a, b, Carey et al. 1997, 1999a, b). As late-seral forests develop, interactions of complexes of habitat elements at fine spatial scales allow simultaneous increases in the abundance of each of the squirrel species, despite overlap in their food, den, and space requirements (Carey 1995, Carey et al. 1997, 1999a). Thus, management strategies purported to accelerate development of late-seral forest conditions can be evaluated by (1) the absolute abundances of the three species of squirrels relative to their abundances in old growth, and (2) simultaneous increases in abundance over time. Low abundances (relative to old growth) and divergent population trends among the species would suggest important ecosystem processes are being mismanaged (Carey et al. 1999a, b).

In this paper, I report the response of forest squirrel populations to management by legacy retention and management with thinnings in a retrospective quasi-experiment (Cook and Campbell 1979, Hoaglin et al. 1991). I compare my quasi-experimental results with results reported from other retrospectives of natural and managed forests in the Pacific Northwest. My data also are baseline data for a 20-yr management experiment that was subsequently imposed on the stands (Carey et al. 1999c).

STUDY AREAS

Building upon a region-wide search for retrospective study areas (Thomas et al. 1993), I contacted private and public landowners in western Washington and inspected the areas they had available for study and experimental manipulation. I was particularly interested in homogeneously treated blocks of forests that would allow replication of experimental treatments and whose

TABLE 1. Means and standard errors (in parentheses) of salient features of the study areas in Thurston County, Washington, USA (1991–1993).

Feature	Star	Stellar	Farley	Hill
Number of stands	4	4	4	4
Management strategy	Legacy retention	Legacy retention	Thinnings	Thinnings
Tree diameter at 1.5 m (cm)	43 (2)	43 (2)	63 (3)	58 (3)
Density of trees >10 cm diameter (no. trees/ha)	598 (63)	642 (99)	224 (26)	236 (34)
Diameter of tree crowns (m)	6.5 (0.2)	6.2 (0.4)	9.0 (0.5)	7.9 (0.5)
Total understory cover (%)	34 (4)	34 (4)	89 (8)	87 (6)
Cover of shrubs <2 m (%)	19 (4)	17 (5)	30 (4)	31 (18)
Cover of fallen trees (%)	7 (0.0)	8 (0.0)	2 (0.0)	3 (0.0)

past history was representative of currently recommended management strategies of legacy retention and management with thinnings. I found both suitable study areas and interested managers on Fort Lewis Military Reservation, in Thurston County, in the Puget Trough Physiographic Province, Washington, USA. The study areas were just south of the Nisqually River, and sampling began in 1991 (Carey et al. 1996*b*, 1999*c*). The Rainier Training Area has low relief (100-140 m), ample precipitation (mean, 91 cm/yr), and a mild climate (minimum January temperatures range 0-2.5°C). The area is composed of ~6000 ha of second-growth Douglas-fir (*Pseudotsuga menziesii*) stands with various management histories. The homogeneity of management compartments made the area ideal for comparing forests of differing histories. Its isolation from old-growth Douglas-fir forest eliminated potentially confounding effects of adjacency to old forest.

Four 13-ha stands were demarcated in each of four large management compartments (referred to as blocks in analysis of variance results): Farley, Hill, Star, and Stellar (Table 1; Carey et al. 1999*c*). Within-compartment variation was less than among-compartment variation, but within-compartment differences in slope position, plant species composition, and vegetation structure were apparent (Carey et al. 1999*c*). For example, low shrub cover varied two- to threefold among stands within compartments, and cover of coarse woody debris varied 1.5-fold. Both Farley and Hill had been clear-cut in ~1927, but not necessarily in the same year or season or by the same operator. Depth of crown and increment cores of dominant trees suggested trees had grown widely spaced. The forests had been commercially thinned twice before the age of 60 yr (>10 yr prior to this study). Standing and fallen dead trees had been removed during cuttings. Coarse woody debris was scarce (Table 1). Few legacy trees (alive or dead) had been retained (< 1 tree/ha combined). All the stands were well stocked with large Douglas-fir. Understory cover (shrubs, ferns, and forbs) was high. No significant regeneration of shade-tolerant conifers was found.

