

Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon

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We compared density, sex ratio, body mass, and annual recapture rate of northern flying squirrel (*Glaucomys sabrinus*) populations in second-growth and old-growth Douglas-fir (*Pseudotsuga menziesii*) stands in the Oregon Cascade Range. Densities averaged 2.0 and 2.3 squirrels/ha in second- and old-growth stands, respectively. Although densities varied between years within stands, average densities were similar between years. Body mass and annual recapture rate were similar between stand-age classes, although a higher proportion of females was recaptured in subsequent years in second-growth than in old-growth stands. Similarly, there was a higher proportion of females than males in second-growth but not in old-growth stands. Squirrel densities were not correlated with habitat characteristics; we concluded that flying squirrels may be habitat generalists, and not a species associated with old-growth stands, as was previously hypothesized. We suggest that studies be carried out with radiotelemetry to more accurately assess the habitat associations of this species.

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Nous avons comparé la densité, le rapport mâles:femelles, la masse corporelle et le taux annuel de recapture chez des populations de Grands Polatouches (*Glaucomys sabrinus*) de forêts secondaires et de forêts climaciques de Sapins de Douglas (*Pseudotsuga menziesii*), dans la chaîne des Cascades, en Oregon. La densité était en moyenne de 2,0 individus/ha dans les forêts secondaires et de 2,3 dans les vieilles forêts. Les densités variaient d'une année à l'autre dans chacune des forêts, mais les valeurs moyennes des densités étaient semblables d'une année à l'autre. La masse corporelle et le taux annuel de recapture étaient semblables dans les deux types de forêts, mais au cours des années subséquentes, une plus grande proportion de femelles ont été capturées dans les forêts en croissance que dans les vieilles forêts. De même, il y avait une plus grande proportion de femelles que de mâles dans les forêts secondaires que dans les vieilles forêts. La densité des polatouches n'était pas reliée à des caractéristiques de l'habitat; nous croyons que les polatouches sont des généralistes quant à leurs préférences d'habitat et non pas des espèces associées nécessairement aux vieilles forêts, comme on l'a généralement cru à ce jour. Nous conseillons l'emploi de techniques radiotéléométriques pour évaluer plus justement les préférences d'habitat chez cette espèce.

[Traduit par la rédaction]

Introduction

Northern flying squirrels (*Glaucomys sabrinus*) are widely distributed in northern North America, occurring in high-elevation forests in the southern Appalachians, extending north into central Canada, and throughout forests in the Pacific Northwest (Wells-Gosling and Heaney 1984). In the Pacific Northwest, several reports have suggested that flying squirrels may be more abundant in old-growth stands than in young second-growth stands (Harris and Maser 1984; Brown 1985, p. 164; Franklin 1988).

Flying squirrels are known to nest and den in cavities in large snags (Weigl and Osgood 1974; Maser 1981) and to feed primarily on lichens and the fruiting bodies of hypogeous fungi (McKeever 1960; Maser et al. 1985; Maser et al. 1986), all components that may be more abundant in old-growth than in young second-growth stands (hereafter referred to as second-growth). Therefore, the hypothesis that flying squirrels may be more abundant in old-growth stands seems reasonable. Although nesting sites and food may be more abundant in old-growth stands, they may not limit flying squirrel densities in second-growth stands. Lower predation rates and use of other nesting substrates may make second-growth stands more

suitable for flying squirrels than was previously believed.

Old-growth forests once dominated the forested landscape in the Pacific Northwest (Harris 1984, p. 27), but have increasingly been replaced by second-growth forests as a result of intensive forestry practices. Concern for wildlife in old-growth forests (e.g., Meslow et al. 1981) has motivated investigators to study the species associated with these forests. In this paper we compare population characteristics of flying squirrels in second- and old-growth Douglas-fir forests to test the hypothesis that squirrel population characteristics do not differ between these two forest types.

