

AN ABSTRACT OF THE THESIS OF

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The forested landscape in western Oregon has become increasingly dominated by young, second-growth forests (i.e., those regenerated after clear-cutting of previously uncut forests) as a result of intensive and extensive timber harvesting. There have been few investigations on how wildlife populations respond to these forests. This study compared population characteristics and habitat relationships of 2 sciurids between second- and old-growth Douglas-fir forests.

An important parameter in the characteristics of wildlife populations is abundance, but estimation of abundance is a problem for animals that are not easily captured. I applied various estimators (enumeration, jackknife, moment methods) to data from northern flying squirrel (Glaucomys sabrinus) populations that had low, heterogeneous capture probabilities ($\bar{X} \approx 0.10$) and low densities (≈ 2 animals/ha). The enumeration method (i.e., the number of individuals captured) would have performed poorly because capture probabilities appeared to vary spatially and temporally. The jackknife estimator-selection procedure was sensitive to small changes with the data, and estimates did not stabilize with time. Similarly, the moment estimator performed poorly when there were < 16 trapping occasions. Computer simulations confirmed these results. Specifically, the first-order jackknife estimator produced the most reliable results compared to the other estimators. I used this estimator to determine abundance of northern flying squirrels and Townsend's chipmunks (Eutamias townsendii) in second- and old-growth forests.

Flying squirrels are one of the major prey species of the spotted owl (Strix occidentalis), a species that is listed as threatened under the Endangered Species Act. Estimated densities ranged from 1.1 - 3.3 squirrels/ha, and averaged 2.0 and 2.3 in second- and old-growth stands, respectively. Body mass and survivorship were also similar between stand-age class; however, there was a higher proportion of females in second-growth stands. The findings of similar densities of flying squirrels in these stand types are contrary to expected patterns of abundance and suggests that spotted owls select old-growth forests for reasons other than flying squirrel abundance. Flying squirrel densities were not correlated to the measured habitat variables, and models relating habitat characteristics at a particular trap station failed to predict squirrel occurrence.

Townsend's chipmunks comprise a major proportion of small-mammal biomass in the central Oregon Cascades, and therefore may be ecologically important. I examined differences of Townsend's chipmunk populations in second- and old-growth forests. Densities ranged from 0.4 to 10.3 chipmunks/ha, and averaged 2.6 and 5.2/ha in second- and old-growth stands, respectively. Chipmunk densities were positively correlated with density of large hard-snags, although this relationship was only true in old-growth stands. Chipmunks had smaller home ranges, a greater proportion of females, and a greater proportion of animals believed young-of-the-year in old- than in second-growth stands. Based on these differences, old-growth stands appeared to provide better habitat for Townsend's chipmunks than second-growth stands.

CHARACTERISTICS OF NORTHERN FLYING SQUIRREL AND TOWNSEND'S
CHIPMUNK POPULATIONS IN SECOND- AND OLD-GROWTH FORESTS

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PREFACE

The original aim of my thesis was to compare abundance of spotted owl prey between second- and old-growth forests in the central Oregon Cascades in an effort to determine if the owl's selection of old-growth may be related to differences in prey abundance. I compared abundance of northern flying squirrels, the major prey item of spotted owls in the central Oregon Cascades, in the 2 stand types. I found that flying squirrels had characteristics that made estimation of population-size with previously published models difficult. An evaluation of this problem led to chapter I, Estimation Of Animal Abundance When Capture Probabilities Are Low. Chapter II, Habitat-Selection And Abundance Of Northern Flying Squirrels In Second- and Old-Growth Douglas-Fir Forests, reflects the initial research objectives. Through the trapping efforts, we were able to quantify many characteristics of Townsend's chipmunk populations, a common prey for many diurnal predators; the results are reported in chapter III, Characteristics Of Townsend's Chipmunk Populations In Second- and Old-Growth Coniferous Forests.

POPULATION CHARACTERISTICS OF NORTHERN FLYING SQUIRRELS
AND TOWNSEND'S CHIPMUNKS IN SECOND- AND OLD-GROWTH FORESTS

CHAPTER I

ESTIMATION OF ABUNDANCE OF SMALL MAMMALS
WITH LOW CAPTURE PROBABILITIES

INTRODUCTION

Animal abundance is central to basic and applied ecology, but its estimation is a recognized problem for animals not easily observed or captured. Capture probabilities often vary among individuals (Hammond 1990), further complicating estimates (Otis et al. 1978, Seber 1986). The generalized jackknife model (Burnham and Overton 1978, 1979) was developed to provide reliable estimates of abundance when capture probabilities are heterogeneous and the population is assumed closed during the sampling period (Otis et al. 1978).

The jackknife model includes a set of estimators that are linear functions of the capture frequencies, i.e., the number of animals captured i times. Burnham and Overton (1978, 1979) developed a statistical procedure to select the estimator that reduced bias with a minimum increase in variance; however, the estimator-selection procedure may not perform well when either capture probabilities or sample sizes are low (K. Burnham, pers. commun.), which is often the case for many small-mammal studies (Hammond 1990). Several researchers (Otis et al. 1978, Burnham and Overton 1978, 1979; Pollock 1982, Chao 1988, Menkens and Anderson 1988) have evaluated the jackknife estimator with computer simulations, but none have evaluated each order of the jackknife estimator separately. Instead, results were from simulations whereby a different order could have been selected for any of the replications; therefore, the estimator used could have varied during the usually >50 replications. This would affect the bias of the estimate and its variance and the percent of times the estimate is within the 95% confidence interval (confidence-interval-coverage). Low coverage has been a recognized problem with the jackknife estimator (Otis et al. 1978:34).

The moment estimator was proposed by Chao (1988) as an alternative to the jackknife when capture probabilities are low and most individuals are captured ≤ 2 times. The moment estimator, like the jackknife, is based on the capture frequencies. Although confidence-interval-coverage with the moment estimator was generally better than that achieved with the jackknife estimator, estimates were often imprecise (Chao 1988).

Otis et al. (1978) and White et al. (1982) cautioned against using model-based estimators when capture probabilities or sample sizes are low. Unfortunately, many studies of animal abundance fail to meet their suggested levels of sample size ($N \geq 25$) and average capture probabilities (≥ 0.10). When results of field data fail to meet these criteria, many researchers use the number of individuals captured (enumeration) as an estimate of relative abundance. Estimates of relative abundance by enumeration for intra- and interspecific comparisons often are biased because capture probabilities frequently differ among species, times, and places (Nichols and Pollock 1983, Nichols 1986). Bias probably is greater when a small proportion of the population is captured, as would occur when capture probabilities and number of trapping occasions are low.

For this chapter, I evaluated the performance of the enumeration method, the moment estimator, the set of jackknife estimators and its estimator-selection procedure on data from northern flying squirrel (*Glaucomys sabrinus*) populations and Monte Carlo simulations. I propose a specific jackknife-estimator rather than that selected by the model-selection procedure.

METHODS

Field Studies

The field study was conducted in the Blue River and McKenzie Ranger Districts, Willamette National Forest, Oregon, an area characterized by mild, wet winters and warm, dry summers (Franklin and Dyrness 1973). I established live-trapping grids (13 ha) in 10 stands; each grid consisted of 100 trapping stations spaced 40-m apart and

arranged as closely as possible to a 10 X 10 array but varied from 10 X 10 to 16 X 6, depending on stand size and shape. Two baited Tomahawk #201 traps (41 X 13 X 13 cm) were placed at each station. Animals were ear-tagged with monel #1 tags.

We trapped for 8 to 21 consecutive nights in each grid during the fall of 1987 to 1989. In 1987, we trapped in 6 of the 10 grids for 8 consecutive nights during dry weather (1.5 cm cumulative precipitation; i.e., the amount of rain after the summer dry period) and trapped in 4 grids during wet weather (11.1 cm cumulative precipitation). In 1988, we trapped in 5 grids for 21 consecutive nights; the first 8 nights of trapping were considered dry weather (0.5 cm precipitation) and the remaining nights (13) during wet conditions (9.6 cm). We trapped in the second set of 5 grids for 16 consecutive nights, operated entirely within the wet period (27.8 cm). In 1989, we trapped in all 10 grids for 21 consecutive nights. Conditions were wet before the trapping session, thus there was not a comparable dry period as there was in previous years. I compared the proportion of animals captured once as a measure of relative susceptibility to being trapped between seasons (dry-wet) with Wilcoxon rank-sums test and relative consistency between years with Spearman rank-correlation analysis. I used the first 8 nights of trapping for seasonal comparisons and the first 8 (1987 - 1988) or 16 nights (1988 - 1989) for comparisons between years.

The capture frequencies (f_i) are used in the estimation of population-size (N^{\wedge}) with the jackknife and moment estimators. Each of the jackknife estimators are linear functions of the f_i such that $N^{\wedge} = \underline{S} + \sum a_{ik} f_i$, where \underline{S} , a_{ik} , and f_i represent the number of individuals captured, coefficients computed for each k^{th} order ($a_{ik} = 0$ for $i > k$), and number of animals captured i times, respectively (Burnham and Overton 1978, 1979). Estimates from the moment estimator are computed as $N^{\wedge} = \underline{S} + f_1^2/2f_2$ (Chao 1988). A variance estimator (SE^{\wedge}) was developed for each estimator (Burnham and Overton 1978, 1979; Chao 1988).

I compared N^{\wedge} and standard error ($SE^{\wedge}_{N^{\wedge}}$) among the first 5 jackknife estimators, the selected jackknife estimator, and the moment

estimator. I modified the estimators (field and simulated data) by making all estimates less than the number of individuals captured (\underline{S}) equal to \underline{S} . I did not estimate squirrel abundance in 1987 because of the low number of captures and recaptures that were obtained from 8 occasions. I compared \underline{N}^{\wedge} and $SE_{\underline{N}^{\wedge}}$ for 1988 and 1989 data from the values computed for the last night of trapping ($\underline{t} = 16$ or 21).

I calculated the coefficient of variation for \underline{N}^{\wedge} during 8 to 21 nights ($CV = SE_{\underline{N}^{\wedge}}/\underline{N}^{\wedge}$) to evaluate the stability of \underline{N}^{\wedge} . I computed the CV only for the 1989 data because this was the only year we trapped in all grids for 21 nights. I compared CV, \underline{N}^{\wedge} , and $SE_{\underline{N}^{\wedge}}$ among estimators by use of analysis of variance (ANOVA) with a randomized-block design (Sokal and Rohlf 1981:348). The estimators were used as the treatment effect, and the grids were treated as the block (replicates) to account for differences in characteristics of each squirrel population (grid). F -statistics were reported for the estimator effect only. Animals that died in the traps at first capture (1988: $\underline{n} = 11$, 3.7%; 1989: $\underline{n} = 15$, 5.0%) were excluded from analyses.

Computer Simulations

I established guidelines for the simulation procedure from the results of the field data. I set population size (\underline{N}) at 40, and established capture probabilities (\underline{p}_i) for 5 groups of "animals" as follows: $\underline{p}_1 = 0.05$ (18 animals, 45% of the population), $\underline{p}_2 = 0.10$ (11 animals, 27.5%), $\underline{p}_3 = 0.15$ (5 animals, 12.5%), $\underline{p}_4 = 0.20$ (3 animals, 7.5%), $\underline{p}_5 = 0.50$ (3 animals, 7.5%). Percentages of animals within each of these groups were chosen to resemble closely the capture frequencies and percent recapture rates for the 10 grids sampled during 1988 and 1989 (Table 1.1). For each estimator, I computed the mean estimate (\underline{N}^{\wedge}), mean percent relative bias (MPRB = $\{[\underline{N}^{\wedge} - \underline{N}]/\underline{N}\}100$), and root mean square error (RMSE = $\{1/\underline{n}\sum(\underline{N}^{\wedge}_i - \underline{N})^2\}^{1/2}$). RMSE is equivalent to standard error except that the true population size is subtracted from each estimate. I compared accuracy of relative abundance measures by comparing two simulated populations, \underline{N}_1 and \underline{N}_2 . I used the population size and the distribution of capture probabilities specified earlier

Table 1.1 Capture frequencies^a of northern flying squirrels on 10 trapping grids, Willamette National Forest, Oregon, 1987 - 1989.