Star and Stellar had been clear-cut in ~1937, but many live and dead trees had been left during clearcutting (Carey et al. 1996*b*, 1999*c*). The forests regenerated naturally into even-aged Douglas-fir. No further manipulation of stands was undertaken, except that a few retained old-

growth trees that projected well beyond the overstory and that appeared to be hazards to helicopters had been felled and left on the forest floor. As in the thinned forest, significant among-stand, within-compartment variation was apparent in slope position, species composition, and vegetation structure. Forest floors had several kinds of coarse woody debris: tall stumps of old-growth trees (mean density, 48 trees/ ha); old well-decayed, fallen trees (5.0-9.5% cover); a few lightly to moderately decayed felled old-growth trees; and abundant (2-4% cover) fallen small-diameter trees that had died from suppression or root rot (*Phellinus weirii*). Understory ranged from absent to moderate cover of salal (*Gaultheria shallon*). Numerous residual large snags (3.5 trees/ha) and large live trees (2.7 trees/ha) were still standing. Contemporary Douglas-fir were small and crowded (Table 1).

The 16 stands exemplify the results of two commonly suggested strategies for long-rotation (70-130-yr) management. They were past the common harvest age for industrial forestlands and approaching the age at which forests are commonly harvested on public lands. They were in the most prevalent stages of forest development that would be expected in landscapes managed under the respective strategies. Thus, the stands represent the typical potential for maintaining biodiversity in a managed landscape, including complexity of trophic pathways, that would be expected under each strategy as modeled by Carey et al. (1999*b*). However, management strategies were not randomly assigned to management compartments and many variables other than those directly related to the management strategies could not be controlled; thus, the potential for confounding factors exists and the data we measured are only quasi-experimental (Cook and Campbell 1979, Hoaglin et al. 1991).

METHODS

Squirrels were trapped, and capture data analyzed, following procedures suggested by Carey et al. (1991), except trapping-grid size was 8 X 8 (64 stations, 40 m apart, and enclosing 7.8 ha) instead of 10 X 10 (enclosing 16 ha), because previous harvest practices and road networks produced stands too small for 10 X 10 grids. Grids were separated by ≥ 80 m. I placed two

Tomahawk 201 traps (Tomahawk Co., Tomahawk, Wisconsin) at each station (one on the ground and one 1.5 m high in a tree; total no. traps = 2048) and baited them with peanut butter, molasses, and oats. I left them open for two four-night periods, separated by three nights in fall 1991 and spring and fall 1992 (~45 000 trap nights). The effectiveness of these procedures has been demonstrated for northern flying squirrels and Townsend's chipmunks, and they have been widely used for Douglas' squirrels (Carey et al. 1991, Carey 1995). Trapping in 1991 was too late in the fall to trap Townsend's chipmunks effectively; the chipmunk is a facultative hibernator and a signify-cant portion of the population seemed to be hibernating.

Population sizes of Townsend's chipmunks, in 1992, and northern flying squirrels, in 1991 and 1992, were estimated with Chapman's modified Lincoln-Peterson index using two sampling periods to reduce the effects of small numbers of captures per day on density estimates (Menkens and Anderson 1988, Carey et al. 1991). Areas sampled were calculated by adding one-half the mean maximum distance moved (MMDM) between subsequent recaptures to the grid dimensions (Otis et al. 1978, Wilson and Anderson 1985). Density was calculated by dividing population size by area sampled. Four estimates of the density of flying squirrels still seemed abnormally large, due to chance variation in numbers of recaptures. Thus, I used number of individuals of a species captured per unit effort (ICPUE) as an index to a species' activity within a trapping grid, with effort calculated as number of total trap nights minus one-half the numbers of sprung-but-empty traps and traps containing animals (Nelson and Clark 1973, Carey et al. 1999a). This metric avoids multiplicative errors in density estimates arising from mark-recapture calculations and estimates of MMDM (Skalski and Robson 1992). It also avoided errors in estimating population size from counts (the minimum-number-known-alive [MNKA] method), which arise from reductions in trapping effort for a species due to weather and captures (Nelson and Clark 1973). I used MMDM as an independent index of habitat quality, which was the area used by individuals while foraging (Carey 1995). The number of individuals captured is, nonetheless, a good predictor of population sizes (as estimated from various mark-recapture analyses) of flying squirrels and chipmunks, over a wide range of densities in the Pacific Northwest, yielding the following values: R^2 = 0.84, slope = 1.1, and intercept = 0.0 for flying squirrels; and R^2 = 0.99, slope = 1.1, and intercept = 0.0 for chipmunks (Carey et al. 1991). I performed a general linear model analysis (SPSS 1997) of MNKA on estimated population size for this data set for flying squirrels (R^2 = 0.82, F = 206.5, df = 1, 46, P = 0.0; slope = 1.16, t = 14.37, P = 0.00; intercept = 1.07, t = 1.97, P = 0.055), and used the marginal means for each block to compare to densities from other areas. For chipmunks (R^2 = 0.99, F = 435.2, df = 1, 30, P = 0.00; slope = 1.07, t = 66.0, P = 0.00; intercept = 0, t = 0.82, P = 0.43), I used the grand marginal mean for