Methods and materials

Study sites

We selected five second-growth (30-60 years old) and five old-growth (>400 years old) Douglas-fir stands on the west slope of the Cascade Range in the Blue River or McKenzie River ranger districts, Willamette National Forest, near the towns of Blue River and McKenzie Bridge, Lane County, Oregon. Selection criteria were that stands be dominated by Douglas-fir (*Pseudotsuga menziesii*), large enough to accommodate a 13-ha grid with a 50-m buffer, and accessible by road. Selected stands were at between 375 and 900 m elevation, and slope ranged from 10 to 60%. Climate in the study area was

characterized by mild, wet winters and warm, dry summers (Franklin and Dymess 1973, p. 38). Stands were dominated by Douglas-fir and western hemlock (*Tsuga heterophylla*). Western red cedar (*Thuja plicata*) and incense-cedar (*Libocedrus decurrens*) were common canopy species in old- and second-growth stands, respectively. The understory (2-4 m in height) was dominated by vine maple (*Acer circinatum*), Pacific dogwood (*Corpus nuttallii*), California hazel (*Corylus cornuta*), and western hemlock; and the lower understory (<2 m in height) by Oregon grape (*Berberis nervosa*), salal (*Gaultheria shallon*), swordfern (*Polystichum munitum*), *Vaccinium* spp., and Pacific rhododendron (*Rhododendron macrophyllum*).

Four of five second-growth stands were planted after clear-cut logging; the fifth stand was naturally regenerated after wildfire. Silvicultural treatments varied from intensive clear-cuttings to stands with some large trees retained (about 1.2 trees > 79 cm diameter at breast height (dbh)/ha). The five old-growth stands were not logged previously, except for small areas where a few individual trees were salvage logged; < 5 % basal area was removed.

Population size

We established one livetrapping grid in each stand; grids consisted of 96-100 trap stations spaced at 40-m intervals. Grids (≈ 13 ha) varied from an array of 10 X 10 to 16 X 6 trap stations, depending on the size and shape of stands. Two Tomahawk No. 201 (41 X 13 X 13 cm) live traps were placed at each station. One trap was placed ≈ 1.5 m high on the largest tree within 5 m of the trap station; the second trap was placed on the ground within 2 m of the tree (Witt 1991). Traps were baited with a mixture of peanut butter, whole oats, molasses, and a high-protein pellet. We ear-tagged squirrels with Monel No. 1 tags (National Band and Tag Co., Newport, Ky.) and recorded body mass and sex at first capture.

In 1987, we trapped from 1 October to 5 December. We trapped on two grids (one old-growth and one second-growth stand) simultaneously for 8 consecutive nights for each of five sets of grids. Because of a low number of recaptures in 1987, we increased the number of nights in 1988 and 1989. In 1988, we trapped on five grids (old-growth and second-growth stands) simultaneously for 21 consecutive nights (19 October to 8 November), and trapped on the remaining five grids (three second-growth and two old-growth stands) simultaneously for 16 nights (15-30 November). We reduced the number of trapping nights to 16 because of inclement weather; however, population estimates appeared reliable when ≥ 14 nights of trapping were used (Rosenberg 1991). In 1989, we trapped on all 10 grids for 21 consecutive nights (10-30 October and 7-27 November).

We did not estimate squirrel abundance in 1987 because of the small number of recaptures; instead, we used the number of individuals captured to estimate relative abundance. For 1988 and 1989 data, we used the first-order jackknife estimator (Burnham and Overton 1979) to estimate flying squirrel abundance (\hat{N}). We computed an effective trapping area around the grids by using one-half of the mean maximum distance moved (MMDM; Wilson and Anderson 1985), averaged for all grids. MMDM was estimated from animals captured ≥ 2 times and was added to the perimeter of the grid to estimate the effective area trapped (\hat{A}). Density (\hat{D}) was estimated as \hat{N}/\hat{A} . Grids in second- and old-growth stands were treated similarly because there was no significant ($P = 0.7$) difference in MMDM between the two stand types, and because the low recapture rates, which varied among stands (Rosenberg 1991), could potentially bias the results towards a higher MMDM in stands that had a higher recapture rate. We provide density estimates using MMDM as a crude estimate of the distance to be included around the perimeter of the grid; however, more accurate estimates of distances moved, such as could be obtained from radiotelemetry, would improve the accuracy of density estimates.