Year	\underline{t}^b	grids (\underline{n})	Mean (SE) percent of animals captured \underline{f}_i times				
			$\underline{i} = 1$	$\underline{i} = 2$	$\underline{i} = 3$	$\underline{i} = 4$	$\underline{i} \geq 5$
1987	8	10	76.4(4.7)	18.0(3.0)	3.9(2.1)	0.4(0.04)	2.4(1.0)
			[52.0-100.0] ^c	[0-32.3]	[0-16.0]	[0-4.0]	[0-8.0]
1988	16	5	56.1(3.3)	21.9(2.8)	8.6(2.1)	8.6(0.6)	4.6(0.4)
			[44.8-60.0]	[14.3-27.3]	[2.8-13.1]	[7.1-10.5]	[3.6-5.7]
	21	5	39.8(6.0)	30.6(6.3)	14.0(2.2)	8.1(3.0)	7.6(2.6)
			[22.6-60.0]	[16.7-52.6]	[5.3-27.0]	[0-16.7]	[0-16.1]
1989	21	10	50.9(4.4)	21.9(2.6)	8.4(2.3)	5.5(1.4)	13.2(2.7)
			[32.4-75.0]	[9.0-34.3]	[0-22.7]	[0-13.5]	[0-24.3]

^a proportion of animals captured \underline{i} times
^b number of consecutive trapping nights (occasions)
^c range

for N_1 ; for N_2 , $N = 40$, but I doubled the capture probabilities of N_1 . I computed mean difference between populations ($MD = \Sigma[N_{1i}^{\wedge} - N_{2i}^{\wedge}] / R$, where R is the number of replications), mean percent absolute relative bias among estimators ($MPARB = |(MD/N)|100|$) and RMSE. The number of individuals captured (S) was included as one of the estimators.

For comparison of absolute (single population) and relative (2 populations, N_1 and N_2) abundance, 2,000 replications of the simulated data sets were made for occasions (t) = 6, 12, and 21. $RMSE \geq 20\%$ of population size ($RMSE \geq 8$) was considered unacceptably large (sensu Pollock et al. 1990:70 for coefficient of variation, analogous to RMSE).

RESULTS

Field Data

Flying squirrel populations had relatively low densities and low, heterogeneous capture probabilities. We captured 201, 294, and 301 flying squirrels during 1987, 1988, and 1989, respectively. The number of individuals captured per hectare averaged 1.5 in 1987 and 2.2 in 1988 and 1989. Number of captures per individual averaged 1.4, 2.1, and 2.7 in 1987 - 1989, respectively. Capture frequencies varied by grid (Table 1.1). Most ($\geq 39\%$) animals were captured once (Table 1.1), although several animals were captured ≥ 11 times (1988: 2, 0.6%; 1989: 7, 2.3%).

The proportion of animals captured >1 time for the 10 grids ranged from 0 to 0.77 (Table 1.1), and was greater during the wet (0.39) than dry (0.13) period in 1987 (Wilcoxon rank-sums test, $z = -2.5$, $p = 0.01$) and tended to be greater for the wet (0.25) than dry (0.13) period during the first 8 nights of trapping in 1988, but not significantly ($z = -1.5$, $p = 0.14$). For each grid, there was a weak relationship between years for proportion of animals captured >1 time (1987 and 1988: $r_s = 0.51$, $p = 0.13$, $n = 10$, 8 occasions; 1988 and 1989: $r_s = 0.58$, $p = 0.08$, $n = 10$, 16 occasions).

Estimates of population-size and SE^{\wedge} varied among estimators for the flying squirrel populations. N^{\wedge} on the last occasion ($t = 16$ or

21) varied among estimators in 1988 ($F = 4.8$, $p < 0.01$) and 1989 ($F = 2.7$, $p = 0.02$). \bar{N}^{\wedge} increased for first- through fifth-order jackknife estimators (Table 1.2). The SE^{\wedge} differed among estimators in both years ($F \geq 2.6$, $p < 0.05$, Table 1.2). SE^{\wedge} of the moment estimator was similar to SE^{\wedge} of the third-order jackknife estimator. The lowest SE^{\wedge} was produced by the first-order jackknife estimator and the highest SE^{\wedge} by the fifth-order jackknife estimator. SE^{\wedge} of the selected jackknife estimator was similar to that of the first- and second-order jackknife estimator; these estimators usually were chosen by the order-selection procedure by $\underline{t} \geq 16$. The order of the jackknife estimator chosen by the selection procedure varied with the number of trapping nights (\underline{t}) and tended to be < 3 when \underline{t} was ≥ 16 . When $\underline{t} = 21$, the first or second order was selected in 13 of 15 data sets.

The coefficient of variation of \bar{N}^{\wedge} over time (8 to 21 occasions) ranged from 0.4 to 17.4% within individual grids and \bar{CV} of the 10 grids ranged from 3.4 to 10.6% among the estimators (Table 1.2). The moment estimates and fifth-order jackknife estimates had significantly higher CV's than did the other estimators. The first-order estimates had the lowest CV, but not significantly lower than second-order jackknife estimates (Table 1.2).

Simulated Data

Bias generally decreased with increasing \underline{t} for the first-order jackknife and moment estimates of absolute abundance (Table 1.3). RMSE $> 20\%$ were produced by all estimators at $\underline{t} = 6$ and all jackknife estimates were biased negatively. This condition changed as \underline{t} increased, and at $\underline{t} = 21$, all \bar{N}^{\wedge} were positively biased. At $\underline{t} = 12$, the moment estimator provided the least biased \bar{N}^{\wedge} , but RMSE was high; only the first-order jackknife estimator produced reliable results. At $\underline{t} = 21$, moment estimates were essentially unbiased but RMSE was $> 20\%$; first-order jackknife estimates had low bias and the lowest RMSE. Higher-order jackknife estimates had greater bias and RMSE than lower-order estimates. The selected jackknife estimates had bias and RMSE similar to second-order jackknife estimates (Table 1.3).

Table 1.2 Population estimates, estimated standard error, and coefficient of variation^a among estimators for flying squirrel populations ($n = 10$), Willamette National Forest, Oregon, 1988 - 1989.

Statistic	Year	Order of Jackknife Estimator ^b						
		first	second	third	fourth	fifth	selected	moment ^c
\bar{N}^{\wedge}	1988 ^c	40.7 C ^d	46.0 ABC	48.8 AB	51.0 A	51.8 A	42.9 C	44.6 BC
	1989	41.8 B	49.1 AB	52.7 A	54.2 A	56.3 A	49.7 AB	48.1 AB
$\overline{SE}_{N^{\wedge}}$	1988	4.8 E	8.1 D	12.4 C	18.5 B	26.8 A	5.6 DE	11.7 C
	1989	5.0 D	8.4 D	12.7 C	18.6 B	26.6 A	7.9 D	14.5 C
$\overline{CV}(SE)$	1989	3.4(0.8)E	4.0(0.9)DE	5.4(1.0)D	7.2(1.1)C	9.2(1.2)AB	8.0(1.3)BC	10.6(1.2)A
Range		0.4-8.9	1.8-9.9	2.4-10.8	3.3-14.1	4.4-17.4	4.2-17.4	4.4-18.5

^a CV was computed from successive population estimates from 8 to 21 trapping nights ($CV = \overline{SE}_{N^{\wedge}} / \bar{N}^{\wedge}$)

^b Burnham and Overton (1978)

^c Chao (1988)

^d Means with the same letter are not statistically different ($P > 0.05$), Duncan's multiple range test.

Table 1.3 Performance of the 5 orders and selected order of the jackknife estimator^a and the moment estimator^b for estimates of absolute abundance. Results are from 2,000 replications of simulated data.

t^c	Statistic	Jackknife order					selected	moment
		first	second	third	fourth	fifth		
6	MPRB ^d	-30.5	-16.5	-7.9	-3.2	-0.5	-9.1	5.5
	RMSE ^e	9.3	7.3	9.6	12.4	14.7	12.7	21.1
12	MPRB	-5.8	7.6	13.7	17.1	20.1	8.1	4.0
	RMSE	5.4	8.2	12.2	16.0	19.9	13.6	14.5
21	MPRB	5.8	11.8	13.0	16.2	24.0	10.1	2.0
	RMSE	4.8	8.4	11.6	15.7	22.1	10.1	7.9

^a Burnham and Overton (1978)

^b Chao (1988)

^c Number of trap occasions

^d Mean percent relative bias = $([(\bar{N} - N)/N]*100)$

^e Root mean square error

I found similar patterns when two populations of equal size but different capture probabilities were compared (Table 1.4). At $\underline{t} = 6$, only moment estimates and the selected jackknife estimates had low bias, but had high RMSE. All of the other estimators, including the number of individuals captured, produced estimates with high bias. Bias was reduced for all jackknife estimates at $\underline{t} = 12$, but the RMSE remained high. By $\underline{t} = 21$, bias was <3% for moment, first-order jackknife, and selected jackknife estimates. RMSE was lowest for first-order jackknife estimates, reasonably high for moment estimates, and unacceptably high for selected jackknife estimates (Table 1.4).

The proportion of replications that each order was selected by the order-selection procedure changed with the number of occasions. At $\underline{t} = 6$, the first-order jackknife was selected in 29% of the 2,000 replications, and at $\underline{t} = 21$ it was selected 91% of the time. Conversely, the other orders were selected more often when $\underline{t} = 6$ (Table 1.5).

DISCUSSION

Densities of northern flying squirrel populations in the central Oregon Cascades were low and capture probabilities ($\bar{X} \approx 0.10$) differed both spatially and temporally. Similarly, Carey et al. (in press) reported capture probabilities that varied among grids for flying squirrels in the Coast Ranges of Oregon. The number of animals captured would have been a poor measure of relative abundance when considering these temporal and spatial differences in capture probabilities. The results of our simulations comparing two populations support this contention; the number of individuals "captured" (enumeration) produced relative abundance estimates with high bias and low precision.

Estimates of flying squirrel abundance were not stable during the trapping period for some estimators. Therefore, assuming the true population size did not change with each trap occasion, these estimators appeared unreliable. Population estimates were highly variable among number of trap occasions (8 to 21) for higher-order

Table 1.4 Performance of the number of individuals captured (\underline{S}), the 5 orders and selected order of the jackknife estimator^a, and the moment estimator^b for estimates of relative abundance. Results are from 2000 replications of simulated data.

\underline{t}^c	Statistic	\underline{S}	Jackknife order						
			first	second	third	fourth	fifth	selected	moment
6	MPARB ^d	21.6	24.3	22.3	19.2	16.6	15.1	2.3	0.9
	RMSE ^e	9.0	10.9	11.6	12.5	13.6	14.3	13.9	25.2
12	MPARB	19.6	12.8	3.4	3.3	6.5	6.8	2.3	1.1
	RMSE	8.2	7.1	8.8	13.5	18.9	24.5	14.8	15.1
21	MPARB	13.6	1.4	6.6	9.1	9.0	7.9	2.5	0.4
	RMSE	5.8	4.4	8.4	12.8	18.1	26.2	10.2	8.3

^a Burnham and Overton (1978)

^b Chao (1988)

^c Number of trap occasions

^d Mean percent absolute relative bias = $|[\sum [N^1_{1i} - N^2_{2i}] / R] / N * 100|$, where
 R = number of replications

^e Root mean square error

Table 1.5 Percentage of each order selected by the jackknife model selection-procedure^a for different trap occasions. Results are from 2,000 replications of simulated^b data.

