

# Townsend's chipmunk populations in Douglas-fir plantations and mature forests in the Oregon Coast Range<sup>1</sup>

John P. Hayes, Eric G. Horvath, and Patrick Hounihan

**Abstract:** Despite the abundance and ecological importance of Townsend's chipmunks (*Tamias townsendii*) in coniferous forests in the northwestern United States and southwestern Canada, little is known about either the habitat associations of the species or the influence of forest structure on population density. We live-trapped chipmunks in three mature, fire-regenerated coniferous forests (>140 years old) and nine 10- to 35-year-old Douglas-fir plantations in the Oregon Coast Range to examine patterns of their population density and habitat associations. Estimations of density of chipmunk populations among stands ranged from 0.0 to 23.8/ha. Population density within a stand did not significantly change between autumn and spring. Population density, mean maximum distance moved, and sex ratio did not differ significantly between young and mature stands, although mean body mass of chipmunks in mature forests was greater than mean body mass of those in young stands during autumn. Chipmunk population density was correlated with the percentage of salal (*Gaultheria shallon*) in the understory, suggesting that forest stand structure plays an important role in determining habitat quality for this species. Habitat characteristics in the Oregon Coast Range are highly favorable to Townsend's chipmunks, probably because of mild winters, high rates of primary production, structural characteristics of the stands, and minimal competition from other species of sciurids.

**Résumé :** Malgré l'abondance et l'importance écologique du *Tamias townsendii* dans les forêts de conifères du nord-ouest des États-Unis et du sud-ouest du Canada, les relations entre l'espèce et l'habitat ont été peu étudiées et on ignore l'influence qu'a la structure de la forêt sur la densité des populations. Nous avons procédé au piégeage de tamias dans trois forêts âgées, brûlées et régénérées (>140 ans), et dans neuf forêts de sapins de Douglas de 10–35 ans de la Chaîne côtière de l'Oregon afin d'étudier les fluctuations de densité de la population et les choix d'habitats. La densité des populations dans les différentes forêts variait de 0,0 à 23,8 tamias/ha. La densité de la population dans une forêt ne variait pas significativement de l'automne au printemps. La densité, la distance moyenne maximale parcourue et le rapport mâles:femelles des tamias ne différaient pas significativement entre les jeunes forêts et les forêts âgées, mais la masse corporelle moyenne des tamias était plus élevée dans les forêts âgées à l'automne. La densité de population était reliée au pourcentage de salal (*Gaultheria shallon*) dans la végétation de la strate herbacée, ce qui semble indiquer que la structure de la forêt a une influence importante sur la qualité de l'habitat. Les caractéristiques des habitats dans la Chaîne côtière de l'Oregon sont très favorables aux populations de *Tamias townsendii*, probablement à cause des hivers doux, des taux élevés de production primaire, de la structure des forêts et de la compétition minimale exercée par les autres espèces de sciuridés.

[Traduit par la Rédaction]

## Introduction

Townsend's chipmunk (*Tamias townsendii*) is a dominant species in many small-mammal communities in western

Oregon (Hooven and Black 1976; Doyle 1990). In the ecology of Northwest forests, chipmunks play important roles as prey for diurnal predators (Maser 1981) and as dispersers of mycorrhizal fungal spores (Maser et al. 1978; McIntire 1984; McIntire and Carey 1989).

Several studies have found higher population densities of Townsend's chipmunks in late seral-stage forests than in younger stands. Raphael (1984) found that abundance of chipmunks increased with stand age in Douglas-fir (*Pseudotsuga menziesii*) forests in northern California. Carey (1991) reported that Townsend's chipmunk densities were 1.7 times greater in old-growth stands than in young, managed stands in southwestern Oregon. In the Oregon Cascade Range, Rosenberg and Anthony (1993) found that the density of chipmunks in old-growth stands averaged twice that in

Received April 8, 1994. Accepted October 7, 1994.