Habitat characteristics

We used concentric circular plots modified from Spies et al. (1988) to sample vegetation at every third trapping station. Large (≥ 50 cm diameter) trees, snags, downed wood, and stumps (< 1.5 m tall) were recorded in 0.12-ha (20 m radius) plots centered at the trap station.

Smaller trees ($\geq 5-49$ cm dbh), snags ($\geq 10-49$ cm dbh), and downed wood ($\geq 25-49$ cm diameter) were measured in 0.05-ha (12.6 m radius) plots. We recorded the species and diameter at breast height of live trees and the diameter and condition (percent limbs remaining) for snags (≥ 1.5 m tall) and downed wood. Vegetation was measured from July through September 1988.

We established size classes for trees, snags, and downed wood. Live trees were grouped into three size classes (5-10, >10-49, ≥ 50 cm dbh) and snags into two size classes (10-49, 2-50 cm dbh) and two condition categories (soft: $\leq 2\%$ limbs remaining; hard: > 2% limbs), and downed wood volume (m^3) was computed for two size classes (25-49 and ≥ 50 cm diameter). We computed the percent coefficient of variation ($(SE/\bar{x} \times 100)$) of tree diameters as a measure of tree-size diversity.

Percent cover of understory plants (Oregon grape, fern, salal, conifer, rhododendron, deciduous) and percent ground cover (herb, woody debris <25 cm diameter, moss) were visually estimated for each category in eight 1-m² plots. These were placed 4 and 7 m from the trap station along each cardinal direction. We used the average of the eight plots in the analyses. Organic soil depth was measured to the nearest 1 cm up to 10 cm, and then recorded as > 10 cm in each of the eight 1-m² plots by placing a trowel marked in 1-cm increments into the soil. The median value of the eight samples was used in the analyses.

Statistical analyses

We used Wilcoxon rank-sum tests to compare the number of individual squirrels captured (1987) and estimated densities (1988 and 1989) between second- and old-growth stands for each year separately. Relative densities (1988-1989) and sex ratios (1987-1989) among grids were compared between years with Spearman rank correlations. Sex ratios (pooled by stand age-class) were compared using χ^2 tests for each year separately, under the hypothesis that equal proportions of males and females were captured. Body mass and MMDM were analyzed using a split split-plot and a split-plot analysis of variance, respectively (Sokal and Rohlf 1981, p. 394); this analysis was used because the same stands were used in each year. The nested effect of stand within stand age-class was used as the error term to test the main effect of stand age-class, and sex X year X stand (stand age-class) was used as the error term to test the main effects of year and sex for the body mass analysis. Annual recapture rate was compared between stand age-classes for each sex separately using χ^2 tests by testing for equality of proportions of squirrels recaptured 1 year after their initial capture.

One hundred and forty animals were recaptured approximately a year after their initial capture and were thus considered to be adults. The lowest mass for this group of squirrels was 104 g, so animals weighing less than this were considered to be juveniles. We were unable to evaluate the proportion of animals ≥ 104 g that were juveniles, but to facilitate reporting the results, we refer to this group as adults. The proportion of animals estimated to be juveniles was compared between stand age-classes using χ^2 tests for each year.

Relationships between flying squirrel density (1988 and 1989) and habitat characteristics were evaluated with Spearman rank correlations for each year separately. We used the mean values from all plots within each of the 10 stands (see Appendix).

Results

Population estimates

In 1988 and 1989 there were sufficient recaptures to compute MMDM, which ranged from 60 to 88 m ($\bar{x} \pm SE$, 77.8 ± 2.9 m) in 1988 and from 62 to 134 m (92.4 ± 6.9 m) in 1989. There was no significant difference between second-growth (86.6 ± 6.1 m) and old-growth (83.5 ± 5.5 m) stands ($F = 0.1$, $df = 1$, $P = 0.7$), but MMDM tended to be greater in 1989 ($F = 3.9$, $df = 1$, $P = 0.08$).