\underline{t}^c	Jackknife order				
	first	second	third	fourth	fifth
6	29.3	29.7	12.0	4.4	24.7
12	63.1	25.1	4.8	3.3	3.8
21	90.8	5.9	1.9	0.7	0.9

^a Burnham and Overton (1978)

^b $\underline{N} = 40$, Capture probabilities are 0.05 ($\underline{n} = 18$), 0.10 ($\underline{n} = 11$), 0.15 ($\underline{n} = 5$), 0.20 ($\underline{n} = 3$), 0.50 ($\underline{n} = 3$)

^c Number of trap occasions

jackknife estimators and the moment estimator. The first-order jackknife estimator provided the least variable estimate of flying squirrel abundance. Population-size estimates became more similar among estimators as the number of trapping occasions increased, especially for the lower-order jackknife estimators and the moment estimator. At $\underline{t} = 21$, the estimator-selection procedure usually chose the first-order estimator for field data; I found a similar pattern with the simulated data. This was not surprising, because lower bias is expected when a larger proportion of the population is captured, as occurred with a greater number of trapping occasions. The estimator-selection procedure should select lower orders when bias is low (Burnham and Overton 1978, 1979). The first-order jackknife estimates tended to be the most precise and least biased of the jackknife estimators. The first-order jackknife, selected jackknife, and moment estimates had low bias by $\underline{t} = 21$, but RMSE for the selected jackknife estimates was unacceptably high (i.e., $RMSE \geq 20\%$), and RMSE for moment estimates was greater than that for the first-order estimator. Higher-order jackknife estimators (≥ 3) and the selected order provided estimates with unacceptably large RMSE, and these estimators should be considered unreliable for both absolute and relative abundance estimates under the conditions we investigated. When capture probabilities are < 0.05 , the second-order estimator may be more appropriate than the first-order (W. S. Overton and D. Rosenberg, unpubl. data) because of the lower proportion of animals captured and the resultant higher inherent bias.

The jackknife model is a frequently used estimator of population size for small-mammal studies and is 1 of 5 estimators available in program CAPTURE (Otis et al. 1978, White et al. 1982). The jackknife estimate most often used and that suggested by Otis et al. (1978) and White et al. (1982) is that from the estimator chosen by the selection procedure. Greenwood et al. (1985:388) used the first-order jackknife estimator to estimate population size of striped skunks (Mephitis mephitis) with known population-size and found it provided the best estimate as compared to the 10 other estimators evaluated. They

compared only the first-order of the jackknife estimators, and chose it because "of its simplicity and low variance." Our findings support the use of the first-order jackknife estimator because of its accuracy and precision under the conditions I considered (i.e., small population size with low and heterogeneous capture probabilities).

Chao (1988) found that when few animals were captured >2 times, moment estimates were less biased than the selected jackknife estimates; however, imprecise estimates for the real and simulated data sets she used were obtained by use of these estimators. I found the moment estimator produced more reliable results than the selected jackknife estimator, but less reliable than the first-order jackknife estimator when \underline{t} was >12 .

Performance of the 5 estimators of the jackknife model were not compared by previous evaluations of the jackknife estimator (Burnham and Overton 1978, 1979; Otis et al. 1978, Pollock 1982, Chao 1988, Menkens and Anderson 1988). Different ordered-estimators would likely have been chosen by the selection procedure within a simulation study, as I found to be true. This produces estimates with varying degrees of bias. The large RMSE I found for the selected jackknife estimates may be the reason for the findings (Otis et al. 1978, Chao 1988) of low confidence-interval-coverage (≤ 5 to 87%). I recommend that the selection procedure for choosing a specific jackknife estimator not be used for small sample sizes and low capture probabilities; the first-order jackknife estimator should be used instead.

Our field and simulation results indicate that <12 days are inadequate to provide reliable estimates of absolute or relative abundance when capture probabilities are low and differ among individuals and populations. Although the first-order jackknife estimator provided reliable estimates at $\underline{t} \geq 12$, estimates were inaccurate and imprecise at low \underline{t} . Otis et al. (1978) recommended 5 to 10 trap occasions; however, they considered this inadequate when capture probabilities are <0.10 or population size is <25 . The models I evaluated were developed with the assumption of a closed population. Increasing the number of trap occasions may increase the degree to

which closure is violated. An increase in the number of traps per home range may increase capture probabilities; this would allow the number of trap occasions to be reduced. Larger grid sizes may reduce the influence of immigration and emigration, thereby lessening the degree to which closure is violated.

My analysis of simulated data included only a single distribution of capture probabilities. Performance of the set of jackknife estimators and the moment estimator needs to be compared to other distributions of capture probabilities to evaluate the robustness of each estimator. Furthermore, these estimators should be evaluated with other sources of variation in capture probabilities (e.g., behavior) that probably exist in real animal populations.

CHAPTER II
HABITAT SELECTION AND ABUNDANCE OF NORTHERN FLYING SQUIRRELS
IN SECOND- AND OLD-GROWTH DOUGLAS-FIR FORESTS, OREGON

INTRODUCTION

The northern flying squirrel (*Glaucomys sabrinus*) is considered a common resident of coniferous forests in the Pacific Northwest (Maser 1981:166) and is a prey item for many vertebrates (reviewed in Wells-Gosling and Heaney 1984). Flying squirrels were the principal prey item of the spotted owl (*Strix occidentalis*), comprising more than 50% of the biomass of prey in the north central Cascades (Forsman et al. 1984:41). It is one of the few small mammals that remains active and accessible to predators in winter; it constituted a greater proportion (up to 72%) of the spotted owl's diet during this season (Forsman et al. 1984).

The spotted owl is listed as threatened under the Endangered Species Act. The decline of the spotted owl has been attributed to declines in the availability of old-growth Douglas-fir (*Psuedotsuga menziesii*) forests (Forsman et al. 1977, 1982, 1984) and an avoidance of second-growth forests <60 years old has been documented (Forsman et al. 1984, Carey et al. 1990; G. Miller, pers. commun.). The spotted owl's selection of old-growth forests may be related to higher prey abundance (Forsman et al. 1982, 1984:53, Gutierrez and Carey 1985, Carey et al. 1990). Several workers have suggested that flying squirrels were more abundant in old-growth forests than in other age classes (Harris and Maser 1984:50, Brown 1985:164, Franklin 1988); however, there are no published quantitative studies of which I am aware.

This study was initiated to understand the ecology of northern flying squirrels to manage more effectively for the spotted owl (Gutierrez and Carey 1985). Our objectives were to a) compare abundance of flying squirrels in second- (i.e., those regenerated after clear-cutting of previously uncut forests) and old-growth Douglas-fir forests, and b) to determine forest characteristics with which flying squirrels are associated.

STUDY AREA AND METHODS

Study Sites

I selected 5 second- (30 to 60 years old) and 5 old-growth (>400 years) Douglas-fir stands on the Blue River and McKenzie Ranger Districts, Willamette National Forest in the central Oregon Cascades. Stands were between 375 and 900-m elevation and percent slope ranged from 10 to 60% (Appendix A). Climate in the study area was characterized by mild, wet winters and warm, dry summers (Franklin and Dyrness 1973).

Forests were dominated by Douglas-fir and western hemlock (*Tsuga heterophylla*). Western red cedar (*Thuja plicata*) and incense cedar (*Calocedrus decurrens*) were common canopy species in old- and second-growth stands, respectively. The understory (2 to 4 m in height) was dominated by vine maple (*Acer circinatum*), dogwood (*Cornus nuttallii*), hazelnut (*Corylus cornuta*), and western hemlock, and the lower-understory (<2 m in height) by Oregon grape (*Berberis nervosa*), salal (*Gaultheria shallon*), sword fern (*Polystichum munitum*), *Vaccinium* spp., and rhododendron (*Rhododendron macrophyllum*).

Four of the 5 second-growth stands were regenerated after clear-cutting; the fifth stand was partially fire regenerated (Appendix A). Treatments varied from intensive clear-cuttings to those with seed tree retention. The 5 old-growth stands were not logged previously, except for small areas where a few individual trees were removed. There was a broad range of values for most of the habitat variables measured within and between stand age-class (Table 2.1). Second-growth stands were characterized by greater densities of trees and smaller-diameter snags than old-growth stands. Densities of large trees and large snags were greater in old- than second-growth stands (Table 2.1), and in some second-growth stands these components were rare or absent (Appendix B).

Population-Size

I established live-trapping grids in each of the 10 stands. Each grid consisted of 100 trap stations spaced 40 m apart. Grids were arranged as close as possible to a 10 X 10 array (~13 ha), but varied

Table 2.1 Habitat characteristics (\bar{X} [SE]) on trapping stations in second- and old-growth Douglas-fir stands, Willamette National Forest, Oregon, 1988.

Characteristic	Second-growth (\bar{n} = 165)	Old-growth (\bar{n} = 164)	p^a
Deciduous shrub (<5 cm DBH) cover (%)	7.3 (0.8)	5.6 (0.6)	NS
Coniferous (<5 cm DBH) cover (%)	2.6 (0.3)	6.2 (0.3)	*
Rhododendron cover (%)	0.7 (0.2)	2.7 (0.5)	*
Small-size coniferous trees (#/ha)	155.0 (12.0)	125.4 (10.3)	NS
Medium-size coniferous trees (#/ha)	516.0 (9.4)	196.0 (9.4)	*
Large-size coniferous trees (#/ha)	10.4 (1.1)	65.6 (2.0)	*
Small-size deciduous trees (#/ha)	135.6 (14.9)	54.6 (6.0)	*
Medium-size deciduous trees (#/ha)	69.9 (7.5)	15.0 (1.9)	*
Large-size down-wood (m ³ /ha)	52.8 (3.2)	65.8 (4.2)	*
Small-size snags (#/ha)	61.2 (6.0)	23.8 (3.0)	*
Large-size snags (#/ha)	8.0 (1.0)	17.4 (1.3)	*

^a Students' t -test, NS = not significantly different ($p > 0.05$), * $p < 0.05$

from 10 X 10 to 16 X 6, depending on size and shape of stands. Two Tomahawk #201 traps (41 X 13 X 13 cm) were placed at each station. One trap was placed approximately 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 trap. Traps were baited with a mixture of peanut butter, whole oats, molasses, and a high protein (>30%) pellet. Animals were ear-tagged with monel #1 tags; body mass and sex were recorded.

In 1987, traps were operated on the grids from 1 October to 5 December. Traps were operated on two grids (1 old- and 1 second-growth) simultaneously for 8 consecutive nights for 5 sessions, with a different pair of grids in each session. Because of the low number of recaptures, I increased the number of nights in 1988 and 1989. In 1988, traps were operated on 5 grids simultaneously for 21 consecutive nights (19 October to 8 November) and trapped on the remaining 5 grids simultaneously for 16 nights (15 to 30 November). In 1989, trapping was done on all 10 grids for 21 consecutive nights (10 to 30 October and 7 to 27 November). I did not estimate squirrel abundance in 1987 because of the small number of recaptures. Instead, the number of individuals captured was used to evaluate relative abundance, although I preferred to compare abundance with model-based estimators because capture probabilities differed among stands and seasons (Chapter 1). For the 1988 and 1989 data, the first-order jackknife estimator (Burnham and Overton 1979) was used to provide estimates of flying squirrel abundance. I computed a boundary width around the grids by using one-half of the mean maximum distance moved (MMDM, Wilson and Anderson 1985) averaged from all grids for animals captured ≥ 2 times and added this distance to the perimeter to include the effective area trapped. Second- and old-growth grids were treated similarly because there was no significant ($P > 0.05$) difference in MMDM between the two stand types.

Habitat Characteristics

I used nested circular-plots modified from Spies et al. (1988) to sample vegetation at every third trapping station. Large (≥ 50 -cm-diameter) trees, snags (standing dead trees), down-wood (coarse woody debris), and stumps (< 1.5 m tall) were recorded in 0.12-ha (20-m-radius) plots centered at the trap station. Smaller trees (≥ 5 to 49 cm diameter at breast height, dbh), snags (≥ 10 to 49 cm dbh), and down-wood (≥ 25 to 49-cm-diameter) were measured in 0.05-ha (12.6-m-radius) plots. The species and dbh were recorded for live trees and recorded the diameter and condition (% limbs remaining) for snags (≥ 1.5 m tall) and down-wood. Vegetation was measured once in each plot during July through September 1988.