J.P. Hayes,<sup>2</sup> E.G. Horvath, and P. Hounihan. Coastal Oregon Productivity Enhancement Program, Hatfield Marine Science Center, Newport, OR 97365, U.S.A., and Department of Forest Science, Oregon State University, Corvallis, OR 97331, U.S.A.

<sup>1</sup> Paper 2990, Forest Research Laboratory, Oregon State University, Corvallis.

<sup>2</sup> Author to whom all correspondence should be addressed.

second-growth stands, and found a correlation between the number of hard snags and chipmunk density in old-growth stands. In contrast, Anthony et al. (1987) found that in riparian zones in the Oregon Cascade Range, Townsend's chipmunks in young (25- to 50-year-old) stands were 5 times more abundant than in mature (130- to 200-year-old) forests and twice as abundant as in old-growth (400- to 450-year-old) forests.

In this paper, we present the results of mark-recapture analyses for Townsend's chipmunks in Douglas-fir plantations and mature forests in the Oregon Coast Range, and we discuss patterns of habitat and seral-stage associations of Townsend's chipmunks in the Oregon Coast Range.

## Methods

### Study sites

We selected three areas of the Oregon Coast Range in the Waldport District of the Siuslaw National Forest in Lincoln County, Oregon, for study. In each area, one stand was selected in each of four age-classes: 10- to 15-, 20- to 25-, and 30- to 35-year-old Douglas-fir plantations, and mature forests (> 140 years old). For selection, each stand had to be > 15 ha, accommodate a 120 × 240 m grid with an 80-m buffer, and be accessible by road within 5 km of the other study sites in the area. Overstory vegetation in the study sites was dominated by Douglas-fir in plantations and by western hemlock (*Tsuga heterophylla*) or Douglas-fir with substantial amounts of western redcedar (*Thuja plicata*) and Sitka spruce (*Picea sitchensis*) in mature stands. Dominant understory species included salmonberry (*Rubus spectabilis*), salal (*Gaultheria shallon*), vine maple (*Acer circinatum*), sword fern (*Polystichum munitum*), evergreen huckleberry (*Vaccinium ovatum*), and western hemlock.

All the plantations were planted after clear-cut logging. The mature stands were naturally seeded and regenerated following large-scale fires. Logging had been conducted in two of the mature stands, but < 20% of the timber volume had been removed.

### Livetrapping

In each stand we established a 32-station grid (4 × 8) with 40-m spacing between stations. Edges of the grid were situated at least 80 m from the edge of the stand. We set two No. 201 Tomahawk live traps (41 × 13 × 13 cm) at each station, one about 1.5 m off the ground in the largest tree within 5 m of the grid station and one on the ground or on a log within 3 m of that tree. Techniques for setting traps followed Carey et al. (1991) and Hayes et al. (1994). Traps were baited with a mixture of oats, molasses, and peanut butter and were checked daily for 8 consecutive days. During a given 8-day period, one stand of each age-class was trapped. Trapping was conducted during autumn 1992, between 6 October and 10 November, and spring 1993, between 30 March and 4 May.

All chipmunks captured were identified to sex and weighed to the nearest gram with a 300-g spring scale. Chipmunks were marked with a unique combination of zero to three holes in each ear and one or no toes clipped on one hind foot, and were released at the site of capture.

### Habitat analysis

Habitat characteristics were measured at each grid station. In each of the quadrants defined by the cardinal directions, the diameter at breast height (DBH), species, and distance from the grid station of the nearest tree ≥ 5 cm DBH was recorded. We estimated overstory tree density for each stand by the point-centered quarter method (Bonham 1989). The proportion of each species in the stand was calculated and mean DBH for the stand was determined. Four 28.3-m<sup>2</sup> circular plots were centered 5 m from the grid point in each of the cardinal directions. Percent cover of salmonberry, salal, vine maple, sword fern, conifers < 5 cm DBH, and other shrubs was visually estimated in each of the circular plots. Logs ≥ 2 m long with a maximum diameter of 25–49 cm and those with a maximum diameter ≥ 50 cm that were partially or completely in a circular plot were counted. Each standing dead tree or stump ≥ 1.5 m tall in each plot was considered to be a snag; these were counted and identified as hard conifer (bole of tree intact, exterior wood generally of sound texture), soft conifer (bole of tree generally not intact, exterior wood generally soft and chunky in texture), or red alder (*Alnus rubra*). The numbers of snags and logs per hectare in each category were extrapolated from these data.

