

# DENS OF NORTHERN FLYING SQUIRRELS IN THE PACIFIC NORTHWEST

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**Abstract:** Silvicultural prescriptions to enhance northern flying squirrel (*Glaucomys sabrinus*) habitat have been suggested as an aid for recovery of the threatened northern spotted owl (*Strix occidentalis caurina*). Flying squirrels are hypothesized to be limited by den sites (cavities in trees) and by food (truffles). However, no quantitative information exists on den sites of flying squirrels. Therefore, during 1986-94, we used radiotelemetry to locate 604 different den sites in the southern Coast Range of Oregon, the southern Olympic Peninsula, and the Puget Trough of Washington. Den sites included cavities in live and dead old-growth trees; cavities, stick nests, and moss nests in small (10-50 cm dbh) second-growth trees; dens in cavities in branches of fallen trees; and dens in decayed stumps of old-growth trees and suppressed young trees. Two-thirds of all dens located were in live trees. Most dens were located during a study of second-growth forests in the Puget Trough. Females selected cavities for maternal dens. Squirrels used multiple dens; denning partners varied with den. Dens of males were  $211 \pm 7$  m apart; dens of females were  $108 \pm 4$  m apart. Males used  $2.2 \pm 0.1$  dens per month; females  $2.3 \pm 0.1$  dens per month. Dens, except maternal dens, were often occupied simultaneously by several adult squirrels. Many fragile den sites were used by females. Secure cavities are scarce and may limit reproductive success. Management for cavity trees and dens could prove fruitful in owl recovery and habitat restoration efforts.

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Although widespread in boreal North America (Wells-Gosling and Heaney 1984), the arboreal, nocturnal flying squirrel is difficult to observe. Consequently, little is known about specifics of its life history. Only a few dens were found during the last century (e.g., Cooper 1862); even recent literature is anecdotal (Carey 1991). There are 2 general categories of dens: cavities in trees and nests on tree branches and boles (Cowan 1936). Cavities are formed as a result of decay following damage or disease or created in decaying wood by woodpeckers (Picidae) and large tree squirrels (*Sciurus* sp.; rev. in Carey

and Sanderson 1981). Nests are built next to the bole of the tree or on platform-like branches and are varied in composition (Wells-Gosling and Heaney 1984). Dens in the Pacific Northwest include cavities in live trees and dead trees; hanging nests of lichen; nests of twigs, moss, and shredded bark; and nests of other arboreal rodents and birds (Bailey 1936, Maser et al. 1981a,b; Carey 1991, Witt 1992). Flying squirrels are reported to use cavities in winter and nests in summer (Banfield 1974).

Others suggest that flying squirrels prefer cavities over nests (Bailey 1936, Carey and Sanderson 1981, Maser et al. 1981a,b; Wells-Gosling and Heaney 1984) and scarcity of cavities may account for use of nests (Weigl and Osgood 1974). The extensive use of nests in western Oregon may have resulted from extensive logging that reduced numbers of snags (and

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consequently, cavities; Maser et al. 1981a). Because no quantitative data on dens and denning behavior have been reported, it would be difficult even to design an experiment to test hypotheses or critically examine speculations about dens as limiting factors.

Here, we present data from 9 years of radio-telemetry of northern flying squirrels in 26 forest stands across the Pacific Northwest to describe: (1) types of dens used, (2) statistical preferences (use vs. availability; Johnson 1980) for particular types of dens and supporting structures, (3) numbers of dens and distances between dens used by individuals, and (4) use of dens in different geographic areas, stand conditions, and seasons. We provide data that are necessary for designing experiments to test hypotheses about dens and we discuss ecological and management implications of our results.

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## STUDY AREA

We studied flying squirrels in 8 stands in the Coast Range, Douglas County, Oregon (1986-87, 1989-91): 4 old-growth stands 280-330 years old, one 110-year-old stand with substantial residual old-growth components such as snags and logs (combined with old growth for analysis), and 3 managed second-growth stands 40-60 years old. Douglas-fir (*Pseudotsuga menzeisii*) was the dominant species in all stands although most stands had a mix of overstory species. Flying squirrel densities averaged  $1.9 \pm 0.1$  squirrels/ha in old forests and  $0.9 \pm 0.2$  squirrels/ha in second-growth forests (Carey et al. 1992). We chose 1 old-growth stand (Lost Creek) for intensive study during 1989-91.

We examined use of dens in 2 stands in 60-year-old managed second-growth forest in Grays Harbor County, southcentral Olympic Peninsula, Washington, during 1987-88. The stands were Douglas-fir and western hemlock (*Tsuga heterophylla*) with an understory of salal (*Gaultheria shallon*). Densities averaged 0.8 (range 0.2-1.75)

squirrels/ha during our study of these 2 stands (Carey 1995a; Carey, unpubl. data)

In the Puget Trough, we studied 8 stands in each of 2 second-growth Douglas-fir forests 3 km apart in Thurston County during 1991-94: 1 intensively managed 65-year-old forest that had been thinned twice in the past 20 years (managed with thinning [MT]) and one 56-year-old unthinned forest with a residual component of large live trees, snags, and fallen dead trees (managed with legacies [ML]). Densities averaged 0.32 squirrels/ha in MT and 0.63 squirrels/ha in ML (Carey et al. 1996b). Artificial cavities were added (2.5/ha) to 8 stands (4 in each forest) in 1992, but rarely were used by the squirrels in our study. We included artificial dens only in our analyses of distances moved between dens and numbers of dens used per month. In addition, 8 stands (4/forest) received experimental variable-density (EVD) thinnings during the spring of 1993.

## METHODS

### Trapping and Radiotelemetry

Live-trap grids were established in all 26 stands. Grids were 13 ha (Puget Trough) or 20 ha (Coast Range and Olympic Peninsula). Squirrels were live-trapped in spring and fall; some ( $\geq 120$  g) were anesthetized with methoxyflurane, fitted with replaceable collar-style radiotransmitters that were  $<3\%$  (1989-94, Holohil Ltd., Carp, Ont.; 4.0 g) or  $<5\%$  (1986-88, AVM Instrument Co., Ltd., Livermore, Calif.; 6.0 g) of squirrel mass and released.

The 1986-91 studies were pilot studies. Squirrel dens were located with hand-held receivers and H-antennas at irregular, but frequent, intervals. In the Puget Trough, dens were located twice weekly, December 1991-August 1994, except during 2-4 week trapping sessions each spring and fall. During December 1991-April 1993, we monitored 20-30 individuals; during April 1993-August 1994, we tracked all ( $\geq 60$ ) adults captured.

### Describing Dens

In the Coast Range and Olympic Peninsula, most large trees were in old growth or were residual old-growth trees in second growth. The height and complexity of old-growth canopies made determination of den type from the ground difficult; we could not evaluate den type consistently. We did not climb old-growth trees and snags because most are difficult and dangerous to climb. Only the physical structure that supported the den was described consistently: species; structure type (live tree or snag); and diameter at breast height (dbh) class: large ( $>50$  cm) or medium (10-50 cm). The

dbh classes separated 40-70 year second-growth trees from residual, older trees.