I established size-classes for trees, snags, and down-wood. Live trees were grouped into 5-10, >10 - 49, and ≥ 50 -cm-dbh classes, snags into 10-49, and ≥ 50 -cm-dbh classes and condition categories (soft: $\leq 2\%$ limbs remaining, hard: $>2\%$ limbs), and down-wood volume (m^3) was computed for 25 - 49, and ≥ 50 cm diameter classes. I computed the CV of tree diameters as a measure of tree-size diversity.

Percent cover of understory plants was estimated for three common species and three life forms (Oregon grape, salal, rhododendron, fern, conifer, deciduous, and total) and percent ground cover (herb, woody debris < 25 -cm-diameter, moss) was estimated visually in 8 1-m^2 quadrats. These were placed 4 and 7 m from the trap station along each cardinal direction. I used the average of the 8 quadrats in the analyses. Organic soil depth (depth from the surface to mineral soil) was measured to the nearest 1 cm to 10 cm, then recorded as >10 cm in each of the quadrats. The median value of the 8 samples were used in the analyses.

Statistical Analyses

I used Wilcoxon rank-sums test to compare number of individual squirrels captured (1987) and estimated densities (1988 and 1989) between second- and old-growth stands. Sex ratios (pooled by stand age-class) were compared with chi-square goodness-of-fit tests under

the model of equal proportions of males and females captured. Relative sex ratios in each stand were compared among years with Spearman rank-correlation. Body mass was compared among sex, stand age-class, and years with analysis of variance.

I included only the 1987 and 1988 locations of flying squirrel captures to develop the models relating squirrel presence at a trap station and habitat characteristics. The 1989 data were used to test the models developed from the 1987 and 1988 data. Stepwise discriminant function analysis (DFA) was used to identify which habitat variables were most influential in determining whether a trap station was a site of squirrel captures (CAP) or not (NOCAP). I used prior probabilities of group membership equal to the proportion of observations in each group. Inclusion of variables in the stepwise procedure was allowed at $p \leq 0.15$, but only variables with $p \leq 0.05$ were retained. I used the jackknife procedure to calculate the classification error rate (Morrison 1976) with the variables selected by the stepwise procedure for each age-class and for both classes pooled. The jackknife procedure uses the discriminant equation derived from all observations except for the observation being classified. This procedure is more reliable than classification rates determined from the discriminant equation based on all observations (Morrison 1976, Capen et al. 1986). Cohen's kappa statistic was used to determine the improvement of classification rates over chance (Titus et al. 1984). Separation of group means was tested with Wilks' lambda. I report results of the DFA to give a general overview of the data rather than a conclusive statement because nonlinear response and violation of the assumption of multivariate normality are difficult to test and often occur in ecological data (Williams 1983).

I compared the mean of each variable selected by the stepwise DFA procedure between stations where flying squirrels were captured and not captured within and between stand age-class with analysis of variance and Duncan's multiple-range test. I also compared characteristics of stations at which 0, 1, 2, or ≥ 3 individuals were captured with Kruskal-Wallis analysis of variance. I did this analysis because the

number of different animals captured on a station may be more indicative of its habitat suitability for flying squirrels than presence-absence comparisons. I used a nonparametric test because of the unequal and relatively small sample sizes in some groups. Pearson correlation coefficients were used to evaluate the correlations between variables. I eliminated the variable in a correlated ($r > 0.70$) pair based on my ability to interpret the variables' biological importance. Total cover was positively correlated ($r > 0.70$) with deciduous cover; total cover was the only variable eliminated. Variables not distributed normally were \log_{10} (salal, deciduous, Oregon grape, all stem and snag classes) or square-root transformed (rhododendron, down-wood) for all statistical tests. However, we report only untransformed values to facilitate numeric comparisons. Relationships of flying squirrel density (1988 and 1989) to habitat variables were evaluated with Spearman rank-correlations. I used the mean values from all plots within each of the 10 stands (Appendix B).

RESULTS

Population-Size and Densities

In 1987, 201 flying squirrels were captured 282 times with an average of 20.1 squirrels/grid (Table 2.2). Eighty-one recaptures were recorded (1.4 captures/animal), but numbers of recaptures were too low to estimate population size for 7 of the 10 grids (Chapter 1). The grids with the most and fewest squirrels captured were in old-growth stands. Numbers of individuals captured were almost identical between stand age-class: 99 squirrels were caught in second- and 102 in old-growth stands.

In 1988, 294 flying squirrels were captured 618 times, with an average of 29 squirrels/grid. MMDM ranged from 60 m to 88 m with an average of 78 m; there was no significant difference of MMDM between second- ($\bar{X} = 81$ m) and old-growth ($\bar{X} = 74$ m) stands (Wilcoxon rank-sums test, $p > 0.05$). Estimated population sizes ranged from 27 to 56 ($\bar{X} = 42$) and estimated densities (area included a 39-m-wide boundary around each grid) ranged from 1.4 to 2.9 animals/ha ($\bar{X} = 2.1$; Table 2.2).

Table 2.2 Number of flying squirrels captured and estimated densities (number/ha) in second- and old-growth Douglas-fir stands, Willamette National Forest, Oregon, 1987-1989.

Stand Age-class	1987		1988				1989			
	No. Occasions	Individuals Captured	No. Occasion	Individuals Captured	Population Size ^a	Density ^b (#/ha)	No. Occasions	Individuals Captured	Population Size	Density ^c (#/ha)
Second-growth	8	11	21	24	33	1.7	21	28	39	1.9
	8	10	21	33	40	2.0	21	37	48	2.2
	8	32	16	25	39	1.9	21	37	53	2.5
	8	21	16	24	35	1.8	21	13	22	1.1
	8	25	16	29	46	<u>2.4</u>	21	24	33	<u>1.6</u>
						$\bar{X} = 2.0$				$\bar{X} = 1.9$
Old-growth	8	42	21	25	37	1.9	21	45	68	3.3
	8	4	21	39	51	2.6	21	32	43	2.1
	8	12	21	20	27	1.4	21	19	30	1.5
	8	17	16	40	56	2.9	21	33	44	2.1
	8	27	16	35	54	<u>2.8</u>	21	33	53	<u>2.6</u>
						$\bar{X} = 2.3$				$\bar{X} = 2.3$

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

^b Density estimates were computed from the population estimate with a 39-m-boundary width ($\frac{1}{2}$ mean-maximum-distance moved) included around the trapping grid (Wilson and Anderson 1985).

^c Same as ^b but with 46-m-boundary width.

Densities were not significantly different between second ($\bar{X} = 2.0$) and old-growth ($\bar{X} = 2.3$) stands (Wilcoxon rank-sums test, $p = 0.3$). The highest and lowest densities occurred in old-growth stands. The old-growth stand with the lowest density was different from the one that had the fewest individuals captured in 1987. Both of these were the only grids that were near (<500 m) active spotted owl nests (G. Miller, pers. commun.).

In 1989, 301 squirrels were captured 819 times, with an average of 30 animals/grid. MMDM ranged from 62 to 134 m ($\bar{X} = 92$ m for second- and old-growth grids). Estimated population-sizes ranged from 22 to 68 squirrels ($\bar{X} = 43$) and densities (area included a 46-m-wide boundary) varied from 1.1 to 3.3 animals/ha. Densities were not significantly different between second- ($\bar{X} = 1.9$ squirrels/ha) and old-growth ($\bar{X} = 2.3$ /ha) stands (Wilcoxon rank-sums test, $p = 0.4$).

Relative densities among stands in 1988 were not related to those in 1989 ($r_s = 0.42$, $p = 0.2$). I did not compare 1987 with 1988 and 1989 because we were unable to estimate densities in 1987 and the number of individuals captured is not a reliable measure of relative abundance (Chapter I).

Sex Ratio

Seventy-seven animals were recaptured in 1988 that were first captured in 1987. I considered this group as known adults. Body mass for this group was measured from the animal's second year of capture. The lowest mass recorded was 104 g, so animals less than this were considered young of the year. All animals captured in 1989 that were initially caught in 1988 were >104 g.

Second-growth stands had a higher proportion (62 to 66%) of females ≥ 104 g than expected by chance under the model of equal sex ratios; however, sex ratios in old-growth stands were not significantly different from 1:1 (Table 2.3). Sex ratios of animals ≥ 104 g in individual grids (males:females) ranged from 0.3 to 2.1 in 1987, 0.3 to 1.6 in 1988, and 0.3 to 1.5 in 1989, and were generally similar among years (1987-1988 and 1987-1989: $r_s = 0.63$, $p = 0.06$;

Table 2.3 Sex ratios of flying squirrel populations in second- and old-growth Douglas-fir stands, Willamette National Forest, Oregon, 1987 - 1989.

Animal Age-class	Year	Second-growth		Old-growth	
		<u>n</u>	males:females	<u>n</u>	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 ^c
Adult ^b	1987	83	0.6	78	1.0
	1988	112	0.5	136	1.0
	1989	108	0.5	124	0.9

^a animals <104 g

^b animals \geq 104 g

^c Sex ratio differed from a 1:1 ratio ($P < 0.05$)

1988-1989: $r_s = 0.71$, $p = 0.03$). There was no deviation from a 1:1 sex ratio for squirrels <104 g 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 2.3).

Body Mass

I compared body mass between sexes and stand age-classes for animals <104 g and animals ≥ 104 g. I did not detect significant differences in body mass among sex and stand age-classes in any of the 3 years ($F \leq 1.5$, $p > 0.20$ for each year) for squirrels <104 g. Significant differences in body mass were found for animals ≥ 104 g. In general, females were heavier than males, although this relationship was not consistent in each of the stand age-class comparisons among the 3 years (Table 2.4). Body mass of males in old-growth stands was greater in 1988 than in 1987 and 1989 and females in second-growth stands were heavier in 1988 than in 1989 (Table 2.4). There was no significant difference in body mass of squirrels captured in second- and old-growth stands in 1987 for either sex (Table 2.4), but in 1988 and 1989 males were significantly heavier in old- than second-growth stands (Table 2.4). However, this difference was small in 1989 (1.9 g, 1.5%) and may be due to the larger sample sizes of males captured in old-growth stands. Body mass of animals considered young of the year (<104 g) ranged from 59 to 103 g and body mass of animals ≥ 104 g ranged from 104 to 188 g for males and 104 to 190 g for females.

Age Structure and Survivorship

Thirty-one of 191 (16%), 37 of 285 (13%), and 64 of 296 (22%) of animals captured that were weighed and sex determined were considered young-of-the-year (i.e., <104 g) in 1987, 1988, and 1989, respectively. There was no significant difference in the proportion 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 animals captured (including both body-mass classes) were recaptured the following year after their

Table 2.4 Body mass (g) of flying squirrels^a in second- and old-growth Douglas-fir stands, Willamette National Forest, Oregon, 1987-1989.

Year	Second Growth						Old Growth					
	Males			Females			Males			Females		
	n	\bar{x}	SE	n	\bar{x}	SE	n	\bar{x}	SE	n	\bar{x}	SE
1987	31	130.2	2.8AB ^b § ^c	52	136.3	2.3A§*	38	127.2	2.1B§	39	137.2	2.9A§
1988	38	125.1	2.5B§	74	137.9	1.8A§	69	135.0	2.1A*	67	137.4	2.2A§
1989	38	124.2	2.0B§	70	130.9	1.9A*	58	126.1	1.7A§	66	131.6	2.3A§

^a Only animals ≥ 104 g were included (i.e. those < 104 g were believed to be young-of-the-year).