### Statistical analysis

We estimated abundance of chipmunks for each stand and season with CAPTURE (Otis et al. 1978). We used the jackknife estimator (Burnham and Overton 1979) because heterogeneity was a dominant factor influencing population estimates. We estimated the effective area trapped by adding a buffer of one-half the mean maximum distance moved (MMDM) around the area encompassed by the trapping grid. Point estimates and confidence intervals for population densities were calculated by dividing the estimates for numbers of chipmunks and confidence intervals by the effective area trapped (Wilson and Anderson 1985). Densities were considered to be statistically different if the 95% confidence intervals did not overlap.

Because of differences in MMDM values (and, consequently, in effective areas trapped) for males and females, we calculated effective areas trapped separately for each sex. Sex ratios (number of males per female) were calculated for autumn and spring based on the number of individuals captured per effective area trapped for that sex.

All other statistical analyses were conducted with the SAS statistical software package for personal computers (Version 6; SAS Institute Inc. 1987). For analyses of chipmunk body mass, multiple masses of individuals from a season were averaged to obtain a single seasonal body mass estimate for each individual. Preliminary statistical analyses of differences in body mass of chipmunks among seasons and sexes were tested for statistical significance with PROC GLM in a two-way ANOVA. Because of statistical interactions in the overall model, main effects due to sex and season could not be tested. Simple effects due to sex and season were examined separately by *t* tests with PROC TTEST. We used contrasts in PROC GLM with site as a class variable to test for differences in body mass of chipmunks between mature stands and plantations. Data on chipmunk body mass were not used from site R20 or for females from site RM during the spring for stand-level analyses because of small sample sizes. We

used PROC CORR to examine correlations of chipmunk population densities with mean body mass, MMDM, and habitat characteristics. Because of the small sample size for females in site RM and the absence of recaptures during either season in site R20, these sites were omitted from the analysis of MMDM data. As a preliminary analysis, differences among MMDM values for chipmunk populations among seasons and sexes were tested for statistical significance in a two-way ANOVA using PROC GLM. Main effects due to sex and season could not be tested because of statistical interactions in the model; simple effects due to sex and season were examined separately by *t* tests using PROC MEANS, with data paired by stand. Differences in mean chipmunk population density and sex ratio between mature stands and plantations were tested with PROC TTEST.

**Results**

**Habitat characteristics**

Variation in some, but not all, of the measured habitat characteristics was associated with the seral stage of the stand (Table 1). Mature stands had significantly larger mean diameters of overstory trees, fewer trees per hectare, lower proportions of Douglas-fir and higher proportions of western hemlock in the overstory, higher percent cover of small conifers, sword fern, and "other shrub" species (primarily evergreen huckleberry) in the understory, greater numbers of logs with a maximum diameter of 25–50 cm, and greater numbers of soft snags than the younger stands (*P* < 0.05). Percent cover of salmonberry, salal, and vine maple in the understory, number of alder and hard conifer snags, and number of logs per hectare with a maximum diameter >50 cm did not differ significantly between mature and younger stands.

**Chipmunk population density**

We caught a total of 873 individuals (3384 captures in total); during the autumn trapping season we captured 528 individuals (1324 captures) and during the spring trapping season we captured 701 individuals (2060 captures). At site R20, no chipmunks were captured in autumn and one animal was caught once during the spring. Point estimates for chipmunk densities at all other sites varied from 5.3 to 23.8/ha for autumn and 3.8 to 20.4/ha for spring (Table 2). Estimates of population densities were not significantly different between autumn and spring trapping sessions for any stand.