comparisons with other areas. Because relatively few Douglas' squirrels were captured or recaptured, densities were calculated by dividing MNKA by area sampled, as was done in the other studies (Carey 1995).

I compared the densities I found to published estimates of densities from other areas in western Washington and western Oregon that included estimates for chipmunks and flying squirrels in both managed and old-growth forests. The areas differed in forest type (dominant vegetation). The Northern Cascades and Olympic Peninsula forests of Washington were cooler and more moist than the forests of the Puget Trough, and they were dominated by western hemlock (*Tsuga heterophylla*), Pacific silver fir (*Abies amabilis*), or Sitka spruce (*Picea sitchensis*). Forest in the Western Cascades of Oregon were Douglas-fir and western hemlock. The forests in the Coast Ranges of Oregon were most similar to the Puget Trough climatically and phytologically and were dominated by Douglas-fir. Carey (1995) reported that warmer, drier forests dominated by Douglas-fir seemed to support denser populations of arboreal rodents than the cooler, wetter forests dominated by western hemlock, Pacific silver fir, or Sitka spruce.

Densities, ICPUE, and MMDM were analyzed with general linear model factorial analysis of variance incorporating management strategy (legacy vs. thinning) and trapping period (fall 1991 vs. spring 1992 vs. fall 1992). Data were checked for normality and homoscedasticity; transformations were not necessary (Dowdy and Wearden 1983). I did not consider the periods to be simple repeated measures, because they incorporated variation in weather, food production, and other phenological and temporal effects known to produce changes in squirrel populations. Because sampling periods were not randomized, potential existed for overinflation of statistical significance. Thus, I repeated these analyses with repeated-measures analysis of variance as a check on statistical significance and obtained results similar to the factorial analysis. As separate measures of demographic performance, I examined (1) differences in proportions of the fall adult populations that were females, with external anatomical evidence of pregnancy or lactation (Carey 1995); and (2) the proportions of total fall populations that were newly recruited, nulliparous females <1-yr-old. Proportions were calculated by minimum number of individuals known to be alive (actually captured and marked), not mark-recapture estimates of population size. Reproduction and recruitment data from Douglas' squirrels were too few to test.

RESULTS

I captured 327 individual flying squirrels 605 times, 240 individual chipmunks 747 times, and 33 individual Douglas' squirrels 50 times. Flying squirrel ICPUE

TABLE 2. General linear model marginal means, standard errors, 95% confidence intervals, and statistically significant Waller-Duncan (W-D) groups of blocks for the numbers of individual northern flying squirrels and Townsend's chipmunks trapped.

Block	Management strategy	Mean†	1 SE	CI	W-D group	General linear model results
Flying squirrel						
Star	Legacy retention	0.81	0.83	0.64–0.98	1	Model $F = 8.44$, df = 11, 36, $P < 0.01$;
Stellar	Legacy retention	1.15	0.83	0.98–1.32	2	Blocks $F = 10.02$, df = 3, 36, $P < 0.01$;
Farley	Thinnings	0.66	0.83	0.49–0.83	1, 3	Period $F = 27.98$, df = 2, 36, $P = 0.00$
Hill	Thinnings	0.54	0.83	0.37–0.71	3	
Chipmunk						
Star	Legacy retention	0.19	0.13	−0.07–0.45	1	Model $F = 16.35$, df = 7, 24, $P < 0.01$;
Stellar	Legacy retention	0.28	0.13	−0.02–0.54	1	Blocks $F = 36.52$, df = 3, 24, $P < 0.01$;
Farley	Thinnings	1.11	0.13	0.85–1.38	2	Period $F = 2.12$, df = 1, 24, $P = 0.16$
Hill	Thinnings	1.82	0.13	1.56–2.08	3	