In 1987, we captured 201 flying squirrels 282 times, averaging 1.4 captures/individual (20.1 ± 3.7 squirrels/grid; Table

TABLE 1. Numbers of flying squirrels captured and estimated densities (number/ha) in second-growth and old-growth Douglas-fir stands in Willamette National Forest, Oregon, 1987-1989

Stand ^a	1987 ^b		1988 ^c		1989 ^d		
	Number captured	Number captured	Population size ^e	Density (no./ha) ^f	Number captured	Population size	Density (no./ha) ^g
Second-growth stands							
SG-1	11	24	33	1.7	28	39	1.9
SG-2	10	33	40	2.0	37	48	2.2
SG-3	32	25*	39	1.9	37	53	2.5
SG-4	21	24*	35	1.8	13	22	1.1
SG-5	25	29*	46	2.4	24	33	1.6
Avg.	18.5	27.0	38.6	2.0	27.8	39.0	1.9
Old-growth stands							
OG-1	42	25	37	1.9	45	68	3.3
OG-2 ^h	4	39	51	2.6	32	43	2.1
OG-3 ^h	12	20	27	1.4	19	30	1.5
OG-4	17	40*	56	2.9	33	44	2.1
OG-5	27	35*	54	2.8	33	53	2.6
Avg.	20.4	31.8	45.0	2.3	32.4	47.6	2.3

^a Trapping grid configurations were approximately a 10 x 10 array of traps, except for stands SG-2 (approximately 8 x 13) and SG-3 (approximately 6 x 17).

^b Eight trap occasions (approximately 24 h each).

^c Sixteen to 21 trap occasions (approximately 24 h each); 16 occasions are denoted by an asterisk.

^d Twenty-one trap occasions (approximately 24 h each).

^e Population estimates were derived from the first-order jackknife estimator (Burnham and Overton 1979).

^f Density estimates were computed from the population estimate, with a 39-m boundary width (one-half mean maximum distance moved) included around the trapping grid (Wilson and Anderson 1985).

^g Same as footnote f but with 46-m boundary width.

^h Trapping grid was near (<500 m) an active spotted owl nest (occupied at least once during 1987-1989).

1). Numbers of recaptures were too low to allow population size to be reliably estimated or to compute MMDM for 7 of 10 stands. Numbers of individual squirrels captured were almost identical between stand age-classes: 99 were caught in second-growth and 102 in old-growth stands. Stands with the most and fewest squirrels captured were old-growth stands.

In 1988, we captured 294 flying squirrels 618 times, averaging 2.1 captures/individual (29.4 ± 2.2 squirrels/grid). Estimated population sizes ranged from 27 to 56 (41.8 ± 3.0), and estimated densities ranged from 1.4 to 2.9 animals/ha (2.1 ± 0.2 ; Table 1). Densities were not significantly different between second-growth (2.0 ± 0.1 animals/ha) and old-growth (2.3 ± 0.3 animals/ha) stands ($z = 0.94$, $P = 0.30$). Highest and lowest squirrel densities occurred in old-growth stands.

In 1989, we captured 301 squirrels 819 times, averaging 2.7 captures/individual (30.1 ± 3.0 animals/grid). Estimated population sizes ranged from 22 to 68 squirrels (43.3 ± 4.2), and densities ranged from 1.1 to 3.3 animals/ha (2.1 ± 0.2 ; Table 1). Estimated densities were not significantly different between second-growth (1.9 ± 0.2 squirrels/ha) and old-growth (2.3 ± 0.3 squirrels/ha) stands ($z = 0.8$, $P = 0.4$). The highest density was in an old-growth stand, and the lowest in a second-growth stand.