In the Puget Trough, tree crowns usually were visible from the ground and we could record more comprehensive data: den type (cavity, nest); condition of the supporting structure (live trees-no visible defects, irregular forks on which a nest was built, or rot producing a cavity; snags or other dead structures-well decayed, moderately decayed, or sound); den height; and den location (Universal Transverse Mercator [UTM] coordinates). Initially, when we could not identify den type from the ground, we climbed the tree. In 12 climbs, all dens were determined to be nests high in the crown. We discontinued climbing because in all but 2 climbs, squirrels left their dens and did not return (based on telemetry). Thereafter, den type was included in analyses if (1) the bole was visible through the canopy and the possibility of a cavity could be ruled out (den type was assumed to be a nest but no nest height was recorded), or (2) telemetry could not distinguish between adjacent trees but den types and structure species were equivalent (we did not record den ht, structure ht, or structure dbh). Den type was excluded from analyses if (1) telemetry could not distinguish between  $\geq 2$  structures and both cavities and nests were present, (2) both a cavity and a nest were found in the same structure, or (3) the bole was not visible through the canopy and the possibility of a cavity could not be eliminated. We did not evaluate den type in residual, live, old-growth trees because their crowns were difficult to see and many had both cavities and nests. Four structures with undetermined den types were used only to assess numbers of dens used, distances moved between dens, and occupancy of dens by  $>1$  radiocollared squirrel.

### Assessing Den Availability and Use

Most of our data did not meet assumptions of normality, therefore we used the nonparametric Mann-Whitney-*U* test ( $\alpha = 0.05$ ) corrected for ties (Norusis 1993) to examine differences among forests. We used  $\chi^2$  analyses for categorical data. Because of low sample sizes on the Olympic Peninsula, statistical comparisons were made only for Oregon Coast Range and Puget Trough forests. We used 3 methods and  $\chi^2$  goodness-of-fit tests with Bonferroni inequalities (Byers et al. 1984) to compare use to availability.

*Method 1.*—In Lost Creek (Coast Range), we compared the frequency of squirrels denning in different structures to the frequency of the structures in 100 350-m<sup>2</sup> plots around grid points. This method determines statistical preference (or avoidance for fourth order selection; Johnson 1980) for denning

in structures classified as live trees or snags, deciduous or coniferous trees, and medium or large dbh. However, the method assumes that all trees surveyed had equal potential for supporting dens, including healthy, medium-dbh live trees with no decay or nests evident. No inferences were made about preferences for den types (nests vs. cavities).

*Method 2.*—In the Puget Trough, we compared dens used to an inventory of potentially available dens in 9 categories based on type of den (cavity or nest) and type of tree: (1) residual or contemporary (current, dominant-age cohort), (2) live or dead, and (3) coniferous or deciduous. We inventoried 4,096 400-m<sup>2</sup> plots. Flying squirrel dens were naturally-formed cavities, cavities excavated by woodpeckers, and nests built by Douglas' squirrels (*Tamiasciurus douglasii*) or flying squirrels. Dens were used by flying squirrels and by Douglas' squirrels, Townsend's chipmunks (*Tamias townsendii*), long-tailed weasels (*Mustela frenata*), woodpeckers, and unidentified birds (Carey, pers. obs.). Method 2 differed from method 1 in excluding structures not suitable for dens and, thus, limiting comparisons of use to availability to items known to be used by squirrels.

*Method 3.*—To determine if flying squirrels in the Puget Trough used some combinations of dens and supporting structures more repetitively than others, we compared numbers of telemetry relocations by type and structure to what would be expected if each actual den received equal use. We assumed that dens used once by squirrels were continually available to squirrels, i.e., that competition from other species or other unknown factors did not reduce the availability of the dens. Higher than expected use of particular categories would suggest differences in den quality.

### Estimating Number of Dens Used

To determine the number of checks per week that would be needed to estimate the number of dens used by individual squirrels, we followed a subset of 16 squirrels for 5 consecutive days over a 4-week period during January-February 1992. We tracked 4 squirrels/week, alternating weeks between MT and ML. We compared sampling days 1 and 3 (2 checks/week with  $\geq 1$  day between checks) to sampling all 5 days for each squirrel, using weekly averages and the mean of weekly averages. Twice-weekly checks recorded 95% of the dens and 86% of den changes recorded during daily checks. We decided to check twice weekly, realizing that squirrels might change dens more often than our data would show, but that we would find most, if not all, dens. Thus, we also minimized problems

Table 1. Dens of northern flying squirrels and supporting structures in the Coast Range of Oregon and the Olympic Peninsula of Washington, 1985-89.

Type <sup>b</sup>	Oregon Coast Range				Olympic	
	Old growth <sup>a</sup>		Managed		Managed	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Live trees	63	67.7	5	41.7	4	44.4
Residual, >50 cm dbh	N/A	N/A	1	8.3	1	11.1
Contemporary <sup>c</sup>						
Large conifers	46	49.5	1	8.3	3	33.3
Medium conifers	6	6.5	2	16.7	0	0
Large deciduous	9	9.7	0	0	0	0
Medium deciduous	2	2.2	1	8.3	0	0
Dead trees (>2 m ht)	30	32.3	7	58.3	5	55.6
Residual	N/A	N/A	6	50.0	2	22.2
Contemporary <sup>c</sup>						
Large conifers	24	25.9	0	0	0	0
Medium conifers	6	6.5	1	8.3	3	33.3
Low structures <sup>d</sup>	0	0	0	0	0	0

<sup>a</sup> Residual type not applicable (N/A) for old-growth stands.

<sup>b</sup> Trees in managed stands were either residual or contemporary (current cohort).

<sup>c</sup> Two dbh classes: large (>50 cm) and medium (10-50 cm).

<sup>d</sup> Dens in dead structures <2 m ht, in fallen trees, and nests on the ground.

associated with non-independent data.

### Determining Distances Between Dens

In Lost Creek, we measured the distance and bearing from den to nearest trapping grid point. In the Puget Trough, locations were given UTM coordinates. The location of each trap grid was determined with a Global Positioning System (GPS; Laurini and Thompson 1992). Grid cells were divided into 10- X 10-m blocks and UTM coordinates were calculated for the center of each block. Dens located within grids were recorded by block. For dens located outside grids, 1 of 3 methods was used to determine location: (1) distance and bearing to nearest trap station, if the den was ≤100 m from a grid, (2) distance and bearing to a nearby, previously located den if grids were >100 m away, or (3) GPS. For (1) and (2), bearings were measured with a hand compass and distances were measured with a tape- or electronic measure (Sonin Inc., Brewster, N. Y.).

## RESULTS

### Sample Sizes and Experimental Effects

We tracked 4 flying squirrels (2M, 2F) to 12 dens in Coast Range second growth, 31 squirrels (13M, 18F) to 93 dens in Coast Range old growth, and 4 squirrels (1M, 3F) to 9 dens in Olympic Peninsula second growth (Table 1). In the Puget Trough, we

tracked 140 squirrels (74 M, 66 F) to 490 natural dens 5,560 times (Table 2). Sample size varied with season, number of individuals captured during trapping, mortality of radiocollared squirrels, and operational life of transmitters. Sampling frequency varied with 80% from twice-weekly checks (>1 day apart), 14% from 1 check/ week, and 6% from additional checks during some weeks. Frequency of use of artificial dens was <5%.

The EVD thinnings in 1993 significantly decreased 2 types of potential dens in ML: live-conifer cavities that were not apparent when trees were marked for thinning and residual stumps that could not be avoided while removing logs ( $U = 0.0$ ,  $P = 0.03$  for both). There were no significant effects on other den categories ( $P > 0.10$ ). The EVD thinnings did not affect our results because: (1) dens actually being used and trees with obvious potential as dens were not affected, (2) most animals we tracked used areas outside the EVD thinnings (which received only 3-4% of use), (3) squirrels under-used live trees with cavities in ML, and (4) residual stumps were numerous relative to use, even after EVD thinnings, in ML (63 stumps/ha before vs. 34 stumps/ha after).