Notes: The table reports data for northern flying squirrels (*Glaucomys volans*) trapped in fall 1991 and spring and fall 1992, and for Townsend's chipmunks (*Tamias townsendii*) trapped in spring and fall 1992 in four stands in each of four management compartments (blocks) on the Rainier Training Area of Fort Lewis, Washington, USA.
† Mean no. individuals captured per 100 trap nights.

were highest in Stellar and lowest (50% lower) in the thinned stands in Farley and Hill (Table 2). Flying squirrels used smaller foraging areas (had smaller mean maximum distance moved [MMDM]) in stands managed with legacies, than in thinned stands (Table 3); MMDM in Stellar were significantly shorter than in the other compartments. There was significant variation among sampling periods for individuals captured per unit effort (ICPUE) and MMDM (Tables 2 and 3). Populations in the spring were 56-61 % of fall populations, and MMDM were exceptionally long in fall 1992 (153 ± 20 m in thinned stands, and 96 ± 8 m in legacy stands). The percentages of the fall adult populations that were reproductive females (38 ± 4%) and the percentage of newly recruited nulliparous females (18 ± 2%) did not differ among compartments (reproductive, $F = 0.82$, df = 7, 24, $P = 0.58$; newly recruited, $F = 0.79$, df = 7, 24, $P = 0.83$). Overall, ICPUE was 50% higher in legacy stands (0.98 ± 10) than in thinned stands (0.60 ± 0.14; $F = 17.1$, df = 1, 42, $P = 0.00$). Densities in legacy stands were comparable to densities in managed stands to the south, but lower than in old-growth Douglas-fir. Densities in legacy stands were higher than in managed or old-growth hemlock forests in Washington. Mean densities in thinned stands (95% confidence interval = 0.3-0.7 squirrels/ha) were significantly

lower than in managed or old-growth Douglas-fir forest (lowest end of 95% confidence intervals = 1.5 squirrels/ha) and similar to extensively managed Douglas-fir, managed western hemlock, and old-growth western hemlock forests in other parts of Washington (Table 4).

Chipmunk ICPUE were highest in Hill (where flying squirrels were few) and very low in Star and Stellar (Table 2). Chipmunk mean ICPUE was 0.24 ± 0.04 in legacy forests and 1.47 ± 0.12 in thinned forests ($F = 65.0$, df = 1, 28, $P = 0.00$). Chipmunk movements showed a mean of 112 ± 8 m (all stands combined) and did not differ between sampling periods ($F = 0.36$, df = 1, 76, P = 0.56), strategies ($F = 1.62$, df = 1, 76, $P = 0.22$), or compartments ($F = 0.543$, df = 3, 74, $P = 0.65$). Fall MMDM was 92.5 ± 8.3 m. Percentages of the adult population that were reproductive female (20 ± 6.7%) or percentages of newly recruited, young females (10 ± 3%) did not differ among compartments (reproductive, $F = 1.17$, df = 3, 12, and $P = 0.36$; newly recruited, $F = 0.96$, df = 3, 12, and $P = 0.44$). Densities of chipmunks were four times greater in thinned stands as in legacy stands (a difference of 0.67 ± 0.12 chipmunks/ha), but still much less than in Douglas-fir old growth to the south. Densities in

TABLE 3. General linear model marginal-mean maximum distances moved by northern flying squirrels (*Glaucomys sabrinus*), standard errors, 95% confidence intervals, Waller-Duncan (W-D) homogeneous groups, and estimated area sampled by trapping grids.