Old-growth stands in which the fewest animals were captured (1987) or with the lowest densities (1988 and 1989) were the only stands that were near (<500 m) active spotted owl nests (G. Miller, personal communication). Lowest squirrel densities in old-growth stands occurred in the same grid in 1988 and 1989 (Table 1). Densities among stands in 1988 were not related to those in 1989 ($r_s = 0.42$, $P = 0.2$), so changes

TABLE 2. Sex ratios of flying squirrel populations in second-growth and old-growth Douglas-fir stands in Willamette National Forest, Oregon, 1987-1989

Squirrel age-class	Year	Second-growth stands		Old-growth stands	
		<i>n</i>	Males:females	<i>n</i>	Males:females
Juvenile ^a	1987	13	0.6	18	0.9
	1988	22	1.0	15	1.5
	1989	29	1.2	35	2.2 ^b
Adult ^c	1987	83	0.6 ^b	78	1.0
	1988	112	0.5 ^b	136	1.0
	1989	108	0.5 ^b	124	0.9

^a Animals weighing < 104 g.

^b Sex ratio differed from 1:1 ($P < 0.05$).

^c Animals weighing ≥ 104 g.

in density between years were not similar among stands.

Sex ratio

The sex ratios (males:females) of adult squirrels (i.e., those weighing ≥ 104 g) in individual stands ranged from 0.3 to 2.1, and were related among years (1987-1988 and 1987-1989; $r_s = 0.63$, $P = 0.06$; 1988-1989: $r_s = 0.71$, $P = 0.03$). The sex ratios of adults in old-growth stands were not significantly different from 1:1; however, second-growth stands had a significantly greater proportion (62-66%) of females than males (Table 2). There was no deviation from a 1:1 sex ratio for juveniles in second- or old-growth stands in 1987 or 1988, but sex ratios were skewed in favor of males in old-growth stands in 1989 (Table 2).

TABLE 3. Body mass (g) of flying squirrels in second-growth and old-growth Douglas-fir stands in Willamette National Forest, Oregon, 1987-1989

Year	Second-growth stands						Old-growth stands					
	Males			Females			Males			Females		
	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE
1987	31	130.2	2.8	52	136.3	2.3	38	127.2	2.1	39	137.2	2.9
1988	38	125.1	2.5	74	137.9	1.8	69	135.0	2.1	67	137.4	2.2
1989	38	124.2	2.0	70	130.9	1.9	58	126.1	1.7	66	131.6	2.3

NOTE: Only animals weighing ≥ 104 g were included because those weighing < 104 g were believed to be young of the year.

TABLE 4. Number and percentage of flying squirrels recaptured in subsequent years of trapping in Willamette National Forest, Oregon, 1987-1989

Year first captured	Number recaptured					
	Males			Females		
	<i>n</i>	1988	1989	<i>n</i>	1988	1989
Second-growth stands						
1987	35	11 (31.4)	8 (22.9)	59	30 (50.1)	10 (16.9)
1988	47	-	10 (21.3)	80	-	23 (28.7)
Old-growth stands						
1987	47	17 (36.2)	12 (25.5)	48	18 (37.5)	6 (12.5)
1988	75	-	16 (21.3)	68	-	14 (20.6)

NOTE: Values in parentheses denote the percentage of squirrels recaptured of those initially captured. *n*, number of squirrels initially captured.

Body mass

We compared body mass between sexes and stand age-classes for juvenile and adult squirrels. Body mass of juveniles ranged from 59 to 103 g, and body mass of adults ranged up to 188 g for males and 190 g for females. We did not detect significant differences in body mass between stand age-classes ($F = <0.0$, $df = 1$, $P = 0.9$) or sexes ($F = 2.0$, $df = 1$, $P = 0.2$), or among years ($F = 2.0$, $df = 2$, $P = 0.2$) for juveniles. Significant differences in body mass were found for adult animals. Females were heavier than males ($F = 36.5$, $df = 1$, $P = 0.0001$), but there was no significant difference between stand age-classes ($F = 0.5$, $df = 1$, $P = 0.5$) or among years ($F = 2.5$, $df = 2$, $P = 0.12$; Table 3).