There were no apparent associations between stand age and chipmunk density for either season. Population densities in mature stands were not significantly different than in young stands for either season (*P* > 0.05). The two stands with the highest estimated density were a 10- to 15-year-old plantation (R10) and a mature stand (PM). Densities varied substantially within all age-classes.

Percent cover of salal was positively correlated with chipmunk density in autumn (*r* = 0.680, *n* = 12, *P* = 0.015) and spring (*r* = 0.756, *n* = 12, *P* = 0.004). Chipmunk densities were not significantly correlated with any other measured habitat characteristic.

**Body mass**

Females were significantly heavier than males during autumn (females,  $\bar{x}$  = 84.4 g, *n* = 246; males,  $\bar{x}$  = 81.1 g, *n* = 274;

**Table 1.** Habitat characteristics of study sites.

Stand age (years)	Site	Overstory trees										Understory vegetation (% cover)				Mean no. of logs/ha		Mean no. of snags/ha	
		Mean DBH (cm)		No. of trees/ha	Percent composition				Salmonberry	Salal	Other shrubs	Sword fern	Vine maple	Conifer	Diameter 25–49 cm	Diameter ≥50 cm	Hard conifer	Soft conifer	Alder
		Mean DBH (cm)	Western hemlock		Douglas-fir	Other													
10–15	L10	17.5	96.7	844	3.3	0.0	66.7	9.4	6.1	0.4	0.0	0.2	92	112	0.0	8.6	0.0		
	P10	10.9	70.9	2251	23.6	5.5	16.2	29.0	3.8	1.4	0.2	11.3	307	209	2.8	16.6	0.0		
20–25	R10	18.0	99.2	687	0.8	0.0	55.6	34.1	3.4	1.5	0.0	0.9	159	206	11.1	8.3	0.0		
	L20	28.1	94.5	704	2.3	3.1	17.9	13.1	2.6	2.9	1.0	1.0	246	248	5.5	2.8	0.0		
	P20	28.6	90.6	245	3.1	6.2	10.5	1.5	2.2	9.8	12.9	0.0	162	45	2.8	11.1	0.0		
	R20	21.8	91.4	922	3.1	5.5	17.0	2.2	0.4	2.3	0.0	0.5	84	153	24.9	13.8	0.0		
30–35	L30	30.3	64.8	575	30.5	4.7	10.0	24.4	10.8	0.9	0.0	1.9	215	371	16.6	11.1	0.0		
	P30	29.4	85.8	286	8.7	5.5	20.2	19.3	10.2	10.6	27.3	1.4	92	84	2.8	0.0	0.0		
	R30	33.3	86.7	455	9.4	3.9	30.0	10.5	1.1	22.9	0.0	1.1	170	106	16.6	16.6	0.0		
>140	LM	49.5	34.4	257	47.7	18.0	31.0	12.0	14.3	17.5	2.8	5.5	248	179	2.8	55.3	0.0		
	PM	52.8	26.6	233	61.7	11.7	21.8	23.3	16.3	21.8	0.0	6.5	218	246	11.1	52.5	0.0		
	RM	52.9	32.0	220	35.9	32.0	21.8	0.9	9.0	21.6	0.0	4.2	229	153	16.6	55.3	11.1		