^b Means within a row that are not significantly different ($p > 0.05$) share a common letter (Duncan's multiple-range test).

^c Means within a column that are not significantly different ($p > 0.05$) share a common symbol (Duncan's multiple-range test).

initial capture and 19% (36 of 189) were recaptured during their second year following their initial capture (Table 2.5). There was a greater proportion of females recaptured between years in second- than in old-growth stands, and a greater proportion of females were recaptured than males in both stand types. However, these differences were not significant among sex and stand-age class ($\chi^2 = 6.1$, $P = 0.11$, $df = 3$; Table 2.5). The lack of a statistical difference may reflect small sample sizes rather than equal survivorship.

Habitat Characteristics

Habitat variables were sampled at 329 trap stations; 165 were in second- and 164 were in old-growth stands. Flying squirrels were captured at approximately half ($n = 176$, 53%) of the stations during 1987 and 1988 and were equally distributed in second- ($n = 87$) and old-growth ($n = 89$) stands. The largest proportion ($n = 94$, 53.4%) of stations had 1 animal captured; 53 (30.1%) had 2 captures; 22 (12.5%) had 3; 5 (28.0%) had 4; and 2 (1.1%) had 5 captures. Only different individuals within a year were included in the number captured; individuals captured in both years on the same station ($n = 11$) were counted twice.

Habitat characteristics were different at trap stations at which squirrels were captured and not captured. Stem density of medium-size deciduous trees and rhododendron cover were selected by the stepwise DFA procedure as the variables that best discriminated between CAP and NOCAP stations. The discriminant functions correctly classified 57% of the trap stations and was higher for classifying CAP (66%) than NOCAP (47%) stations (Table 2.6). Stem density of medium-size deciduous trees was higher at CAP ($\bar{X} \pm SE$, 48 ± 6) than NOCAP stations (34 ± 6 ; t -test, $P < 0.01$). Rhododendron cover was also higher on CAP (2.3 ± 0.5) than NOCAP stations (0.9 ± 0.3 ; t -test, $P < 0.05$). All further analyses were done separately for second- and old-growth stands to determine if habitat relationships were different within each stand age-class.

Table 2.5 Number and percent of flying squirrels recaptured in subsequent years of trapping, Willamette National Forest, Oregon, 1987-1989.

Year First Captured	Number Recaptured					
	Males			Females		
	n^a	1988	1989	n^a	1988	1989
Second Growth						
1987	35	11 (31.4) ^b	8 (22.9)	59	30 (50.1)	10 (16.9)
1988	47	--	10 (21.3)	80	--	23 (28.7)
Old Growth						
1987	47	17 (36.2)	12 (25.5)	48	18 (37.5)	6 (12.5)
1988	75	--	16 (21.3)	68	--	14 (20.6)

^a Number that were captured initially

^b Percent of number initially captured

Table 2.6 Comparison of trap stations where flying squirrels were captured (CAP) versus not captured (NOCAP) by stepwise discriminant function analysis.

Stand Age-Class	Variables Selected ^a	Wilks' lambda	% Correctly Classified ^b			
			NOCAP	CAP	Total	kappa
Second-growth (<u>n</u> = 165)	ST2, LDN	0.94*	44.9	66.7	56.4	0.13*
Old-growth (<u>n</u> = 164)	ST1, RHO	0.89**	53.3	67.4	61.0	0.22**
Stand types pooled (<u>n</u> = 329)	ST2, RHO	0.96*	47.1	66.5	57.5	0.15**

^a ST2 = Stem density of medium-size deciduous trees, LDN = volume of down-wood ≥ 50 cm diameter, ST1 = stem density of small-size deciduous trees, RHO = rhododendron cover.

^b Classification rate computed using the jackknife procedure (Morrison 1976).

^c Cohen's kappa statistic is an estimate of the improvement of classification rates over chance (Titus et al. 1984).

* $\underline{p} < 0.05$

** $\underline{p} < 0.005$

Second-growth

The stepwise procedure selected large down-wood volume and stem density of medium-size deciduous trees to best discriminate between CAP and NOCAP stations. The discriminant function had an overall correct classification rate of 56% and was higher in classifying CAP (67%) than NOCAP (45%) stations (Table 2.6). Stem density of medium-size deciduous trees was significantly greater at CAP stations (Table 2.7) and was higher at stations with a greater number of individuals captured (Table 2.8). Stem density of medium-size deciduous trees was similar, on average, at stations with no captures and with 1 capture, but was approximately twice as high at stations with 2 or 3 captures. Large down-wood volume increased most from stations where squirrels were not captured to stations where at least 1 animal was captured (Table 2.8, $p = 0.056$), but there was not a clear increase of volume with number of different animals captured (Table 2.8).

Old-growth

Rhododendron cover and stem density of small-size deciduous trees were selected by the stepwise DFA to best discriminate between CAP and NOCAP stations. The discriminant function correctly classified 61% of the observations and was higher in correctly classifying CAP (67%) than NOCAP (53%) stations (Table 2.6). Rhododendron cover and stem density of small-size deciduous trees were significantly greater on CAP stations (Table 2.7). Rhododendron cover and stem density of small-size deciduous trees were generally higher on stations with >1 capture (Table 2.8). Stem density of small-size deciduous trees increased most from stations with no captures to stations with 1 capture. Rhododendron cover was $>75\%$ higher on stations with ≥ 3 captures than at stations with 1 capture and over 6 times higher than at stations with no captures.

Test of model

In 1989, 158 (48%) of the stations had at least 1 squirrel captured, and were distributed similarly in second- ($n = 72$, 46%) and

Table 2.7 Comparison of habitat characteristics (\bar{X} [SE]) on trap stations where flying squirrels were not captured (NOCAP) and captured (CAP) among second- and old-growth stands, Willamette National Forest, Oregon, 1987 - 1988.

Characteristic	Second Growth		Old Growth	
	NOCAP (\underline{n} = 78)	CAP (\underline{n} = 87)	NOCAP (\underline{n} = 75)	CAP (\underline{n} = 89)
Rhododendron cover (%)	0.9 (0.4)B ^a	0.5 (0.3)B	1.0 (0.4)B	4.1 (0.9)A
Small-size deciduous trees (#/ha)	140.5 (25.4)A	131.2 (17.0)A	35.2 (6.3)C	71.0 (9.4)B
Medium-size deciduous trees (#/ha)	57.9 (10.8)B	80.7 (10.4)A	11.2 (2.7)C	18.2 (2.8)C
Large-diameter down-wood (m ³ /ha)	45.6 (4.8)B	59.2 (4.8)AB	70.4 (7.2)A	61.6 (4.8)A

^a Means with the same letter in a row are not significantly different ($P > 0.05$), Duncan's multiple-range test.

Table 2.8 Comparison of selected habitat characteristics (\bar{X} [SE]) in second- (SG) and old-growth (OG) trapping stations that had 0 to ≥ 3 flying squirrel captures, Willamette National Forest, Oregon, 1987-1988.

Characteristic	Stand Age-Class	Number of Captures				p^a
		0	1	2	≥ 3	
Sample Size	SG	78	47	26	14	
	OG	75	47	23	15	
Rhododendron cover (%)	SG	0.9 (0.4)	0.8 (0.5)	0.2 (0.2)	0 (0)	0.05
	OG	1.0 (0.4)	3.8 (1.2)	3.2 (1.0)	6.7 (2.8)	0.03
Small-size deciduous trees (#/ha)	SG	140.5 (25.4)	118.2 (19.8)	133.8 (28.2)	170.0 (65.2)	0.05
	OG	35.2 (6.3)	66.4 (14.7)	69.6 (14.5)	88.0 (18.4)	0.002
Medium-size deciduous trees (#/ha)	SO	57.9 (10.8)	57.8 (10.3)	92.0 (18.3)	134.2 (40.6)	0.04
	OG	11.2 (2.7)	16.2 (3.5)	20.7 (4.8)	20.0 (8.7)	0.05
Large diameter down-wood (m /ha)	SG	46.2 (4.6)	58.4 (6.4)	63.8 (8.8)	52.0 (8.8)	0.05
	OG	70.4 (7.0)	61.4 (6.4)	62.1 (10.4)	63.2 (12.8)	0.05

^a Significance level, Kruskal-Wallis analysis of variance test.

old-growth ($n = 86$, 54%) stands. The models developed for the 1987 and 1988 data were not successful in predicting squirrel presence. The model developed for second-growth (stem density of medium-size deciduous trees and volume of large down-wood) did not correctly classify occurrence of squirrels at trap stations any better than chance (Cohen's kappa = 0). The model developed for old-growth stands (stem density of small-size deciduous trees and rhododendron cover) also did not significantly improve the classification rate over chance (Cohen's kappa = 0.12, $p > 0.05$).

Relationship of squirrel density to habitat characteristics

The previous analyses compared habitat characteristics at the trap station. To determine if there were stand-level relationships, we computed a mean for each variable within each stand and determined the relationship of squirrel density in 1988 and 1989 to each variable. Flying squirrel density in 1988 was positively correlated to deciduous shrub (<5 cm dbh) cover on the 10 trapping grids ($r_s = 0.72$, $p < 0.05$, $n = 10$). Density in 1988 was not significantly ($p > 0.05$) related to any other variables measured, and density in 1989 was not related to any of the variables measured. There was a wide range of snag and stem densities within and between stand age-class (Appendix B), but no significant relationships with these variables and squirrel densities 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 a lack of a relationship in 1989, suggests that the statistical significance of deciduous cover may be spurious.

DISCUSSION

I found similar flying squirrel densities in second- and old-growth coniferous forests in the central Oregon Cascades. Others have suggested that northern flying squirrels are more abundant in old- than in second-growth forests (Brown 1985, Volz 1986, Franklin 1988), but our study, unlike the others, compared abundance quantitatively. Our findings of similar squirrel abundance in both stand age-classes

indicates that the spotted owl selects old-growth for reasons other than prey abundance. Structural components of second-growth forests may reduce the ability of owls to capture prey, but the prey resource is there. Management to increase prey-base of the spotted owl through silvicultural prescriptions may lead to futile results if availability of prey to the owl is not considered.

The reasons for the female-biased sex ratio in second-growth stands is not clear. Davis (1963) found a 1:1 sex ratio with juveniles captured in summer. I did not detect a skewed sex ratio for animals considered young-of-the-year, except in 1989 when there were more males in old-growth stands than expected by chance. Therefore, it is unlikely that a skewed primary sex ratio (i.e., the ratio at fertilization) would account for the observed differences. Rather, differential mortality or dispersal of males may exist between second- and old-growth stands. The tendency for a higher proportion of females to be recaptured in subsequent years in second-growth stands supports this. Spotted owls, which appear to prey on large numbers of flying squirrels, forage more often in old-growth stands (Forsman et al. 1984, Carey et al. 1990). Therefore, it was surprising that we found a skewed sex ratio in second-growth stands if differential mortality arising from predation existed. We do not have data available to determine if dispersal was different between stand types.

Flying squirrels use nests in cavities of live trees and snags (Cowan 1936, Weigl and Osgood 1974, Maser et al. 1981; C. Maguire, pers. commun.). Large snags, which are more likely to contain cavities than smaller snags, are more abundant in old-growth than managed stands (Mannan et al. 1980). This may have led to the suggestion that flying squirrels may be more abundant in old-growth forests. However, nesting habitat may not be the limiting factor to population-size because flying squirrels use a variety of nesting substrates. Cavities in small snags (B. Biswell, pers. commun.), trees infected with witches broom rust (*Chrysomyxa* spp., Mowrey and Zasada 1984), moss nests (Bailey 1936:164), stick nests (Cowan 1936, Weigl and Osgood 1974) and even a nest in a notched stump (Cowan 1936) have been documented. This

demonstrates that flying squirrels can use a wide range of nesting substrates, although comparisons of nest-site selection with available habitat have not been made. Cavities for winter den sites may be more common in colder climates (Maser et al. 1981). Our findings of similar squirrel densities in second- and old-growth stands do not necessarily reflect similar habitat quality (Van Horne 1983). Different reproductive potential, as affected by survivorship and animal quality, may lead to unequal fitness in second- and old-growth stands.