Age structure and annual recapture rate

Sixteen (31 of 191), 13 (37 of 285), and 22% (64 of 296) of squirrels captured in 1987, 1988, and 1989, respectively, were considered juveniles. There was no significant difference in the proportion of juveniles captured in second- and old-growth stands ($\chi^2 \leq 2.4$, $P > 0.10$, $df = 1$, for all 3 years).

Thirty percent (139 of 459) of all squirrels captured were recaptured the following year, and 19% (36 of 189) were recaptured 2 years following initial capture (Table 4). A greater proportion of females was recaptured in successive years in second-growth than in old-growth stands ($\chi^2 = 3.2$, $P = 0.08$, $df = 1$), but the proportions of males recaptured were similar between stand age-classes ($\chi^2 = 0.2$, $P = 0.7$, $df = 1$; Table 4).

Relationship between squirrel density and habitat characteristics

The density of flying squirrels in 1988 was positively correlated with deciduous shrub (<5 cm dbh) cover on the 10

trapping grids ($r_s = 0.72$, $P = 0.02$, $n = 10$). In 1988 density was not significantly ($P \geq 0.05$) related to any other variables measured, and in 1989 density was not related to any of the variables measured. There was a wide range of snag and stem densities within and between stand age-classes (see Appendix), but no significant relationships between these variables and squirrel density were found. It is expected by chance that 1 variable will be significant at $P < 0.05$ when 20 variables are evaluated (we had 24). This, combined with the lack of a relationship in 1989, suggests that the statistical significance of deciduous cover may be spurious.

Discussion

We found similar densities of flying squirrels in young second- and old-growth coniferous forests in the Oregon Cascade Range. In contrast, others have suggested that northern flying squirrels are more abundant in old-growth than in second-growth forests (Harris and Maser 1984; Brown 1985; Franklin 1988), but they did not compare abundances quantitatively. The second-growth stands we studied contained residual old-growth components, such as large woody debris, snags, and trees. It is not known whether stands that lack these components would be as suitable for flying squirrels. Our findings are not surprising considering the large range of northern flying squirrels in North America and the varied forest types they inhabit (Wells-Gosling and Heaney 1984). The lack of a correlation between habitat variables and squirrel density suggests that flying squirrels are habitat generalists within the conditions we examined. The results of other studies suggest the same. Similar numbers of flying squirrels were captured in riparian and upland coniferous forests despite large differences in vegetation between these habitats (Doyle 1990), and

in experiments with captive animals it was found that flying squirrels were not selective of habitat type within forest-like conditions (Weigl 1978). More intensive studies involving attaching radio transmitters to animals are needed to permit habitat associations to be described and the habitat-generalist hypothesis tested.

Flying squirrels use cavity nests in live and dead trees (Cowan 1936; Weigl and Osgood 1974; Maser 1981). Large snags, which are more likely to contain cavities than smaller snags (Mannan et al. 1980; Rosenberg et al. 1988), are more abundant in old-growth than in second-growth stands (Mannan et al. 1980; this study). These findings may have led to the suggestion that flying squirrels are more abundant in old-growth forests. Nesting habitat for flying squirrels may not limit their abundance because they nest in a variety of substrates, including cavities in small snags (J. Waters, personal communication; P. Weigl and T. Knowles, personal communication), trees infected with witches' broom rust (*Chrysomyxa* spp., Mowrey and Zasada 1984), moss nests (Bailey 1936, p. 164), and stick nests (Cowan 1936; Weigl and Osgood 1974). Our finding that relative squirrel densities among stands varied between years suggests that other factors besides the structural features of the habitat may be limiting squirrel abundance, since the characteristics we measured varied little during the 3 years of our study (personal observation). Food availability, predation, and competition with other species likely have more influence on squirrel abundance than nest-site availability. These factors may vary temporally and could be responsible for the yearly variation in densities of squirrels that we found in this study.