**Table 2.** Population estimates of chipmunks.

Stand	Autumn			Spring		
	No. of individuals captured	Estimated no./ha	95% CI	No. of individuals captured	Estimated no./ha	95% CI
L10	26	5.3a	4.5–7.9	53	7.3a	6.5–9.2
P10	57	11.6b	10.5–14.2	84	13.7c	12.9–16.0
R10	99	22.9d	21.1–26.2	112	20.4e	18.7–23.2
L20	38	6.7ab	5.9–8.8	83	4.9a	4.6–7.8
P20	31	9.2ab	7.0–14.8	60	10.0b	9.0–12.1
R20*	0	0.0	—	1	0.3	—
L30	26	5.3a	4.7–8.0	47	7.1ab	6.5–9.0
P30	71	17.4c	15.6–20.8	86	15.1cd	14.0–18.2
R30	40	10.1b	8.6–13.8	58	11.4bc	9.9–14.4
LM	39	10.0b	8.6–12.9	53	7.8ab	7.3–9.7
PM	78	23.8cd	19.8–30.8	102	17.5de	16.1–20.1
RM	23	5.7ab	4.3–9.2	19	3.8a	3.0–7.9

NOTE: Density estimates followed by the same letter have overlapping 95% confidence intervals (CI). Comparisons are made within seasons only.

\*Density is based on the number of individuals captured divided by the area encompassed by the trapping grid.

**Table 3.** Sex ratios (number of males per effective area trapped/number of females per effective area trapped) for each stand.

Stand	Autumn	Spring
L10	2.08	3.68
P10	0.84	1.10
R10	0.64	0.96
L20	0.80	1.54
P20	3.03	2.18
R20	—	—
L30	0.94	0.95
P30	0.91	1.17
R30	1.03	1.75
LM	1.40	1.25
PM	0.73	1.28
RM	1.78	2.17

$t = 6.46$ ,  $df = 518$ ,  $P < 0.0001$ ) and spring (females,  $\bar{x} = 81.8$  g,  $n = 241$ ; males,  $\bar{x} = 75.2$  g,  $n = 456$ ;  $t = 14.00$ ,  $df = 695$ ,  $P < 0.0001$ ). Mean body mass of chipmunks significantly decreased between autumn and spring for both females ( $t = 4.50$ ,  $df = 485$ ,  $P < 0.0001$ ) and males ( $t = 14.02$ ,  $df = 728$ ,  $P < 0.0001$ ). Body mass did not differ significantly between mature stands and plantations for either sex during autumn or spring ( $P > 0.05$ ). Mean body mass of males in a stand was positively correlated with population density for autumn ( $r = 0.795$ ,  $n = 11$ ,  $P = 0.004$ ) but not for spring ( $P > 0.05$ ). Average body mass of females was not significantly correlated with population density for either season ( $P > 0.05$ ).

#### Distances moved

MMDM for the sexes combined averaged 48.2 m for autumn and 74.5 m for spring. During autumn, MMDM values for

males averaged 12.4 m greater than those for females (females,  $\bar{x} = 41.7$  m; males,  $\bar{x} = 54.1$  m;  $t = 2.79$ ,  $df = 9$ ,  $P = 0.02$ ). During spring, the difference between MMDM values for males and females within stands increased considerably, averaging 47.3 m ( $t = 13.46$ ,  $df = 9$ ,  $P < 0.0001$ ). Most of the increase was due to increases in MMDM for males during the spring. Mean MMDM for males was 98.3 m, representing an average within-stand increase of 44.2 m ( $t = 7.25$ ,  $df = 9$ ,  $P < 0.0001$ ). MMDM for females also significantly increased in the spring, but to a much smaller extent. The average spring MMDM for females was 51.0 m, representing an average within-stand increase of 9.3 m ( $t = 3.29$ ,  $df = 9$ ,  $P < 0.01$ ).

MMDM in mature stands was not significantly different from MMDM in young stands for either sex in either season ( $P > 0.05$ ). MMDM was significantly negatively correlated with population density for fall ( $P = 0.03$ ) but not for spring ( $P > 0.05$ ).

#### Sex ratio

Sex ratios (males to females) varied from 0.64 to 3.03 in autumn and 0.94 to 3.68 in spring (Table 3). The average sex ratio over all stands was 1.29 in autumn and 1.63 in spring. The seasonal change in sex ratio was not statistically significant ( $P > 0.05$ ).

Sex ratios for mature stands did not differ from those for young stands for either autumn or spring ( $P > 0.05$ ). Sex ratios were not significantly correlated with population density for either autumn or spring ( $P > 0.05$ ).