The lack of a correlation of flying squirrel densities with snag densities suggests that snag densities were not limiting squirrel populations in the stands we examined. Small snags were common in all 10 stands, and may not have been at a minimum threshold level that would have affected squirrel population-size. Furthermore, live trees are also known to contain cavities, especially dead limbs of deciduous trees (W. McComb, pers. commun.). Our results on habitat selection suggested that flying squirrels used a wide range of available habitat. Doyle (1990) captured similar numbers of flying squirrels in riparian and upland coniferous forests despite large differences in the vegetation between these habitats. Furthermore, northern flying squirrels were not selective of habitat type in a captive experiment (Weigl 1978).

The low correct classification rate and the inability of the models to predict squirrel occurrence at trap stations in 1989 supported the view that flying squirrels were generalists in habitat use within the range of conditions we examined. Rhododendron cover, stem density of deciduous trees, and volume of large-diameter down-wood were selected as the best predictors of locations of squirrel occurrence in 1987 and 1988. Only deciduous shrub cover was positively correlated with squirrel density, and the statistical significance of this finding was questionable.

Similar results have been found with the southern flying squirrel (*G. volans*). Sonenshine and Levy (1981) found the vegetation structure where flying squirrels were captured had greater limb density and greater density and diversity of shrubs than sites where they were not

captured. Bendel and Gates (1987), based on telemetry work, reported greater shrub densities, greater lower-understory cover, and lower cover of upper-understory (>10 - 15 m) woody plants on areas used for foraging.

Large down-wood was abundant on most old-growth plots we examined; therefore, it would be unlikely that we would have detected down-wood to have been selected for in old-growth stands. However, in second-growth stands fewer stations had high quantities of large down-wood compared to old-growth stands. However, down-wood volume was similar in second- and old-growth stations when only successful stations were compared. Ectomycorrhizal fungi, the sporocarps of which are frequently found in the diet of flying squirrels (McKeever 1960, Z. Maser et al. 1985, Maser et al. 1986), have been found to be more abundant in soil with higher components of decaying wood (Harvey et al. 1978, 1979). Maser et al. (1986) and Harmon et al. (1986) speculated that down-wood also may be selected as direct sites of growth for hypogeous sporocarps. However, in our study, depth of organic soil was not a significant variable relating to sites where squirrels were captured or to squirrel density among stands.

Studies where the investigator does not have knowledge of how the habitat was used (such as in our trapping study) must be viewed as exploratory rather than predictive of habitat use. The use of baited traps is further cause for caution because animals may be trapped in areas they might not otherwise use.

Our findings have demonstrated that the variables we measured were not predictive of flying squirrel abundance. Other factors such as food, predation, and competition may be more important in determining squirrel abundance. An evaluation of flying squirrel habitat selection using radio telemetry may be more successful than our study where trap stations were used as focal points of habitat analyses. Use of radio telemetry to assess how baited traps affect habitat use would be very useful in evaluating the merits of habitat studies of this kind.

CHAPTER III
CHARACTERISTICS OF TOWNSEND'S CHIPMUNK POPULATIONS
IN SECOND- AND OLD-GROWTH CONIFEROUS FORESTS

INTRODUCTION

Timber harvesting of old-growth coniferous forests has changed much of the landscape to young, second-growth forests, and short logging rotations and even-aged management practices will not enable managed forests to attain characteristics of older forests. Old-growth forests provide unique habitat for a variety of wildlife species (Meslow et al. 1981) and may also provide optimum habitat for ecologically important species. Such species may be abundant, thereby playing important roles in food chains and energy transfer. Previous investigators (Nelson 1989, Ruggiero et al. in press) compared wildlife populations in old-growth coniferous forests to those in naturally regenerated (i.e., after wildfire) young (<80 years old) stands, although few workers have investigated intensively managed second-growth stands after canopy closure, despite the fact that these stands are increasingly dominating the forested landscape.

Mammals comprise $\approx 30\%$ of vertebrate species in coniferous forests in the Pacific Northwest (Harris and Maser 1984:47) and the region has the highest number of mammalian species in the continental United States (Simpson 1964). In coniferous forests of the central Oregon Cascades, deer mice (Peromyscus maniculatus), Trowbridge's shrew (Sorex trowbridgii), and Townsend's chipmunks (Eutamias townsendii, sensu Levenson and Hoffmann 1984) are often the dominant species in the small-mammal community (Hooven and Black 1976, Doyle 1990, Gilbert and Allwine in press). Townsend's chipmunks often comprise the largest proportion of the small-mammal biomass (Doyle 1990, Anthony and Rosenberg, unpubl. data). Townsend's chipmunks are prey for many species of carnivores, including raptors (e.g, hawks, Accipiter spp.) and mammals such as weasels (Mustela spp.) and bobcats (Lynx rufus) (Maser 1981:150, Reynolds and Meslow 1984). Townsend's chipmunks have a broad diet (Tevis 1952, 1953; Gunther et al. 1983) and may be important consumers in several energy pathways, thus contributing to higher level food chains. Their diet includes the fruiting bodies

(sporocarps) of mycorrhizal fungi that form symbiotic relationships with many plant species, and because of the importance of fungi in their diet, Townsend's chipmunks may be important dispersers of these fungi (Maser et al. 1978). Because of these ecological relationships, the abundance and population dynamics of Townsend's chipmunks may be important in maintaining natural ecosystem processes.

In this chapter, I report differences in demographic characteristics of Townsend's chipmunk populations in second- (i.e., those regenerated after clear-cutting of previously uncut forests) and old-growth coniferous forests in the central Oregon Cascades.

STUDY AREA AND METHODS

Study Sites

I selected 5 second- (30 to 60 years old) and 5 old-growth (>400 years) Douglas-fir (*Pseudotsuga menziesii*) stands on the Blue River and McKenzie Ranger Districts, Willamette National Forest, located in the central Oregon Cascades. Stands were between 375 and 900 m elevation and percent slope ranged from 10 to 60% (Appendix A). Climate in the study area was characterized by mild, wet winters and warm, dry summers (Franklin and Dyrness 1973). Forests were dominated by Douglas-fir and western hemlock (*Tsuga heterophylla*). Western red cedar (*Thuja plicata*) and incense cedar (*Calocedrus decurrens*) were common canopy species in old- and second-growth stands, respectively. The understory (2 to 4 m in height) was dominated by vine maple (*Acer circinatum*), dogwood (*Cornus nuttali*), hazelnut (*Corylus cornuta*), and western hemlock, and the lower-understory (<2 m in height) by Oregon grape (*Berberis nervosa*), salal (*Gaultheria shallon*), sword fern (*Polystichum munitum*), *Vaccinium* spp., and rhododendron (*Rhododendron macrophyllum*). The herbaceous vegetation was diverse, but twin-flower (*Linnaea borealis*), oxalis (*Oxalis oregana*), and gold-thread (*Coptis laciniata*) were most common.

Four of the 5 second-growth stands were planted after clear-cutting; the fifth stand was in part planted after clear-cutting and in part naturally regenerated after fire. The 4 young stands that were

regenerated after clear-cutting were broadcast burned and planted with Douglas-fir seedlings. Treatments varied from intensive clear-cuttings to those with seed-trees retained (Appendix A). The 5 old-growth stands were not previously logged, except for small areas where a few individual trees were removed. There was high variability in forest stand characteristics within and between stand age-classes (Table 3.1). Second-growth stands were characterized by greater densities of coniferous and deciduous trees and small-diameter snags than old-growth stands. Densities of large trees and large snags were higher in old- than second-growth stands (Table 3.1), and in some second-growth stands these components were rare or absent (Appendix B).

Population Characteristics

I established live-trapping grids in each of the 10 stands. Different trapping procedures were used in the fall and spring because the primary study objectives for fall trapping were different (Chapter 2). During fall, grids consisted of 100 trap stations spaced 40 m apart. Grids were arranged as close as possible to a 10 X 10 array (~13 ha), but varied from 10 X 10 to 16 X 6, depending on size and shape of stands. Two Tomahawk #201 (41 X 13 X 13 cm) traps were placed at each station. One trap was placed approximately 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 trap. During spring, grids consisted of 100 trap stations spaced 20 m apart, were arranged in a 10 X 10 array (3.2 ha), and were placed within the fall-season grids. One Sherman 7.6 X 7.6 X 25.4 cm live-trap was placed at each station. Traps were baited with a mixture of peanut butter, whole oats, molasses, and high protein (>30%) pellets during fall and with whole oats and peanut butter during spring. Animals were ear-tagged with monel # 1 tags or toe-clipped for individual recognition; body mass and sex were recorded.

Animals were trapped in fall 1987, 1988, and 1989 and in spring 1988 and 1989. In fall 1987, traps were operated from October to early December on 2 grids (1 old- and 1 second-growth) simultaneously for 8

Table 3.1 Habitat characteristics (\bar{X} [SE]) on trapping stations in second- and old-growth Douglas-fir stands, Willamette National Forest, Oregon, 1988.

Characteristic	Second-growth ($n = 165$)	Old-growth ($n = 164$)
Herb cover (%)	6.5 (0.5)	7.5 (0.7)
Salal cover (%)	3.5 (0.4)	2.6 (0.4)
Fern cover (%)	5.9 (0.5)	5.9 (0.6)
Deciduous shrub (<5 cm DBH) cover (%)	7.3 (0.8)	5.6 (0.6)
Coniferous (<5 cm DBH) cover (%)	2.6 (0.3)	6.2 (0.5)*
Rhododendron cover (%)	0.7 (0.2)	2.7 (0.5)*
Small-size coniferous trees (#/ha)	155.0 (12.0)	125.4 (10.3)
Medium-size coniferous trees (#/ha)	516.0 (9.4)	196.0 (9.4)*
Large-size coniferous trees (#/ha)	10.4 (1.1)	65.6 (2.0)*
Small-size deciduous trees (#/ha)	135.6 (14.9)	54.6 (6.0)*
Medium-size deciduous trees (#/ha)	69.9 (7.5)	15.0 (1.9)*
Large-size down-wood (m ³ /ha)	52.8 (3.2)	65.8 (4.2)*
Small-size snags (#/ha)	61.2 (6.0)	23.8 (3.0)*
Large-size snags (#/ha)	8.0 (1.0)	17.4 (1.3)*

* Students' t -test, $p < 0.05$

consecutive nights, with a different pair of grids in each of 5 sessions. In fall 1988 and 1989 (October to November), traps were operated on 5 grids simultaneously during 2 sessions in 1988 (10 nights) and 1989 (21 nights). New animals were marked for only the first 10 days; all analyses except for movement data are based on the first 10 days of trapping. During spring (April to June) traps were operated for 8 consecutive nights on 2 grids (1 old- and 1 second-growth) simultaneously for 5 sessions.

I estimated chipmunk densities on each grid for each season and year. Animals that died before the last trapping night were omitted from mark-recapture analyses but were added to the population estimates (White et al. 1982). Program CAPTURE (Otis et al. 1978) was used to analyze mark-recapture data. Capture probabilities appeared affected by heterogeneity (Otis et al. 1978:33) so the first-order jackknife estimator (Burnham and Overton 1979) was used to provide population estimates (\hat{N}). I computed an effective trapping area (ETA) around the grids by adding one-half of the mean-maximum-distance-moved (MMDM) to the grid's perimeter (Wilson and Anderson 1985). I computed MMDM for each grid. Density was estimated as $\hat{D} = \hat{N}/\text{ETA}$.