Block	Management strategy	Mean† (m)	1 SE (m)	CI (m)	W-D group	Area sampled (ha)	General linear model results
Star	Legacy retention	91.3	8.8	73.8–108.6	1, 2	13.8	Model $F = 2.69$, df = 7, 112, $P = 0.013$;
Stellar	Legacy retention	74.5	7.4	59.9–89.2	1	12.6	Blocks $F = 4.06$, df = 3, 112, $P = 0.009$;
Farley	Thinnings	115.7	12.8	90.2–141.1	2	15.7	Period $F = 5.76$, df = 1, 112, $P = 0.018$
Hill	Thinnings	112.6	11.5	89.8–135.5	2	15.4	

Note: The table reports data for northern flying squirrels trapped in fall 1991 and fall 1992 in four stands in each of four management blocks on the Rainier Training Area of Fort Lewis, Washington, USA.
† Mean maximum distances moved by flying squirrels.

TABLE 4. Fall densities (no. individuals/ha) of northern flying squirrels (*Glaucomys sabrinus*), Townsend's chipmunks (*Tamias townsendii*), and Douglas' squirrels (*Tamiasciurus douglasii*) in western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*) forests, in the Pacific Northwest, USA.

Physiographic province	Study area characteristics			Flying squirrel density (1 SE)	Town-send's chipmunk density (1 SE)	Douglas' squirrel density (1 SE)
	State†	Stand age and management history‡	Dominant tree species			
Northern Cascades§	WA	Old, natural	Western hemlock	0.2 (0.2)	0.5 (0.3)	0.5 (0.3)
		Young, mixed management	Douglas-fir	0.3 (⋯)	0.1 (0.0)	0.3 (⋯)
Olympic Peninsula§	WA	Old, natural	Western hemlock	0.5 (0.2)	0.4 (0.2)	0.1 (0.0)
		Young, mixed management	hemlock, Douglas-fir	0.2 (0.1)	0.2 (0.1)	0.1 (0.0)
Puget Trough§	WA	Managed with legacies	Douglas-fir	1.0 (0.1)	0.2 (0.1)	0.1 (0.0)
Puget Trough‖		Managed with thinnings	Douglas-fir	0.5 (0.1)	0.8 (0.1)	0.1 (0.0)
Western Cascades#	OR	Old, natural	Douglas-fir, hemlock	2.3 (0.3)	5.1 (0.4)	⋯
		Young, mixed management	Douglas-fir	1.9 (0.2)	2.8 (0.3)	⋯
Coast Range‡	OR	Old, natural	Douglas-fir	1.9 (0.2)	1.9 (0.1)	0.2 (0.0)
		Young, mixed management	Douglas-fir	0.9 (0.1)	1.0 (0.1)	⋯

† WA, Washington; OR, Oregon.

‡ Stands other than those in Puget Trough are classified as naturally old or young (40–70 yr old).

§ *Sources:* Carey (1995), Carey et al. (1992); Carey, *unpublished data.* Ellipses (⋯) indicate insufficient data for calculation or that the species was not found.

‖ This study.

Sources: Rosenberg and Anthony (1992, 1993); high densities may reflect extended trapping periods or complex estimators. Ellipses (⋯) indicate data not reported.

legacy stands were comparable to densities reported elsewhere in Washington.

Douglas' squirrel abundance did not differ statistically among periods or between strategies ($F = 0.43$, df $= 11, 36, P = 0.93$); captures, however, were relatively few. Too few Douglas's squirrels were caught to reliably estimate proportions of reproductive females.

DISCUSSION

Flying squirrels in the relatively dry second-growth Douglas-fir forests of the Puget Trough were as (or more) abundant than in wet old-growth western hemlock-Pacific silver fir forests to the north in the Cascade Range, or in wet old-growth western hemlock—Pacific silver fir-Sitka spruce forests to the west on the Olympic Peninsula of Washington (Carey 1995). Population densities in Puget Trough legacy stands were similar to those in extensively managed Douglas-fir forests, but considerably less than in dry Douglas-fir old growth in the Oregon Coast Range or mesic old-growth Douglas-fir-western hemlock forests in the west-central Cascade Range of Oregon (Carey 1995). Proportions of reproductive females were similar among second-growth and old-growth stands on the Olympic Peninsula (Carey 1995) and in legacy and thinned stands in the Puget Trough. Distances moved by flying squirrels in the thinned stands were the highest mean maximum distances moved (MMDM) recorded to date (117 m, compared to 76 m in west-central Oregon Cascade Range, 93 m in Oregon Coast Range, and 102 m on the Olympic Peninsula; Carey 1995). Thus, when compared to the climatically and phytologically most similar old growth (Oregon Coast Range), neither legacy nor thinned stands approached expected carrying capacities for flying squirrels.