### Types of Dens Used

We tracked 179 flying squirrels to 604 dens. We found cavity dens in live trees, snags, fallen dead

**Table 2.** Dens of northern flying squirrels and their supporting structures in second-growth forests managed with legacies (ML) and managed with thinning (MT) in the Puget Trough of Washington, 1991–94.

Type <sup>a</sup>	ML		MT	
	n	%	n	%
Live trees	186	63.3	118	60.2
Residual, >50 cm dbh	23	7.8	7	3.6
Contemporary				
Conifer, nest	140	47.6	64	32.7
Conifer, cavity	19	6.5	34	17.3
Deciduous, cavity	4	1.4	9	4.6
Deciduous, nest	0	0	4	2.0
Dead trees (>2 m ht)	86	29.3	67	34.2
Residual	52	17.7	8	4.1
Contemporary				
Conifer, nest	2	0.7	2	1.0
Conifer, cavity	29	9.9	37	18.9
Deciduous, cavity	3	1.0	20	10.2
Deciduous, nest	0	0	0	0
Low structures <sup>b</sup>	22	7.5	11	5.6

<sup>a</sup> Trees (live and dead) are either residual (from the preceding stand) or contemporary (current cohort) and cross-classified by type of den (cavity or nest).

<sup>b</sup> Dens in dead structures <2 m tall, in fallen trees, and nests on the ground.

trees, and stumps. We examined cavities in 4 wind-thrown den trees and 6 low structures in the Puget Trough; they were lined with moss (principally *Eurhynchium oregonum* and *Isothecium stoloniferum*). In a concurrent nestbox study, moss was >90% of the volume of material in 146 nestboxes; bracken fern (*Pteridium aquilinum*), shredded cambium, polyester batting (from traps), paper, and lichen also were present (Carey, unpubl. data). We found nests composed of twigs, moss, bark, and leaves in trees and on the ground; moss lined the 12 nests in trees we climbed.

**Coast Range Forests.**—In old growth, 68% of dens ( $n = 93$ ; 75 from Lost Creek) were in live trees, 73% of which were conifers >50 cm dbh (Table 1). Mean ( $\pm$  SE) dbh and height of live den trees were  $108 \pm 5$  cm and  $40 \pm 2$  m. Most (80%) snags with dens also were >50 cm dbh (Table 1):  $93 \pm 7$  cm dbh and  $22 \pm 2$  m tall. All den snags were conifers. No dens were found in structures <2 m tall.

In second growth, 7 of 12 nests were in residual trees >50 cm dbh, 6 of which were snags (Table 1). The remaining dens were in various structures, including 1 medium-dbh conifer snag, but none were in structures <2 m. Live den trees were  $66 \pm 22$  cm dbh and  $27 \pm 8$  m tall and not significantly smaller than those in old growth ( $U = 83$ ,  $P = 0.08$  dbh;  $U = 81$ ,  $P = 0.08$  ht). Dead den trees were also similar in size to those in old growth:  $77 \pm$

12 cm dbh ( $U = 85$ ,  $P = 0.44$ ) and  $23 \pm 6$  m tall ( $U = 104$ ,  $P = 0.97$ ).

In summary, flying squirrels in old growth used live (50% of use) and dead (26% of use) large-dbh conifers as den structures. Snags were Douglas-fir ( $n = 29$ ) and grand fir (*Abies grandis*,  $n = 1$ ). Residual large snags contained 50% of the dens used in second growth (10 Douglas-fir and 2 western redcedar, *Thuja plicata*; Tables 1 and 3).

**Olympic Peninsula Second-growth Forests.**—We located 9 dens (Table 1); 3 were in residual trees (1 live, 2 dead), 3 in large contemporary conifers, and 3 in medium-dbh snags; thus 5 of 9 dens were in snags. All live trees used as dens were >50 cm dbh. Mean densities of residual snags on the Olympic Peninsula (including stands reported here) were  $2 \pm 1$ /ha; residual live trees were not detected in the stands (Carey 1995a). The residual den trees we located were outside of the trapping grids. No dens were in low structures (but all tracking was outside the breeding season).

**Puget Trough Second-growth Forests.**—We found 294 dens (plus 1 den of undetermined type) in ML: 63% were in live trees, 37% were in dead structures, and 65% were in contemporary Douglas-fir (Table 2). Live-den trees were  $49 \pm 1$  cm dbh,  $33 \pm 1$  m tall, and smaller in dbh, but taller than snags with dens (Table 4). Residual live trees were  $35.0 \pm 1.4$  m tall and  $71.3 \pm 5.7$  cm dbh. All but 2 of 86 dens in snags >2 m tall were cavities; 60% of snags and 22% of all structures used as dens were large, residual trees. Mean dbh for den snags was  $63 \pm 4$  cm dbh. Only 36% of snags >2 m with dens and 10% of all snags with cavities (identified in the inventory) were contemporary Douglas-fir (Tables 2 and 5). Deciduous trees were <5% of the snags used. Eighty-one percent of the snags were well decayed throughout, especially the heart wood. Only 6 recently dead (sound) snags were used; 2 had stick nests built in forked branches and 4 had localized decay before dying. Twenty-two dens (7.5% of all dens) were in cavities in well-decayed low structures; all were occupied by females during May–July, when young are reared (Table 2). Low structures included 16 residual stumps, 1 contemporary stump, and 5 fallen dead trees. Dens in fallen trees included 3 in vertical roots, 1 in a vertical branch, and 1 in the decayed top.

We found 196 dens (plus 3 of undetermined type) in MT: 60% were in live trees, mostly contemporary Douglas-fir (Table 2). Surprisingly, 36% of dens in live trees were cavities; 11% of live den trees were deciduous and <6% were residual (Table 3). Snags supported 34% of dens; 58% of snags were

Table 3. Comparisons of types of structures supporting northern flying squirrel dens in second- and old-growth forests in the Oregon Coast Range.

Comparison	Second-growth <i>n</i> <sup>a</sup>	Old-growth <i>n</i> <sup>a</sup>	Statistical results			Interpretation <sup>b</sup>
			$\chi^2$	df	<i>P</i>	
Live vs. dead trees	12	93	3.167	1	0.075	More live trees used in old-growth
Live trees						
Eight species	5	63	2.269	7	0.943	Douglas-fir used most in both
Conifer vs. deciduous	5	63	0.021	1	0.886	Conifer use > deciduous in both
Dead trees						
Three species	7	30	9.198	2	0.010	Grand fir component in old-growth; western red cedar in managed

<sup>a</sup> Total no. of items (den types or supporting structures) found. Numbers and percentages of each are listed in Table 1.  
<sup>b</sup> Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), western red cedar (*Thuja occidentalis*).

were current-stand conifers, but 30% were deciduous, primarily red alder (*Alnus rubra*). Contemporary snags (0.38/ha) were as available as residual snags (0.40/ha); but both were rare (Table 5). As in ML, few (*n* = 2) dens in snags were nests; both were in sound snags with large branches. Most (80%) snags with dens were well-decayed, with cavities. Eight of the 67 snags were residual. Only 1 tree with a cavity had died recently and it had decay before death.