Habitat Characteristics

I used nested circular-plots modified from Spies et al. (1988) to sample vegetation at every third trapping station on the grids that had 40-m interval spacing. Large (≥ 50 cm diameter) trees, snags, down-wood, and stumps (< 1.5 m tall) were recorded in 0.12-ha (20-m-radius) plots centered at the trap station. Smaller trees (≥ 5 to 49-cm diameter at breast height, dbh), snags (≥ 10 to 49-cm-dbh), and fallen trees (down-wood) (≥ 25 to 49-cm-diameter) were measured in 0.05-ha (12.6-m-radius) plots. The species and dbh were recorded for live trees and recorded the diameter and condition (% limbs remaining) for snags (≥ 1.5 m tall) and down-wood. Vegetation was measured during July through September 1988.

To facilitate habitat comparisons, I established categories of tree, snag, and down-wood size. Live trees were grouped into 5-10, > 10

- 49, and ≥ 50 -cm-dbh classes, snags into 10-49, ≥ 50 -cm-dbh classes and condition categories (soft: ≤ 2 % limbs remaining, hard: > 2 % limbs), and down-wood volume (m^3) was computed for 25 - 49, and ≥ 50 -cm-diameter classes. I computed the CV of tree diameters as a measure of tree-size diversity.

Percent cover of understory plants (Oregon grape, fern, salal, conifer, rhododendron, deciduous, and total) and percent ground cover (herb, woody debris < 25 cm diameter, moss) was visually estimated in 8 1-m^2 quadrats. These were placed 4 and 7 m from the trap station along each cardinal direction. I used the average of the 8 quadrats in the analyses. Organic soil depth was measured to the nearest 1 cm to 10 cm, then recorded as > 10 cm. The median value of the 8 samples were used in the analyses.

Statistical Analyses

I compared both density and MMDM between years and stand age-class with two-way analysis of variance (ANOVA). For the MMDM analyses, density was included as a continuous effect in the ANOVA (Sokal and Rohlf 1981:509), because home range and therefore movements may be related to density (Forsyth and Smith 1973). I compared each season separately for these analyses because different grid size and trap intervals were used. These factors may strongly influence density and movement estimates (Stickel 1954, White et al. 1982:120). I pooled seasons when no differences were found between them. Body mass was compared among sex, stand age-class, and years with three-way ANOVA. Comparisons of body mass were made for individuals ≥ 60 g; animals less than this were considered young-of-the-year. Sex ratios (pooled by stand age-class) and proportion of young-of-the-year (i.e., < 60 g) were compared with chi-square goodness-of-fit tests. The expected number of young-of-the-year in the chi-square analysis was based on the proportion of "adults" (i.e., ≥ 60 g) between stand age-class. Sex ratio comparisons were made for each trapping session separately.

Relationships of chipmunk density to habitat characteristics (stand level) were evaluated with regression analyses. I used the fall

1989 density estimates rather than other sampling periods because 1) selection of trap stations to measure habitat characteristics was made within the fall-season grids and 2) we believed the density estimates in fall 1989 were least effected by hibernation. I selected variables significantly ($P > 0.05$) correlated with chipmunk density and entered those variables into a multiple regression with stand-age class entered as an indicator variable (Weisberg 1980:169-177). Stand-age class was included because of the known differences (see RESULTS) in chipmunk density between second- and old-growth stands.

RESULTS

Population Characteristics

A total of 2137 chipmunks were captured from 1987 to 1989, with an average of 3.8 captures per individual (8239 total captures, ≤ 10 trapping nights). In fall 1989, there was an average of 9.7 captures per individual during 21 nights. Estimated densities ranged from 0.4 to 10.3 chipmunks/ha and were twice as high in old- (5.2 ± 0.4) than second-growth (2.6 ± 0.4) stands in both fall ($F = 12.8$, $P = 0.001$) and spring ($F = 12.9$, $P = 0.002$; Table 3.2). Densities often fluctuated within a stand among years and seasons, although some stands were exceptionally stable, especially in fall (Table 3.2). There was no significant differences in density among years in fall ($F = 1.2$, $P = 0.3$), but densities were almost twice as high in spring 1988 than in spring 1989 ($F = 11.7$, $P = 0.003$, $df = 1$; Table 3.2). Estimated densities in spring (4.8 ± 0.6) were greater than fall (3.4 ± 0.4) densities; these differences were likely due to the different grid sizes used. The smaller size of the spring (3.2 ha) than fall (13 ha) grids made the influence of the trap edge greater (White et al. 1982:120). This may result in over-estimated densities.

MMDM ranged from 52 to 146 m and was more variable for second- (56 - 140 m) than for old-growth (52 - 99) stands. MMDM was similar between spring (82.9 ± 4.9) and fall (86.4 ± 3.9 ; Table 3.3) despite the different trap intervals. After accounting for variance attributed to density, MMDM was higher in second- (92.4 ± 5.2) than old-growth (73.8 ± 2.4) stands ($F = 8.6$, $P = 0.005$; Table 3.3). The difference in

Table 3.2 Number of Townsend's chipmunks captured and density estimates (number/ha) in second- and old-growth Douglas-fir stands, Willamette National Forest, Oregon, 1987-1989.

Stand	Fall 1987		Spring 1988		Fall 1988		Spring 1989		Fall 1989	
	Individuals captured	Density ^a (#/ha)	Individuals captured	Density (#/ha)	Individuals captured	Density (#/ha)	Individuals captured	Density (#/ha)	Individuals captured	Density (#/ha)
SECOND-GROWTH										
1107-86	46	2.9	28	4.6	53	3.8	23	4.4	80	4.1
1303-33	14	0.7	15	2.6	40	2.7	6	0.4	47	2.4
7115-16	70	4.8	43	8.6	29	1.6 ^c	22	1.3	56	2.8
7115-31	4	--- b,c	30	4.8	15	0.8 ^c	8	0.9	17	0.8
<u>7115-83</u>	10	<u>0.7</u>	17	<u>2.5</u>	9	<u>0.6^c</u>	16	<u>2.7</u>	36	<u>2.2</u>
\bar{x} (SE)		2.3(1.0)		4.6(1.1)		1.9(0.6)		1.9(0.7)		2.5(0.5)
OLD-GROWTH										
1109-43	119	8.5	49	8.8	87	4.9	32	5.5	129	8.0
1109-84	60	4.4	38	6.5	84	5.7	22	3.7	79	4.2
1111-44	51	3.9	25	5.0	56	3.9	15	3.4	96	6.1
1110-90	74	5.1	55	10.3	22	1.4 ^c	32	6.4	96	5.2
<u>7116-08</u>	25	<u>1.7^c</u>	42	<u>8.1</u>	33	<u>2.0^c</u>	25	<u>4.8</u>	57	<u>3.2</u>
\bar{x} (SE)		4.7(1.1)		7.7(0.9)		3.6(0.8)		4.8(0.5)		5.3(0.8)

^a Density estimate computed from the population estimate derived from the first-order jackknife estimator (Burnham and Overton 1979) divided by the grid area + 1/2 mean-maximum-distance-moved included around the grid (Wilson and Anderson 1985).

^b No recaptures.

^c Suspected hibernation.

Table 3.3 Mean-maximum-distance-moved^a (m) for Townsend's chipmunks captured in second- and old-growth Douglas-fir stands, Willamette National Forest, Oregon, 1987-1989.

Stand	Fall 1987	Spring 1988	Fall 1988	Spring 1989	Fall 1989
SECOND-GROWTH					
1107-86	90 (30) ^b	80 (23)	92 (43)	72 (17)	115 (71)
1303-33	118 (10)	96 (9)	80 (32)	140 (2)	114 (42)
7115-16	75 (37)	74 (28)	56 (25)	64 (17)	110 (47)
7115-31	(0)	107 (18)	92 (11)	132 (7)	146 (16)
7115-83	<u>83 (7)</u>	<u>91 (16)</u>	<u>88 (7)</u>	<u>98 (10)</u>	<u>106 (26)</u>
\bar{x} (SE)	91 (9.3)	90 (5.8)	82 (6.8)	102 (16.0)	118 (7.1)
OLD-GROWTH					
1109-43	63 (80)	64 (45)	92 (74)	72 (28)	76 (115)
1109-84	52 (43)	72 (32)	76 (64)	78 (18)	88 (70)
1111-44	72 (25)	57 (19)	72 (46)	62 (8)	84 (79)
1110-90	64 (55)	74 (42)	60 (19)	74 (22)	99 (84)
7116-08	<u>76 (17)</u>	<u>73 (28)</u>	<u>68 (29)</u>	<u>78 (17)</u>	<u>99 (48)</u>
\bar{x} (SE)	63 (4.1)	68 (3.3)	74 (5.3)	72 (2.0)	89 (4.4)

^a Computed as the average of the maximum distance between trap stations for animals captured ≥ 2 times by program CAPTURE (Otis et al. 1978).

^b Number of individuals

MMDM between stand-age class was less in fall 1988 than other periods (Table 3.3) and may have been due to 5 stands (2 old- and 3 second-growth) that were trapped during cold and snowy weather.

Sex ratios (males:females) were generally skewed in favor of males, particularly in second-growth stands and in spring (Table 3.4). In spring and fall 1988, there were proportionately more males in second- than old-growth stands, with the highest ratio almost reaching 3 males : 1 female (Table 3.4). Sex ratios in fall were greater than 1:1 in second-growth stands in 1988, but were never significantly different than 1:1 in old-growth stands. Chipmunk populations had higher proportions of males in spring than in fall for 1988 and 1989 ($\chi^2 > 5.2$, $p < 0.05$; second- and old-growth stands combined).

Minimum body mass of chipmunks that were known to have been ≥ 1 year old was 61 g, so animals < 60 g were considered young-of-the-year. However, most young of the year gain adult weight by fall (Gashwiler 1976), thus individuals that were > 60 g could have been young-of-the-year or adults. Body mass did not differ between old- and second-growth stands ($F = 0.08$, $p = 0.8$), but did differ between sex ($F = 154.6$, $p < 0.001$) and sampling periods (season, year) ($F = 17.2$, $p < 0.001$; Table 3.5). Females were $\approx 5\%$ heavier than males. The difference between body mass of males and females varied among years, was higher in spring than in fall (Table 3.5), and was due to the generally greater body mass of females in spring. I found significant differences between second- and old-growth stands when each sampling period was analyzed separately, although the patterns were not consistent. In 1987, females were heavier in old-growth stands and in fall 1989 males were heavier in second-growth stands. In all other sampling periods, there were no detectable differences in body mass between stand age-class (Table 3.5).

There were few young-of-the-year that were distinguishable from adults. Twenty-four chipmunks < 60 g (range: 36 - 59 g) were captured (all in fall), and most ($n = 18$, 75%) in 1989. There were more captured than expected by chance in old- ($n = 22$) than second-growth ($n = 2$) stands ($\chi^2 = 7.3$, $p < 0.01$).

Table 3.4 Sex ratios of Townsend's chipmunk populations in second- and old-growth Douglas-fir stands, Willamette National Forest, Oregon, 1987 - 1989.

Year	Season	Second-growth		Old-growth	
		<u>n</u>	males:1 female	<u>n</u>	males:1 female
1987	Fall	130	1.1	309	1.1
1988	Spring	120	2.9 ^{a,b}	197	1.4 ^a
1988	Fall	154	1.6 ^{a,b}	273	1.1
1989	Spring	75	2.1 ^a	131	1.8 ^a
1989	Fall	233	1.3	452	1.2

^a Sex ratio differed from a 1:1 ratio ($P \leq 0.05$)

^b Sex ratio differed ($P \leq 0.05$) between second- and old-growth stands

Table 3.5 Body mass (g) of Townsend's chipmunks^a in second- and old-growth Douglas-fir stands, Willamette National Forest, Oregon, 1987-1989.