#### Discussion

The association of chipmunk density and percent cover of salal is consistent with previous observations that the abundance of Townsend's chipmunks is associated with the amount of ground cover. Tevis (1956) found that chipmunks in northwestern California were "partial to cover" and increased in number as brush and cover increased in an area.

Gashwiler (1970) found a general correlation between abundance of Townsend's chipmunks and amount of ground cover in the Oregon Cascade Range. In contrast, working in old-growth and second-growth stands in the Oregon Cascade Range, Rosenberg and Anthony (1993) did not find any significant relationship between chipmunk abundance and any measures of vegetation.

We propose three hypotheses, which are not mutually exclusive, to explain the observed relationship between chipmunk density and percent cover of salal. The first hypothesis is that chipmunk abundance is related to percent cover of salal because of the importance of salal fruit as forage. The fruit of salal is a food source for many species of small mammals (Martin et al. 1951). Sullivan et al. (1983) demonstrated that Townsend's chipmunk population densities are sometimes limited by food abundance. In their study, in areas supplemented with food, chipmunk population size increased 40–50%, mean body masses increased, and home-range lengths decreased in comparison with those of chipmunk populations in unsupplemented control areas. However, salal fruit is of short persistence and may not be present in sufficient quantity to influence chipmunk population density significantly. Thus, if food limits chipmunk populations in the Oregon Coast Range, some food source other than salal may be more important.

The second hypothesis is that chipmunk abundance is related to percent cover of salal because of the importance of salal as cover. Salal is a non-deciduous shrub that forms dense, continuous thickets up to 4 m tall in the Oregon Coast Range. These thickets impede or prohibit movements of many species of larger animals because of high stem density and interwoven stems. Chipmunks, however, can move rapidly through salal. Thus, salal thickets may provide chipmunks with refuge from many of their terrestrial and avian predators, including coyotes (*Canis latrans*), western spotted skunks (*Spilogale gracilis*), bobcats (*Lynx rufus*), raccoons (*Procyon lotor*), and Cooper's hawks (*Accipiter cooperi*). In the Oregon Coast Range, predation may limit chipmunk populations in stands with low densities of salal.

The third hypothesis is that chipmunk abundance is related to percent cover of salal because of some unmeasured habitat characteristic that is correlated with salal abundance. On our study sites, salal growth was favored by a noncontinuous overstory canopy with openings that allowed the development of salal and other understory vegetation. The relationship between chipmunk abundance and percent cover of salal may reflect stand characteristics that we did not measure, such as availability of other food sources (e.g., fungi), nest sites, or cover, which respond to stand characteristics that also favor high salal density.

Unlike results from the Oregon Cascade Range (Rosenberg and Anthony 1993) and southwestern Oregon (Carey 1991), we did not find that late seral-stage forests supported higher densities of Townsend's chipmunks than did younger stands. Indeed, some of the highest population densities we observed were in young plantations. The difference between our findings and those of Carey (1991) and Rosenberg and Anthony (1993) may be due to a number of factors. The mature stands in our study were considerably younger than the old-growth stands in the other studies. As a result of the fire and logging history of the Oregon Coast Range, old-growth stands with ages comparable to those found in the

Cascade Range and elsewhere are relatively rare. Nevertheless, pockets of old-growth trees are scattered throughout the Coast Range, and some were present in our mature forest sites. Perhaps if the stands we studied developed for an additional 200 to 300 years, chipmunk densities in those stands would exceed those of younger stands. However, we suspect that this would be unlikely; the population densities found in some of the plantations were extremely high, and may approach the maximum density of this species in the wild. Instead, our data suggest that in the Oregon Coast Range, the habitat structure that influences density of Townsend's chipmunks is not closely associated with stand age. Stands with patchy, noncontinuous canopies, which promote growth of salal and support high chipmunk densities in the Oregon Coast Range, are typical of many old-growth Douglas-fir forests (Franklin and Spies 1991). It may be this characteristic of old-growth stands that is at least partially responsible for the associations between Townsend's chipmunks and seral stage observed in other areas.