Low structures contained 11 (5.6% of total) dens in MT: 6 contemporary stumps, 3 residual stumps, 1 pile of sticks and leaves, and 1 stick nest in a low fork of a live, healthy tree. All but one were used exclusively during May-July by females. During a telemetry check in October 1993, 1 male was found in a small, decayed stump; 2 days later, he was found in his previous den in a live tree.

**ML versus MT Forests.**—We trapped and tracked more squirrels, and found more dens, in ML than MT. The total density of dens identified through radio-telemetry was 1.16/ha in ML and 0.78/ha in MT. Proportionately, more nest dens were found in ML and more cavity dens in MT; relative proportions of live trees, snags, and low structures supporting dens

did not differ. Tree species containing dens differed; MT had more deciduous snags, principally red alder, than ML (Table 6). Mean dbh and mean height of den structures and trees in general were larger in MT than in ML; however, snag heights were not different (Table 4).

**Seasonal Use of Dens in Puget Trough.**—Most (88%) squirrels used ≥2 den types. Cavity use was highest during late spring and summer, peaking in May (71%; Fig. 1). Females increased cavity use in May (81%), then decreased use of cavities throughout the summer and fall (Fig. 1a). Males consistently used cavities (56 ± 2.1%) throughout the year, but increased use of nests during November (58%; Fig. 1b).

Squirrels used live trees as dens 66% of the time, but use varied seasonally. Snag use was high in May and June (≤53% of the checks). Dead structures <2 m tall were used almost exclusively during June and July (Fig. 2). Use of live trees was highest in November and coincided with increased use of nests. Mean height of all den structures was 27.8 ± 0.2 m. Mean monthly height of dens of females, however, dropped during May (17.5 ± 1.5 m) and June (17.1 ± 0.8 m); mean

Table 4. Mean (±SE) dbh and height of flying squirrel den trees in second-growth forests managed with legacies (ML) and managed with thinning (MT) in the Puget Trough of Washington.

Category	ML		MT		ML vs. MT	
	<i>n</i>	$\bar{x}$ (SE)	<i>n</i>	$\bar{x}$ (SE)	<i>U</i> <sup>a</sup>	<i>P</i> <sup>b</sup>
Live trees						
dbh (cm) <sup>c</sup>	186	49.0 (1.4)	118	60.1 (1.9)	7,031.0	<0.001
Total ht (m)	185 <sup>d</sup>	32.6 (0.5)	118	37.6 (0.8)	5,937.0	<0.001
Dead trees						
dbh (cm)	86	63.7 (3.6)	67	41.6 (2.7)	1,734.5	<0.001
Total ht (m)	86	12.6 (0.8)	67	11.0 (0.9)	2,437.0	0.103

<sup>a</sup> Mann Whitney *U* value.

<sup>b</sup> 2-tailed significance, corrected for ties.

<sup>c</sup> Average dbh of canopy dominants was 42.6 cm (± 1.0) in unthinned stands and 61.5 cm (± 1.8) in thinned stands.

<sup>d</sup> Total ht of 1 live tree in the unthinned forest was not recorded due to terrain.

Table 5. The availability of structures supporting possible northern flying squirrel dens in 8 stands managed with legacies (ML) and 8 stands managed with thinning (MT) in the Puget Trough, Washington.

Structure	ML $\bar{x}$ (SE)	MT $\bar{x}$ (SE)	ML vs. MT	
			$U^a$	$P^b$
Live trees/ha				
Residual <sup>c</sup>	2.71 (0.84)	0.39 (0.35)	5.0	0.004
Contemporary <sup>c</sup>				
Conifer, nests	1.67 (0.31)	0.61 (0.08)	3.0	0.002
Conifer, cavity	0.89 (0.18)	0.78 (0.21)	25.5	0.492
Dead trees/ha				
Residual <sup>c</sup>	3.52 (0.70)	0.40 (0.12)	0.0	<0.001
Contemporary <sup>c</sup>				
Conifer, cavity	0.38 (0.09)	0.38 (0.09)	32.0	1.000
Deciduous, cavity	0.00 (0.00)	0.16 (0.10)	N/A <sup>d</sup>	N/A <sup>d</sup>
Residual stumps	48.27 (5.9)	21.23 (2.3)	3.0	0.002

<sup>a</sup> Mann-Whitney  $U$  value.

<sup>b</sup> 2-tailed significance, corrected for ties.

<sup>c</sup> See Table 2 for definitions.

<sup>d</sup> N/A indicates not analyzed due to zero sample from ML forest.

height for males was relatively constant.

When females switched to low dens, they often left dens occupied by  $\geq 1$  other radiocollared squirrel. However, we never found  $> 1$  adult occupying a low den. Males exhibited typical denning behavior year round and did not use low dens. In the absence of females, males denned with other males during the rearing season. We saw little use of exterior nests by females during this period. Only when females returned to tall structures later in the summer did we again note joint occupancy. Females apparently chose new dens in which to raise young. During 3 maternal seasons, females selected only new (previously unrecorded) dens and, once a female left a low structure, it was never used again by any radiocollared squirrel.

### Use versus Availability

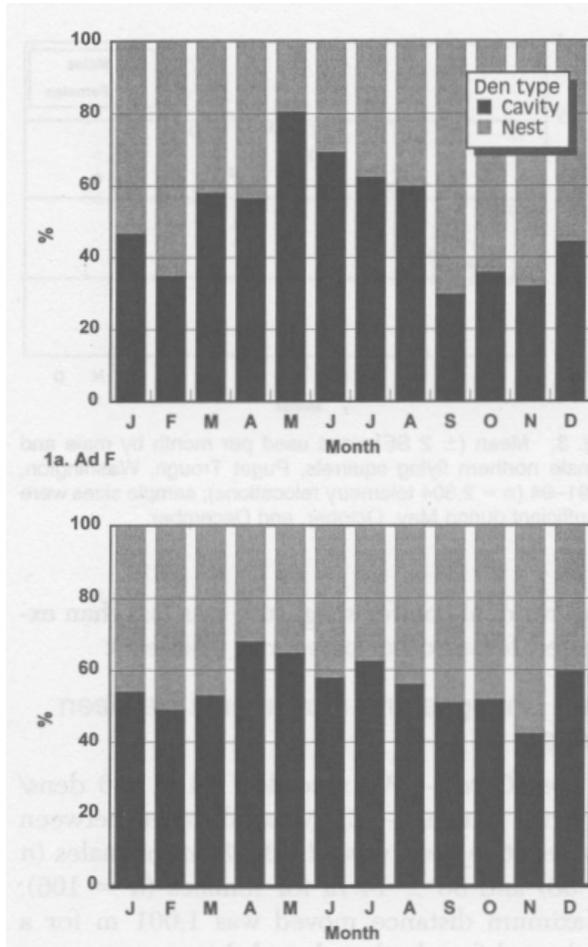
*Coast Range.*—In Lost Creek, squirrels preferentially selected large conifers, live and dead, for den sites; fewer than expected (based on availability) medium-dbh conifers and hardwoods were used (Table 7). This pattern was similar for the entire old-growth sample (Table 3). In second growth, squirrels appeared to select residual snags for den sites (Table 3); residual snags were rare in Coast Range second growth, whereas medium-dbh conifers and hardwoods were abundant (Carey 1995a, Carey et al. 1991).