The potentially high predation on flying squirrels by spotted owls in old-growth forests in the Oregon Cascades (Forsman et al. 1984; Miller 1989) may affect squirrel abundance. The home range of spotted owl pairs in the Oregon Cascades includes an average of about 1000 ha of older-growth forests (Forsman et al. 1984). Based on an average of 2 squirrels/ha (this study), forests used by a pair of spotted owls would contain approximately 2000 squirrels. A pair of spotted owls may consume 500 squirrels per year (E. Forsman, personal communication), which may represent 25% of the population. The lowest squirrel densities we found in old-growth stands were all near spotted owl nests. Investigations of the role played by predation in the population dynamics of flying squirrels will be important in explaining differences, or the lack thereof, in squirrel densities across the landscape.

The greater proportions and higher annual recapture rate of females than males in second-growth than in old-growth stands may have been due to higher survival or lower dispersal rates of females in second-growth stands, assuming that a 1:1 natal sex ratio exists (Davis 1963). The higher proportion of juvenile males in old-growth stands during 1 year of this study suggests that the difference in sex ratios between stand types may also result from differential dispersal or mortality within the juvenile cohort, although further data are needed to determine if the greater proportion of juvenile males than females is characteristic of old-growth stands, or if our finding in only 1 of 3 years is spurious. We could not distinguish between survival and emigration; however, these two factors could be separated by studying the movement patterns of squirrels.

Recent interest in flying squirrels in the Pacific Northwest has resulted partially from studies on the spotted owl (listed as threatened in 1990 under the Endangered Species Act). The owls' diet is principally flying squirrels in parts of the owls' range (Forsman et al. 1984; Miller 1989; Thomas et al. 1990).

The decline of the spotted owl has been attributed to its dependence on, and the reduction of, old-growth Douglas-fir forests (Forsman et al. 1977, 1982, 1984). It has been hypothesized that selection of old-growth forests by spotted owls is related to higher prey abundance in these habitats (Forsman et al. 1982, 1984; Carey et al. 1990). Our finding of similar squirrel densities in both stand age-classes suggests that spotted owls avoid second-growth forests (Forsman et al. 1984; Carey et al. 1990; Solis and Gutiérrez 1990) for reasons other than low flying squirrel (prey) abundance. Young second-growth forests often have high tree densities and homogeneous canopies which may impede flight and inhibit the ability of owls to capture prey.

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Appendix: Habitat characteristics at trapping stations in second-growth and old-growth stands in Willamette National Forest, Oregon, 1988