Chipmunks in legacy stands were less abundant than in any old growth studied to date, and less abundant than in extensively managed stands in Oregon. Densities in Puget Trough thinned stands were higher than in the wet northern forests, but lower than in the mesic and dry forests to the south (Carey 1995). Thus, neither strategy produced populations that would be expected in late-seral forests. The opposing responses of flying squirrels and chipmunks under the alternative management strategies contrasts markedly with their jointly increasing abundance with forest development over a wider chronosequence (Carey 1995). Douglas' squirrel densities in both legacy and thinned stands were higher than in old growth on the Olympic Peninsula, Oregon Coast Range, and northern Washington Cascade Range. This suggests that, at least for squirrels, both strategies failed to achieve the emergent property (synergism resulting from interactions of multiple system components) of niche diversification associated with late-seral Douglas-fir forests (Carey et al. 1999a). Thus, both strategies failed to meet both measures of expectation (species carrying capacities and simultaneously dense populations). Deficiencies were also noted in the forest floor small mammal community (Carey et al. *1996b;* S. M. Wilson and A. B. Carey, *unpublished manuscript*) and in the winter bird community (B. Haveri and A. B. Carey, *unpublished manuscript*).

Retrospective analyses can not demonstrate cause and effect; cause and effect is difficult to demonstrate in most biological and social field studies (Cook and Campbell 1979). Several nonexclusive hypotheses can explain differences between populations of flying squirrels in legacy retention forests and thinned

forests, and among second-growth forests and old-growth forests, around the region. First, the activity, abundance, and carrying capacities of flying squirrels in dry Douglas-fir forests in the Western Hemlock Zone seem tied to coarse woody debris through its influence on the production of fruiting bodies (truffles) of hypogeous ectomycorrhizal fungal associates of Douglas-fir and other members of Pinaceae (Amaranthus et al. 1994, Carey et al. 1999*a*). The thinned forests were depauperate in coarse woody debris and even the legacy retention forests had less coarse woody debris than is commonly found in old-growth Douglas-fir (Spies and Franklin 1991, Carey and Johnson 1995, Carey et al. 1999*a*). I found densities of flying squirrels to be highest in the block of stands with the greatest cover of coarse woody debris.

Second, the closed-canopy legacy retention forest provided a sheltered microclimate in the canopy that was conducive to the use of stick nests by flying squirrels; few stick nests were found in the thinned forests; and cavities in trees (the highest quality den sites for flying squirrels) seemed scarce in both forests (Carey et al. 1997).

Third, closed canopies and relatively open forest floors allowed efficient movement of flying squirrels through the canopies and quick location of truffles in the forest floors of the legacy retention stands. Canopy connectivity had been reduced in the thinned forest and heavy continuous ground cover may have impeded terrestrial foraging and travel. Use of gliding as the primary means of travel may have increased exposure of flying squirrels to predation by owls (Carey 1996). However, heavy understory development in the thinned forest favored ermine (*Mustela erminea*), which prey on small rodents, whereas the open forest floor in the legacy retention forest favored long-tailed weasels (*M. frenata*), which are more likely than ermine to prey on flying squirrels and chipmunks (Wilson and Carey 1996). Diversity of truffles, which has been linked to flying squirrel abundance (Carey 1995), was similar in both forests, but species composition differed as a result of thinning, possibly to the detriment of squirrels (Colgan 1997). Nontruffle food items (Thysell et al. 1997) may have differed in abundance and diversity between thinned and legacy retention stands.

Chipmunks were more abundant in the thinned stands because of understory development, which is a source of food and cover (Harestad 1991, Sutton, 1993, Carey 1995, Hayes et al. 1995, Carey et al. 1999*a*). Both understory development and coarse woody debris are important correlates of forest floor small-mammal abundance (Carey and Johnson 1995). Douglas' squirrels seem limited by their territoriality and consistency of cone production by conifers (Smith 1970, Buchanan et al. 1990, Carey 1995). Old-growth forests generally have a greater variety, abundance, and consistency of seed production than second-growth forests (Buchanan et al. 1990). Puget Trough forests have longer and warmer growing seasons than montane forest; thus, cone production may be greater and more consistent.