*Puget Trough.*—We found  $9.2 \pm 1.3$  potential dens/ha during our inventory of ML (Table 5), including  $3.9 \pm 0.7$  snags/ha, 3.5/ha of which were residual. Documented dens were in contemporary live

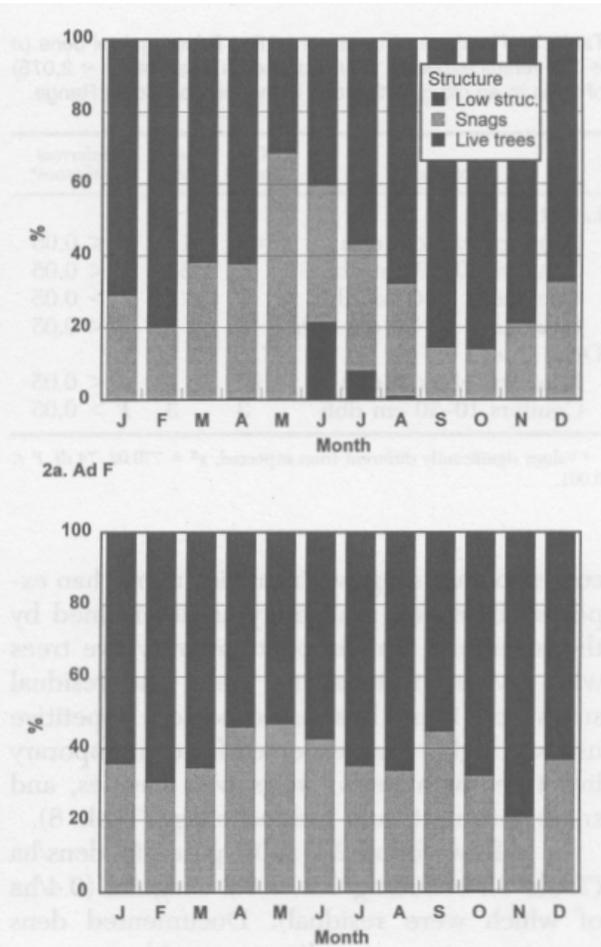
Table 6. Comparisons of flying squirrel den types and types of supporting structures in second-growth forests managed with legacies (ML) and managed with thinning (MT) in the Puget Trough of Washington.

Comparisons	ML		MT		Statistical results			Interpretation
	$n^a$	$n^a$	$\chi^2$	df	$P$			
Nests vs. cavities	271	189	9.852	1	0.002		Nests in ML, cavities in MT	
Live vs. dead vs. low struc.	294	196	1.705	2	0.426		Live > dead > low in both	
Nine tree species	294	195	39.257	7	<0.001		More deciduous in MT	
Live trees								
Nests vs. cavities	163	111	21.904	1	<0.001		More nests in ML	
Healthy vs. forked vs. rot	163	111	21.309	2	<0.001		Forks in ML; cavities in MT	
Eight species	186	118	15.658	7	0.028		More deciduous in MT	
Dominance class	186	118	3.457	3	0.326		Large trees favored in both	
Dead trees >2 m								
Nests vs. cavities	86	67	0.064	1	0.800		>97% cavities in both	
Decay stage	86	67	4.209	2	0.122		Well > moderate > slight in both	
Four species	86	67	23.712	3	<0.001		More <i>Alnus rubra</i> in MT	
Contemporary vs. residual	86	67	37.201	1	<0.001		Residual in ML; contemporary in MT	

<sup>a</sup> Total number of items (den types or supporting structures) found. Numbers and percentages of each are listed in Table 2.



1b. Ad M



2b. Ad M

Fig. 1. Use of nests and cavities by (a) adult female and (b) adult male northern flying squirrels, Puget Trough, Washington, 1991-94 ( $n = 5,053$  telemetry relocations).

Fig. 2. Use of structures containing dens by northern flying squirrels, Puget Trough, Washington, 1991-94 ( $n = 5,602$ ).

live trees with external nests and contemporary snags with cavities more than expected based on availability as determined by the inventory; dens in contemporary live trees with cavities, residual live trees, and residual snags were found less than expected. Repetitive use was higher than expected for contemporary live trees with nests, snags with cavities, and snags with nests and residual snags (Table 8).

In MT, we found  $2.7 \pm 0.7$  potential dens/ha (Table 5), including  $0.9 \pm 0.2$  snags/ha (0.4/ha of which were residual). Documented dens were in contemporary live trees with nests, conifer snags, and deciduous snags significantly more than expected based on the inventory (Table 8). All other den categories, including residual live trees and snags, were used less than expected. However, repetitive use was greater than expected for contemporary live deciduous with nests,

conifer snags, deciduous snags, and residual conifer snags; use was less than expected for all other categories (Table 8).

### Den Changes and Movements Between Dens

*Lost Creek.*—We recorded  $6.1 \pm 0.6$  dens/squirrel (range, 2-12). Mean distance between consecutive dens was  $114 \pm 28$  m for males ( $n = 58$ ) and  $86 \pm 14$  m for females ( $n = 106$ ). Maximum distance moved was 1,001 m for a male and female that shared dens.

*Puget Trough.*—Squirrels changed dens  $1.5 + 0.1$  times/month and used  $2.3 \pm 0.1$  dens/month; but use of dens varied with season and sex. Greater seasonal variation was exhibited by females (Fig. 3),

Table 7. Numbers of trees containing flying squirrel dens ( $n = 75$ ) versus expected values based on a sample ( $n = 2,078$ ) of trees in an old-growth stand in the Oregon Coast Range.

Structure	Observed	Expected	Bonferroni significance <sup>a</sup>
<b>Live trees</b>			
Conifers >50 cm dbh	40	11	$P < 0.05$
Conifers 10–50 cm dbh	5	53	$P < 0.05$
Deciduous >50 cm dbh	6	<1	$P > 0.05$
Deciduous 10–50 cm dbh	1	7	$P < 0.05$
<b>Dead trees</b>			
Conifers >50 cm dbh	20	1	$P < 0.05$
Conifers 10–50 cm dbh	3	3	$P > 0.05$

<sup>a</sup> Values significantly different from expected;  $\chi^2 = 779.02$ , 74 df,  $P < 0.001$ .

who used fewer dens in the winter (Feb mean =  $1.2 \pm 0.1$  dens/month) and more dens in the summer (Jul mean =  $2.9 \pm 0.3$  dens/month). Individuals used 1-27 dens during the course of our study. Males traveled farther, on average, ( $212 \pm 7$  m) when switching dens than females ( $107 \pm 4$  m; Fig. 4). Mean distance moved within a month did not differ between males and females.

**Group Denning**

Because we could not monitor all squirrels (e.g., individuals not captured, with failed transmitters, that only intermittently used the study area, or that were <120 g), we estimated only the minimum number of squirrels denning with other squirrels. During October-April, we found  $\geq 2$  radiocollared squirrels (M and F) using the same den 41% of the time. During June-September, we found females, probably with litters, in dens without other radiocollared

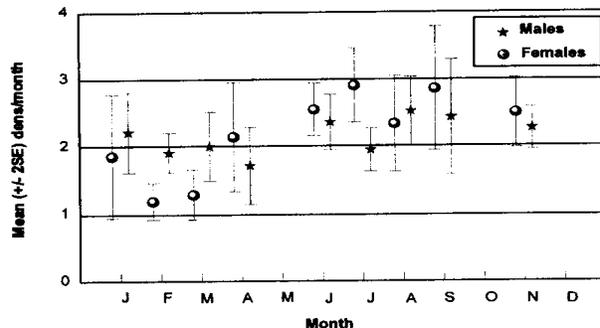


Fig. 3. Mean ( $\pm 2$  SE) dens used per month by male and female northern flying squirrels, Puget Trough, Washington, 1991–94 ( $n = 2,304$  telemetry relocations); sample sizes were insufficient during May, October, and December.

squirrels in 95% of checks (Fig. 5a). We concluded that group denning was nearly universal, with  $\geq 2$  squirrels per den (females occupied dens with litters). We found  $\geq 3$  collared squirrels together about 5% of the time. Squirrels were least likely to cohabitate during August-September and most likely to cohabitate during November-December (Fig. 5b).