	Second-growth stands										Old-growth stands									
	SG-1	SG-2	SG-3	SG-4	SG-5	OG-1	OG-2	OG-3	OG-4	OG-5	SG-1	SG-2	SG-3	SG-4	SG-5	OG-1	OG-2	OG-3	OG-4	OG-5
Herb cover (%)	8.7	1.5	3.0	0.6	9.8	1.5	7.5	1.2	3.5	0.4	6.4	1.2	4.5	0.8	16.7	2.4	6.2	1.0	4.3	0.5
Woody debris cover (%)	17.2	1.2	7.4	0.8	8.8	1.1	8.4	0.9	10.1	0.9	12.7	1.6	8.6	0.7	11.5	1.0	20.6	1.6	10.9	1.1
Moss cover (%)	8.0	1.4	8.5	1.3	5.5	1.3	11.8	1.4	7.1	1.1	7.0	1.8	18.3	2.1	18.7	2.3	11.8	1.9	25.6	2.5
Salt cover (%)	0.1	0.1	2.0	0.6	4.6	1.1	3.5	0.6	7.5	1.1	3.4	0.9	2.3	0.7	0.5	0.2	0	0	6.6	1.2
Fern cover (%)	2.2	0.5	7.8	1.3	4.4	1.0	8.7	1.5	6.4	0.9	4.6	0.9	10.2	1.6	3.2	1.2	3.0	0.9	8.7	1.3
Deciduous cover (<5 cm dbh; %)	1.5	0.4	1.0	0.4	6.2	1.0	16.2	2.1	11.9	2.1	5.8	1.5	4.7	0.8	6.6	1.4	1.4	0.3	9.5	1.9
Conifer cover (<5 cm dbh; %)	5.3	1.0	2.5	0.5	2.3	0.4	1.1	0.3	1.5	0.4	6.1	1.0	6.1	1.5	6.8	1.1	5.5	0.9	6.3	1.3
Rhododendron cover (%)	2.9	1.1	0	0	0.5	0.3	0	0	0	0	5.5	1.6	2.4	0.9	3.8	1.6	0	0	1.8	0.5
Oregon grape cover (%)	8.0	1.1	3.6	0.5	5.1	0.8	7.1	1.1	8.2	1.2	4.9	0.9	4.4	0.6	3.1	0.7	1.3	0.3	7.6	1.1
Downed wood (25-49 cm diam.; m ³ /ha)	27.2	3.8	22.5	2.3	14.2	1.9	13.2	1.7	16.6	2.2	14.0	2.4	16.0	3.0	27.0	2.4	24.0	2.7	17.6	2.6
Downed wood (≥50 cm diam.; m ³ /ha)	22.7	4.3	56.4	6.5	57.2	7.4	46.6	7.7	81.8	6.9	55.2	8.3	41.6	6.6	62.6	8.0	94.0	12.5	75.8	8.5
Snags (10-49 cm dbh; no./ha) ^a	166.6	12.0	16.4	4.0	35.2	6.0	63.0	10.4	24.8	5.1	17.0	4.9	11.5	3.7	36.2	8.5	38.2	8.6	16.4	4.6
Snags (≥50 cm dbh; no./ha) ^a	25.8	3.1	0.7	0.4	2.9	0.7	4.1	0.9	5.8	1.1	25.1	3.2	10.8	1.9	16.7	2.0	23.9	3.8	10.1	1.9
Stumps (no./ha)	30.0	3.5	67.6	5.1	57.0	4.1	56.0	4.3	43.1	4.1	12.4	2.4	8.2	2.6	9.2	1.7	17.6	2.1	15.7	2.5
Conifer stems (5-10 cm dbh; no./ha)	114.6	14.3	311.4	34.1	192.1	28.8	69.6	10.2	87.2	11.6	147.9	40.6	115.6	20.2	113.6	14.1	120.6	14.7	128.4	15.2
Conifer stems (>10-49 cm dbh; no./ha)	509.6	30.8	777.6	35.6	501.8	36.9	446.1	29.7	346.1	24.3	129.6	12.9	169.1	15.3	228.6	25.7	240.6	22.1	210.2	21.7
Conifer stems (≥50 cm dbh; no./ha)	24.7	3.2	1.0	0.5	9.2	1.8	4.6	1.1	11.1	2.7	57.4	3.7	53.6	3.8	75.0	4.4	85.4	4.1	56.7	3.9
Deciduous stems (5-10 cm dbh; no./ha)	3.6	1.4	53.8	14.2	247.2	46.2	174.5	36.8	198.8	26.8	86.6	16.4	50.9	13.7	41.9	9.7	12.1	4.8	81.2	15.2
Deciduous stems (>10-49 cm dbh; no./ha)	6.1	1.8	26.1	8.8	66.1	12.8	132.1	21.8	119.4	18.6	12.7	4.1	18.8	4.8	9.4	3.5	2.4	1.1	31.5	5.4
Deciduous stems (≥50 cm dbh; no./ha)	0	0	0.7	0.5	0	0	1.0	0.5	1.7	0.7	1.0	0.5	0	0	0.2	0.2	0	0	1.0	0.6
Tree diameter CV (%)	25.3	0.9	26.5	0.9	31.9	0.9	25.1	1.4	30.7	1.1	42.4	1.2	36.9	1.5	36.7	1.4	34.3	1.2	40.1	1.0
Soil organic depth (cm) ^b	7.8	1.5	1.5	1.5	3.3	3.3	5.3	5.3	6.7	6.7	7.5	7.5	4.9	4.9	9.9	9.9	8.8	8.8	8.6	8.6

^aSoft and hard snags were pooled for presentation but were treated separately in analyses.

^bValues reported are the mean of the median value of each plot.