It appears that neither forest management strategy was adequate to develop or maintain the complex trophic pathways that support the diverse vertebrate communities associated with old-growth forests (Ruggiero et al. 1991) within a 50-70-yr time frame. Five processes seem preeminent in the development of Douglas-fir-western hemlock forests: crown-class differentiation, decadence, canopy stratification, understory development, and development of habitat breadth (Carey et al. 1999a). Interactions among these processes promotes niche diversification in forests that have significant biological legacies ~100 yr following catastrophic disturbance (Carey 1995, 1998*b*, Carey and Johnson 1995, Carey et al. 1999a). Thinning has the potential to accelerate all the processes but decadence (McComb et al. 1993, Carey 1995, Hayes et al. 1997). However, thinning with even spacing can retard crown-class differentiation and development of habitat breadth; light thinning may fail to advance understory development significantly before the canopy recloses; and heavy thinning may disrupt canopy connectivity, increase wind flow within the forest, and cause the forest to become drier and warmer. Neither the legacy stands nor the thinned stands had developed midstories or the array of plant species (and associated seed, fruit, and nut production) that would be expected in late-seral forests (Spies and Franklin 1989, Canham et al. 1990, Lertzman et al. 1996, Carey et al. 1999*a*, *c*). Carey (1995) proposed variable-density thinning as a surrogate for multiple small- and intermediate-scale disturbances that add diversity to vegetation struc-ture and plant communities in Douglas-fir forests (see also Carey et al. 1999*a*). An experimental test of variable-density thinning was implemented in 1991 (Carey et al. 1999*c*).

Thinning can both reduce decadence (by removing defective, diseased, and decaying trees) and enhance decadence (by emulating the wounding processes of naturally falling trees). Neither the legacy retention strategy nor the thinning strategy produced levels of decadence associated with late-seral forests. Residual snags in the legacy stands were well decayed and rarely used by flying squirrels (Carey et al. 1997), and cover of large fallen trees was below that normally encountered even in dry old-growth Douglas-fir forests (Harmon et al. 1986, Spies and Franklin 1991, Carey et al. 1999*a*). Even though legacy retention is an important strategy for conserving coarse woody debris and decadent live trees (and for carrying over a diverse legacy of vascular and nonvascular plants, fungi, and soil organisms), management of decadence throughout the life of a managed stand may be necessary to maintain ecosystem function.

A third strategy has been proposed for joint production of economic goods and ecological services (Carey and Curtis 1996, Carey 1998a, b, Carey et al. 1999b). This approach uses active, intentional ecosystem management within the construct

of environmental, economic, and social sustainability proposed by Goodland (1995), which he labeled "general sustainability." "Active" means manipulating forest vegetation throughout much of the life of the stand. "Intentional" means making a concerted effort to address all aspects of the ecosystem and general sustainability under the rubric of conservation of biodiversity (Reid and Miller 1989). Active, intentional ecosystem management differs markedly from the two alternatives of this paper in the degree to which scientific information and societal needs are incurporated directly into management prescriptions (see Carey et al. [1996a] for an example). Legacies (a broad variety) are retained at specific, empirically documented levels for specific purposes. Thinnings are done in a novel manner (variable-density thinning) based on empirical studies on natural and managed forest communities formed through self-thinning. and gap formation. Decadence is managed actively to alleviate loss of decadence resulting from reduced tree density. Active, intentional management requires measurement of multiple indices to evaluate progress towards achieving specific conditions and goals. One such index is the abundance of arboreal rodents as a surrogate for nonmerchantable ecological productivity (others include biomass of fungal sporocarps and numbers of wild ungulates). It remains to be seen if this new strategy can reproduce key elements of the biodiversity of old forests in a 70-130-yr period. Similar approaches are being developed elsewhere (e.g., Hunter 1990, Swedish National Board of Forestry 1990, Plochman 1992, Hart 1995, Voller and Harrison 1998).

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