Out of 1,819 observations of group denning, we found male-only groups (50%), female-only groups (13%), and male-female groups (37%). Some (34%) radiocollared squirrels were not observed denning with other radiocollared adults. We observed cases where male-female pairs would remain together (except during maternal denning periods), and groups that, when switching dens, would switch as a group.

We also noted cases where one member of a group would move to a new den and, within a few days, the rest of the group would follow.

Table 8. Observed (5,066 telemetry locations) and expected (occurrences in 4,098 sampling plots) use of den structures by northern flying squirrels in managed with legacies (ML) and managed with thinning (MT) second-growth forests in the Puget Trough of Washington, 1991–94; \* indicates Bonferroni significant difference at  $\alpha = 0.05$ . N/A indicates types were not found in sampling plots.

Structure	ML				MT			
	Type of den <sup>a</sup>		Use of den <sup>b</sup>		Type of den <sup>a</sup>		Use of den <sup>b</sup>	
	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
<b>Live trees</b>								
Residual	23*	78	239	268	7*	24	27*	76
Conifer, nests	140*	48	1,675	1,629	64*	38	508*	695
Conifer, cavity	19	26	141*	221	34*	49	686*	369
Deciduous, cavity	4	N/A	6*	47	9	N/A	47*	98
Deciduous, nest	0	N/A	0	0	4	N/A	80*	43
<b>Dead trees &gt;2 m</b>								
Residual	52*	101	719*	605	8*	25	109	87
Conifer, cavity	29*	11	348	337	37	24	282*	402
Conifer, nest	2	N/A	29	23	2	N/A	4*	22
Deciduous, cavity	3	N/A	8*	35	20	10	299*	250

<sup>a</sup> Statistical results: ML type,  $\chi^2 = 271$ ,  $P < 0.01$ ; ML use,  $\chi^2 = 113$ ,  $P < 0.01$ ; MT type,  $\chi^2 = 64$ ,  $P < 0.01$ ; MT use,  $\chi^2 = 476$ ,  $P < 0.01$ .

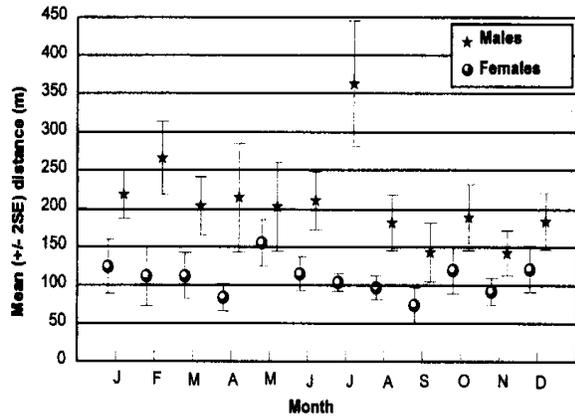


Fig. 4. Mean ( $\pm 2$  SE) distances moved between dens by male and female northern flying squirrels, Puget Trough, Washington, 1991-94 ( $n = 1,382$ ).

**DISCUSSION**

**Study Limitations and Limiting Factors**

Testing hypotheses about dens as factors limiting northern flying squirrels will require experimentation. Denning appeared to be a complex occurrence composed of an array of behavioral aspects that included social, energetic, predator, parasite avoidance, and food resources, but also included behaviorally preferential, statistically preferential, and density-dependent aspects. Interactions with other habitat elements (food, cover) may be important (see Carey 1995b, for a discussion of factors conditioning canopy-arboreal rodent interactions). In our high density populations (i.e., old growth), squirrels denned in live and dead old-growth trees, but not in medium-dbh trees or low structures. In areas of moderate to low densities (Coast Range and Olympic Peninsula second growth), flying squirrels used residual (58 and 33% of dens) and contemporary trees (live and dead). Because residual trees were rare, and contemporary trees abundant (Carey 1995a), we might conclude that the squirrels preferred to den in residual trees. In the lowest density populations (Puget Trough), squirrels used the widest variety of den types and supporting structures and traveled farther between dens than squirrels in old growth. This pattern suggests a relation between the use of large, old trees as den sites and flying squirrel abundance. Indeed, Carey (1995a) reported that, regionally, flying squirrel abundance was correlated with numbers of large snags (our data, however, suggests that large trees with decay, live or dead, are important; large snags might be a correlate of decadence). But the density of residual trees in ML was substantially higher than in

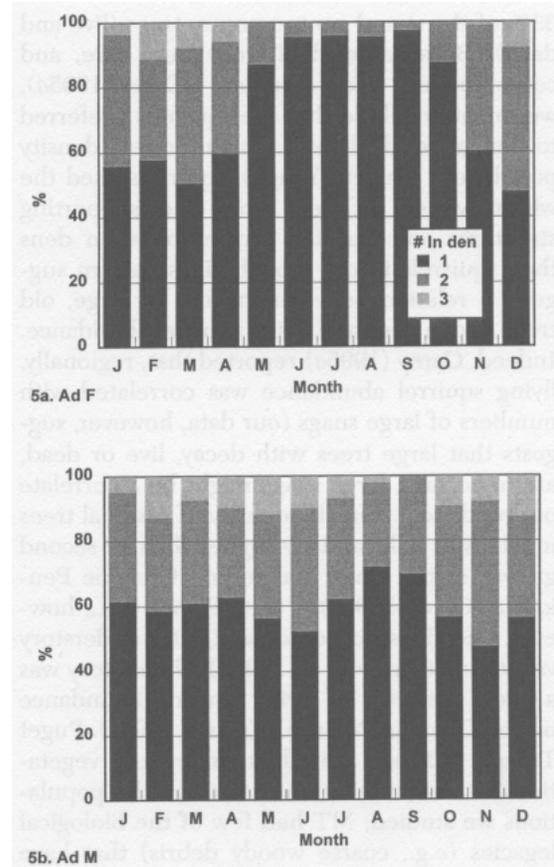


Fig. 5. Percentages of (a) adult female and (b) adult male radiocollared northern flying squirrels occupying dens with or without other radiocollared northern flying squirrels, Puget Trough, Washington, 1991-94 ( $n = 5,330$  telemetry relocations); <2% of dens were known to have  $\geq 4$  squirrels.

second growth in the Coast Range and Olympic Peninsula (Carey 1995a). Puget Trough ML, however, had dense canopies and little understory vegetation (Carey et al. 1996b). Understory was a good predictor of flying squirrel abundance on the Olympic Peninsula (Carey 1995a). Puget Trough MT had abundant understory vegetation but the lowest densities of all the populations we studied; MT had few of the biological legacies (e.g., coarse woody debris) that have been linked to flying squirrel abundance (Carey 1995a; Carey, unpubl. data). Thus, conclusions about dens as limiting factors must await experimental testing with control of extraneous variables and manipulation of selected independent variables, e.g., food and den abundances.