Year	Season	Second Growth						Old Growth					
		Males			Females			Males			Females		
		\bar{n}	\bar{x}	SE	\bar{n}	\bar{x}	SE	\bar{n}	\bar{x}	SE	\bar{n}	\bar{x}	SE
1987	Fall	67	75.6	0.9B ^{b&c}	61	76.8	1.0B\$	161	76.4	0.5B*	144	81.6	0.7A*
1988	Spring	91	77.3	0.6B&	32	83.7	1.4A&	116	76.3	0.6B*	82	82.9	1.0A&*
1988	Fall	93	77.9	1.1B&	60	82.3	1.1A&*	142	78.5	0.7B&	127	82.7	0.8A&*
1989	Spring	46	77.0	1.1B&	23	84.2	1.9A&	80	78.2	0.9B&	40	85.2	1.5A&
1989	Fall	134	77.4	0.6A&	99	78.9	0.8A\$*	242	75.2	0.4B*	203	78.4	0.6A\$

^a animals <60 g (\bar{n} = 24) are not included

^b Means within a row that are not significantly different ($P \geq 0.05$) share a common letter (Duncan's multiple-range test).

^c Means within a column that are not significantly different ($P > 0.05$) share a common symbol (Duncan's multiple range test)

Habitat Characteristics

Density of large snags (≥ 50 -cm-dbh) was the only habitat variable that was correlated ($p < 0.05$) with chipmunk density when stand-age class was included as an indicator variable in the model. Hard ($>2\%$ limbs remaining) large-snags and stand-age class fit best ($R^2 = 95.8$, $p < 0.001$, $n = 10$; Figure 1). Stand-age class was significant in the model ($t = 5.8$, $p = 0.0004$). Chipmunk densities were not significantly correlated with large hard-snags in second-growth stands ($R^2 = 0.12$, $p = 0.6$, $n = 5$), nor with any other snag classes. In old-growth stands, chipmunk densities were highly and positively correlated with large hard-snag densities ($R^2 = 0.96$, $p = 0.002$, $n = 5$).

DISCUSSION

Density consistently differed between stand age-class, and on average, was twice as high in old- than second-growth stands. Chipmunks occur in a wide range of forest types, with similar densities in such widely differing habitats as clear-cuts (Tevis 1956), mature (Hooven and Black 1976), and old-growth coniferous forest (Gashwiler 1959, this study). Chipmunks were also common in riparian areas in second-growth forests (Anthony et al. 1987). In the present study, chipmunk density was correlated with large snag density in old- but not in second-growth stands. There was little variation in the number of large snags in second-growth stands; however, chipmunk densities varied substantially among these stands. The relationship of chipmunk density with large snags warrants further investigation. Rather than directly affecting chipmunk density, large snags may be related to other attributes of the forest that chipmunks respond to, such as forest gaps. Chipmunk populations may be limited by food supply (Sullivan et al. 1983) rather than structural characteristics of their habitat.

Mean-maximum-distance-moved was consistently lower in old- than second-growth stands and can be used as an index to home range size (Wilson and Anderson 1985). Home range size has been extensively studied in chipmunks (*Tamias* and *Eutamias*) and experimental work has suggested that home-range size was a function of food supply (Mares et

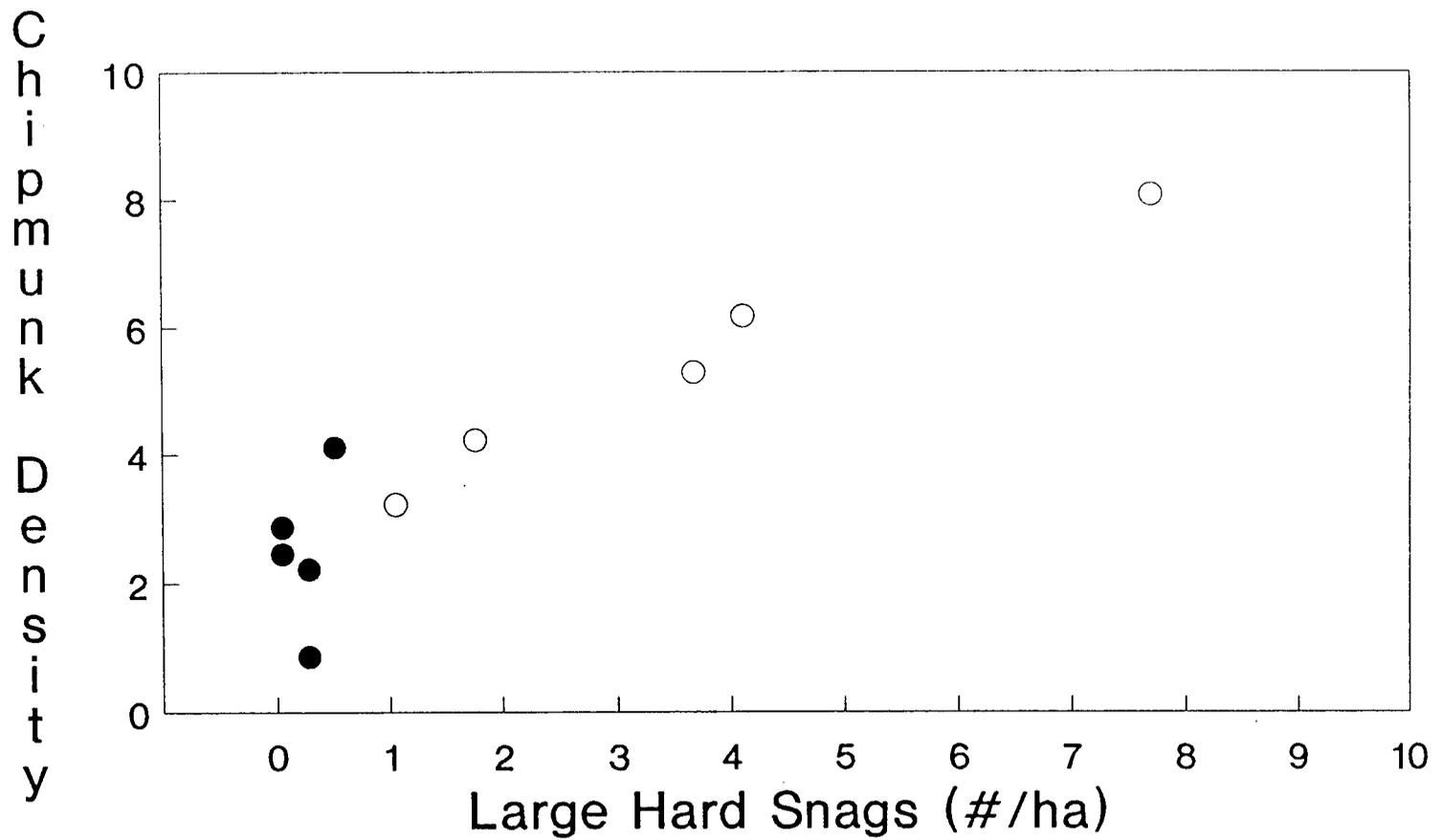


Figure 1. Relationship of chipmunk densities to stand-age class and to density of large hard-snags. Each circle (● = second-growth, ○ = old-growth) represents the densities in a stand (n = 10).

al. 1982). If the size of the home range is related to food resources (Sullivan et al. 1983 for E. townsendii, Mares et al. 1976, 1982 for Tamias striatus; but see Lacki et al. 1984 for a contradictory finding), then animals with a larger home range would spend a greater proportion of their time searching for food or traveling to food patches, activities that may 1) place an animal at greater risk of predation (Dill and Fraser 1984) and 2) allocate a greater amount of energy to maintenance costs rather than growth or reproduction.

I did not find consistent differences in body mass between second- and old-growth stands. Larger home ranges may have allowed chipmunks to acquire sufficient food resources in second-growth stands to achieve normal (i.e., that found in high-quality habitat, sensu Van Horne 1981) adult body mass. Growth rates, however, may be different between second- and old-growth forests. Higher growth rates were found in experimentally fed Townsend's chipmunk populations compared to non-fed populations (Sullivan et al. 1983).

There was clearly a higher proportion of males captured in second- than old-growth stands for most sampling periods. This may have been due to greater immigration rates of males than of females, loss of females via over-winter mortality or emigration, or larger male home-ranges in second-growth stands. Larger home ranges of males could increase the number of males captured and account for the high sex ratios we found in spring. Males are known to travel long distances during the breeding season (Yahner 1978 for T. striatus), and sex ratios favoring males in spring have also been reported by Gashwiler (1976) for Townsend's chipmunk populations.

I was only able to distinguish a small proportion of young-of-the-year from adults. Most (75%) of the individuals believed to be young-of-the-year (i.e., <60 g) were captured during fall 1989. Number of young produced appeared greater in old- than second-growth stands; 91% of animals classified as young of the year were captured in old-growth stands. Reproduction either continued late into the fall, with possible double litters or occurred later in the season in old-growth stands. Despite the low densities in spring 1989, densities in fall

1989 were similar to previous fall densities. Thus, recruitment via in situ reproduction or immigration was high in 1989.

The differences we found in population characteristics between chipmunk populations in second- and old-growth forests suggest that old-growth forests provide better habitat for Townsend's chipmunks than second-growth forests. Because Townsend's chipmunks represent a major proportion of the biomass of the small-mammal community in coniferous forests, they are probably important to food webs and energy flow. The high number of carnivore species in old-growth Douglas-fir forests are believed to be due to the complex food webs that occur there (Harris and Maser 1984:50). Because of the broad diet of chipmunks and their high densities, they may play important functional roles in coniferous forests. The actual role they play in natural and managed forests will require further investigation.

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APPENDICES

Appendix A. Location, aspect, slope, and stand history where live-trapping grids were placed, Willamette National Forest, Oregon.

Stand ^a	Ranger District	Location ^b	Age (yr)	Elev. (m)	Aspect	Slope	Stand History
1107-86	Blue River	14S-5E-1-S	60	900	NW	35	WF ^c , RIC ^d
1303-33	Blue River	17S-4E-20-SW	30	600	E	25	SPC ^e , SFL ^f , REF ^g , FBR ^h , HCC ⁱ
7115-16	McKenzie	15S-4E-5-S	30	800	S	25	SFL, SPC, REF, FBR, HCC
7115-31	McKenzie	16S-4E-9-SW	40	500	SW	10	SFL, RPL ^j , FBR, HCC
7115-83	McKenzie	16S-4E-10-S	40	450	S	20	RIC
1109-43	Blue River	15S-4E-27-S	>400	850	N	55	NPC ^k
1109-84	Blue River	15S-4E-32-W	>400	500	NW	60	NPC
1110-90	Blue River	15S-5E-14-S	>400	800	SW	20	NPC
1111-44	Blue River	15S-5E-19-NW	>400	900	SW	40	NPC
7116-08	McKenzie	17S-4E-20-SW	>400	375	NW	20	SC ^l

^a Numbers represent Forest Service compartment number followed by stand number (last 2 digits)

^b Township-range-section-quadrat

^c Stand originated at least partially from wildfire

^d Forest Service records incomplete

^e Precommercial thinning

^f Fertilization

^g Reforestation

^h Broadcast or spot burn

ⁱ Harvest clear-cut

^j reforestation by planting

^k No previous cutting; small amounts of salvage cutting may have occurred

^l Selective cutting; not extensive

Appendix B. Habitat characteristics (\bar{X} [SE]) at trapping stations in second- and old-growth stands, Willamette National Forest, Oregon, 1988.

Characteristic	STAND NUMBER ^a									
	Second Growth					Old Growth				
	110786 ^a	130333	711516	711531	711583	110943	110984	111090	111144	711608
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)
Salal 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)
Down-wood (25-49 cm dia., 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 (2.1)	16.0 (3.0)	27.0 (2.4)	24.0 (2.7)	17.6 (2.6)
Down-wood (≥50 cm dia., 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, #/ha)	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, #/ha)	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 (#/ha)	30.0 (3.5)	67.6 (5.1)	57.0 (4.2)	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, #/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, #/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, #/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, #/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, #/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, #/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	3.3	5.3	6.7	7.5	4.9	9.9	8.8	8.6

^aNumbers represent Forest Service compartment number followed by stand number (last 2 digits)

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