We suggest that experiments must show (1) sufficient time elapsed for squirrels to find and use artificial dens; (2) artificial dens were actually used by squirrels; (3) increased abundance of dens had demographic effects over time (e.g., increased survival

or population density); and (4) if no demographic effects were observed, that food-den and understory-den interactions were not important. In second growth (e.g., ML and MT), we hypothesize that initial use of dens would be by pregnant females in place of low, fragile structures and use would increase with subsequent generations of squirrels (more squirrels born in, and habituated to, artificial dens).

## Den Types

Types of dens varied regionally and with seral stage. Despite intensive searches for nests of arboreal rodents, from the ground and in felled trees, few exterior nests of northern flying squirrels were found in the Coast Range (Carey et al. 1991, Gillesberg and Carey 1991) where population densities were >3 times those in the Puget Trough, where squirrels used mainly trees with nests. Life history summaries have emphasized use of cavities by flying squirrels, especially abandoned woodpecker holes in snags and cavity use during the winter (Ingles 1965, Banfield 1974, Maser et al. 1981b, Wells-Gosling and Heaney 1984). Cavities provide shelter (from inclement weather and from predators) that is superior to the shelter provided by stick nests (Collias 1964, Short 1979, Maser et al. 1981a, Carey and Gill 1983). Although occasional use of nests by northern flying squirrels has been reported in western North America (Cowan 1936, Booth 1947, Banfield 1974, Maser et al. 1981a), we were surprised at the extensive use of nests in 50-70-year-old trees in the Puget Trough. The Puget Trough, however, is warmer (mean min. Jan temp, 0 to +2.5 C) and drier (precipitation, 80-100 cm/yr) than the Olympic Peninsula (-2.5 C, 300 cm/yr), Coast Range (0 to -2.5 C, 120-160 cm/yr), and other mountainous areas of the Northwest (Franklin and Dyrness 1973). Highest nest use (61%) was seen in the fall (Nov) after juvenile recruitment and before the coldest weather. Denning in nests (vs. cavities) may reflect the less energy-demanding climate of the Puget Trough and a relative lack of suitable cavities. Mild, dry climates in the Pacific Northwest also have been associated with the use of arboreal nests by bushy-tailed woodrats (*Neotoma cinerea*) and dusky-footed woodrats (*N. fuscipes*; Carey et al. 1992). The bushy-tailed woodrat normally uses dens in rock, the dusky-footed woodrat, middens on the ground (Carey 1991).

Alternative explanations exist for the use of nests instead of cavities. Cavity-using animals are not necessarily cavity-dependent (Carey and Sanderson 1981). For example, eastern gray squirrels (*Sciurus carolinensis*) are linked closely with cavities in trees, but still build leaf nests, even when a surplus of

cavities is available—the behavior seems instinctive in some animals (Carey and Gill 1983). Northern flying squirrels might behave similarly in areas with mild climates. The nests we observed were similar to those used in West Virginia by northern flying squirrels (Weigl and Knowles 1992). Capability to build nests close to foraging areas, particularly with ephemeral (e.g., mushrooms and truffles) and rapidly harvested (e.g., nuts and seeds) foods, reduces energetic costs of travel and risk of predation. However, squirrels in the Puget Trough followed relatively fixed travel routes among the same foraging areas, even after changing dens (Carey, unpubl. data).

Two-thirds of all dens were in live trees, regardless of region. These live trees were most often residual trees >50 cm dbh in the Coast Range and contemporary trees (95% CI = 46-64 cm dbh) in the Puget Trough. Cavities can be found in both live trees and snags, yet snags almost always are emphasized in discussions of cavity-trees in the Pacific Northwest, and the West in general (Neitro et al. 1985), because woodpeckers most commonly excavate their holes in snags (Carey et al. 1991, Lundquist and Mariani 1991). Live trees receive less attention, even though many birds and mammals use cavities in live trees (Carey 1983, 1991; Carey et al. 1991). Live trees offer several advantages that snags lack: overhead branches provide extra protection from weather; protection from predators in the form of cover and escape routes; and persistence for a long time, first as a live tree, and eventually as a snag. The high use of live trees suggests that cavity dens of flying squirrels may be best described in terms of decadence and cavity trees (live and dead), rather than snags.

Den shifts by females to low structures around parturition were intriguing. We did not find any low dens in the Coast Range, despite intensive effort. We found only 1 reference to low dens—a female and litter were found in a log about 100 km southwest of our Puget Trough sites (Cooper 1862). Weasels (*M. frenata* and *M. erminea*) were frequent predators of flying squirrels in the Puget Trough (Wilson and Carey 1996) and use of low dens seemed a poor strategy, with both mother and young at risk. We also found weasels in flying squirrel nests 6 and 21 m aboveground in trees.

Females appeared to seek cavity dens to give birth and raise young at the exclusion of other adults, as Urban (1988) suggested for flying squirrels on the Appalachian Plateau. We did not see exclusive use of cavities by all females during May-August possibly because of individual differences in parturition dates and return to non-natal dens after unsuccessful attempts at rearing young. Nests may lack necessary

protection from weather and it may be safer for altricial young to be born in a cavity rather than an exposed nest, as in the case of North Temperate bird species (Nice 1957). There may be a high demand for newly excavated cavities by woodpeckers and their competitors (e.g., flying squirrels) because new cavities are free of parasites (Short 1979). Choice of maternal dens, thus, may be related to “freshness”, rather than size or age. Alternatively, risk of predation may increase markedly with time of occupancy of terrestrial dens.

Why do females choose low structures in which to raise young? High cavities may be limited in managed stands and there may be competition, both intra- and interspecific, for these cavities. We observed Douglas' squirrels occupying cavities in snags recently occupied by flying squirrels. If a female flying squirrel cannot find a suitable cavity high in a tree within her home range, she must use an alternative structure; the only apparent alternatives with cavities were stumps, root wads, fallen trees, and roots. The low structures most often used were large diameter stumps from the harvest of the preceding old-growth stand. Most trees were cut with the use of buckboards and were  $\geq 1$  m tall. Stumps in 1991-94 were well-decayed and easily excavated by a squirrel, yet still rigid (most had a thick ring of bark enclosing a well-decayed heart).

### Use versus Availability of Dens

In the Puget Trough, residual live trees were selected for dens less than expected based on our inventory; we saw few cavities, but many nests, in residual live trees. Flying squirrels showed a preference (through repetitive use) for large, residual snags even though few were selected as dens. Many residual snags were short, well-decayed, and lacking recently excavated cavities; woodpeckers select moderately-decayed snags for excavation (Neitro et al. 1985, Carey et al. 1991, Lundquist and Mariani 1991). Some were being used by the aggressive, territorial Douglas' squirrel (or other species) and may not have been available to flying squirrels. Squirrels used few live conifers with cavities in ML, possibly because the trees were small compared to live trees with cavities in MT; cavities high in the trees may not have been large enough for group occupancy.

In MT, squirrels preferred to use contemporary conifers with cavities, deciduous snags with cavities, and deciduous trees with nests. Unlike ML, conifer nests were used repetitiously less than expected even though they were chosen above their apparent availability. More dens were in live conifers with cavities than in any other category and these were

used almost twice as much as expected. Live conifers were 21% larger ( $61.9 \pm 2.5$  cm dbh) than live cavity trees in ML, thus the likelihood of having a relatively large cavity was high. Flying squirrels also preferred deciduous snags, which were uncommon in ML, but statistically avoided using contemporary conifer snags. We cannot explain why live deciduous trees with nests were preferred.

*Management History and Use of Dens.*—The ML forest regenerated after the preceding old-growth forest was clearcut around 1940. The forest quickly regrew, entered the stem exclusion phase (Oliver 1981), and remained there. Douglas-fir trees composed 99% of the overstory and had short, narrow crowns and small dbh ( $34 \pm 0.5$  cm). Trees with multiple tops or recently-broken leaders were common. Multiple leaders provided platforms of sufficient size to support stick nests, but bole diameters at the point of damage were too small to support cavities. Thus, use of stick nests may have been facilitated by mild climate, suitable substrates for nest building, and tightly closed canopies offering more protection from the elements than open-grown MT canopies.

The contemporary snags in ML were too hard or too small for cavity excavation by woodpeckers. Residual trees possibly were in high demand by Douglas' squirrels, raccoons (*Procyon lotor*), opossums (*Didelphis virginianus*), and owls, especially because few large cavity trees were available. Two snags used by flying squirrels were subsequently occupied by Douglas' squirrels. It has been suggested there was little competition between the 2 squirrels because of a putative preference for nests by Douglas' squirrels and cavities by flying squirrels (Maser et al. 1981b, Carey 1991). However, use of cavities and nest boxes by Douglas' squirrels (Carey, unpubl. data) and use of nests by flying squirrels indicate there may be competition.

The old growth preceding MT was harvested about 1930, regeneration was light, and the second growth had been thinned twice <20 years before our study. Thus, trees were larger, with deeper and wider crowns than in ML, and many dominants maintained live branches to their base. The canopy was 95% Douglas-fir,  $53 \pm 0.6$  cm dbh. Many trees had suffered damage to their tops that resulted in sufficient decay at large enough bole diameters to produce moderately sized cavities suitable for flying squirrels. Twice as many live-tree cavities were used in MT as ML, although overall, dens were 3-4 times more abundant in the ML. Almost 40% of non-maternal den use was in live trees with cavities. In MT, we did not find small trees with platform

branching in areas of closed canopy that we found in ML. Thus, there may have been fewer places for stick nests.

Thinnings had forestalled mortality due to suppression and had removed snags as well; thus, most contemporary conifer snags were large-dbh trees that had died since the last thinning. Large trees produce large snags that remain standing longer and are more likely to be excavated by woodpeckers than small snags. The thinned forest also had more deciduous snags (e.g., red alder) than ML. These snags were about the same age as the conifers but had died after being overtopped by the Douglas-fir. Flying squirrels preferentially used deciduous snags but avoided contemporary coniferous snags; deciduous snags were soft and tended to contain cavities; most coniferous snags were sound. Use of small, soft deciduous snags may reflect the overall lack of dens available.

### Den Changes and Movements Between Dens

Frequent changes in dens could be adaptive by reducing risks of predation (by not leaving and returning to the same den night after night) and parasitism and by facilitating social interactions (den membership often changed with changes in dens). Using multiple dens would be advantageous when foraging patches are dispersed and food abundance is highly variable spatially and temporally. Squirrels would need to monitor highly productive patches to determine when food (primarily truffles and mushrooms of ectomycorrhizal fungi; Maser et al. 1986, Carey 1995a) was available. Fungi fruit and sporocarps deteriorate rapidly; fruiting is variable within and among seasons and years (Luoma 1991). Second-growth forests had fewer species of fungi and flying squirrels had less diverse diets in Washington than in Oregon (Carey et al. 1992, Carey 1995a).

Few observations of distances traveled between dens have been reported (e.g., Maser et al. 1981a, Mowrey and Zasada 1984, Weigl and Knowles 1992), but distances traveled in the Puget Trough were much greater for both sexes than previously reported. Movements between dens by males were long and variable compared to movements of females. Distances between dens of females increased between April and May, as females moved to maternal dens, then decreased during lactation (Jul-Sep). Males moved farthest during July, and least during September. During July, females reared young and denned exclusive of other adults; thus, males may have had to move farther to obtain den companions. Males were still in breeding condition in July, searching for females and traveling farther at

night than during the nonbreeding season (Carey, unpubl. data); thus, males had increased likelihood of encountering other males with which to den. In September, when population levels were highest (with juv recruitment) and females once again were sharing dens, less distance was traveled by males.

Squirrels moved less between dens in the Coast Range than in the Puget Trough. Habitat quality (better foraging) and higher densities of squirrels apparently reduced the need to travel long distances. Thus, the comparatively large distances moved between dens in the Puget Trough may be: (1) an indication of low habitat quality, with squirrels having to travel farther to find food and shelter; and (2) a response to low population density and the benefits of denning in groups.

### Group Denning

We found 2-5 radiocollared animals denning together throughout the year. Certainly, the rate of group denning was higher than we observed. Maser et al. (1981b) reported sexes were segregated in group dens in eastern Oregon and hypothesized that a predominance of males in nestboxes indicated that females were using natural cavities and that natural cavities were superior to nest boxes. We suggest a different interpretation: sexes were not segregated, except before parturition and while females were rearing young. In southern flying squirrels (*G. volans*), denning in groups reduced energy expenditures by 26-33% (Stapp et al. 1991) and it is likely that northern flying squirrels receive similar benefits. Patterns in group denning also suggested that social interactions were important and these patterns may be explained, in part, by kinship among squirrels. Layne and Raymond (1994) concluded that group denning in *Glaucomys* was social behavior that was an evolutionary consequence of, but not related solely to, energy conservation. Selection of dens must therefore be considered in a broader context than energy conservation; avoidance and protection from predation and benefits of social interactions may be important.

### MANAGEMENT IMPLICATIONS

Current logging practices (e.g., cutting small dbh, 40-50-yr-old trees close to the ground) leave few large snags, stumps, and fallen trees in forests. Thinnings often remove all live trees with defects (rot or irregular branching), thus removing actual or potential flying squirrel dens. These practices could eliminate maternal dens. Thinnings combined with cavity tree management and long (70-130 yr) rotations are economically and ecologically viable options for

management of second growth (Carey et al. 1996a). Managers can improve flying squirrel habitat by (1) leaving large fallen trees and large dbh tall stumps at harvest to provide maternal dens and coarse woody debris that is important to the health of forest ecosystems (Carey and Johnson 1995, Carey et al. 1996a); (2) retaining green trees at harvest to provide dens in the future; (3) retaining flying squirrel dens (especially large live trees with cavities or platform branching and trees with obvious nests) during thinnings; and (3) creating cavities in live trees in poor habitat (Carey and Sanderson 1981, Carey and Gill 1983). Options for creating cavities includes excavation with chainsaws (Carey and Gill 1983), inoculating live trees with decay fungi (Parks et al. 1995), and removing the tops of live trees without killing the tree to provide multiple leaders and a site for decay.

Snags have received attention of forest managers because of numerous studies of cavity-using birds (e.g., Neitro et al. 1985). However, live trees are important den structures for mammals (and many birds, including spotted owls), regardless of seral stage. Forest managers should consider live den and nest trees when managing for flying squirrels, spotted owls, and late-successional forests. Leaving large snags is a management option, but current federal safety regulations require leaving a large buffer area around any retained snag (Myers and Fosbroke 1995) and snags may have to be retained in clusters away from management activity. Snag retention may not be feasible in many situations; den tree management can augment cavity tree management. Live trees with cavities can be retained with few safety restrictions. Live trees will continue to grow and persist over a much longer period than snags, eventually develop into snags, and require less management intervention over time.

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