As noted by Van Horne (1983), animal density can be an inaccurate indicator of habitat quality in some cases. Comparisons of demographic parameters, such as MMDM and sex ratio, and measures of animal vigor, such as body mass, can provide valuable additional information for assessing habitat quality. In high-quality habitat, one might expect MMDM to be lower (because animals can extract necessary resources in a smaller home range), sex ratios to be less skewed toward males (because less of the population is composed of dispersing males), and mean body mass to be higher (because individuals have higher vigor) than in low-quality habitat. In the Oregon Cascade Range, Rosenberg and Anthony (1993) found that patterns of distances moved and sex ratios of chipmunks were consistent with expectations based on animal densities; old-growth stands had higher chipmunk densities, higher proportions of females in the populations, and lower MMDM values than did second-growth stands. Body mass, however, was similar in the two age-classes of forest despite differences in population densities. In our study, body mass, MMDM, and sex ratio did not differ significantly between mature and young forests in either autumn or spring. This finding is consistent with the hypothesis that habitat quality for chipmunks is not a function of stand age in the Oregon Coast Range.

Maximum population densities estimated in this study are the highest published values for Townsend's chipmunks. Carey (1991) reported mean densities of about 2.0/ha for autumn and 1.5/ha for spring in southwestern Oregon. Woods (1980) estimated that densities of Townsend's chipmunks may approach 5.0/ha in British Columbia. Previous studies conducted in the Oregon Cascade Range reported maximum densities of Townsend's chipmunks ranging from 10.6 to 12.0/ha (Gashwiler 1970; Hoooven and Black 1976; Rosenberg and Anthony 1993). Our point estimates of chipmunk densities exceeded previously reported maximum densities in 4 of the 12 stands, and were nearly double the previously reported maximum densities in two stands.

Direct, quantitative comparison of results between studies is problematic, as differences between studies may result from methodological differences. For example, grid sizes used by Carey (1991) and Rosenberg and Anthony (1993) were larger than ours, which could account for differences in estimated population densities among studies. However, it

is unlikely that the high population densities observed in our study are an artifact of methodology. Our effective trapping area would have to be twice as large as we estimated to account for the differences between population densities from our study and other studies. Rather, the high densities observed in some stands in our study are probably a function of the physical and biological characteristics of the area, including high rates of primary productivity and the structural characteristics of Coast Range forests. Minimal competition from other sciurids in the Oregon Coast Range may also contribute to high population densities of Townsend's chipmunks; the region has no other species of chipmunks and only one other forest-dwelling diurnal sciurid, the Douglas squirrel (*Tamiasciurus douglasii*). In addition, in contrast to the Cascade Range, relatively moderate winter temperatures and reduced snow cover in the Oregon Coast Range promote growth of non-deciduous understory vegetation, which may provide greater cover and increased survival of chipmunks.

The substantial increase in MMDM for males from autumn to spring reflects seasonal changes in home-range size. The seasonal increase may be due to males increasing home-range size in attempt to maximize encounters with females during the breeding season. MMDM for females also increased between autumn and spring, but the increase was only one-fifth that observed for males. Rosenberg and Anthony (1993) found that MMDM for males was greater than for females in spring, but did not observe a difference in MMDM for males and females in autumn. Resolution of the factors responsible for the observed seasonal changes in MMDM is beyond the scope of this study and warrants further investigation.

It should be noted that we conducted our fieldwork during a relatively short time period, autumn 1993 and spring 1994. It is conceivable that the results would differ if the study were conducted at other times. Specifically, during years when resources were more limiting, such as years with extremely harsh winters or periods of extreme drought, habitat associations may have differed from those we observed.

We conclude that in the Oregon Coast Range, Townsend's chipmunks are generalists with respect to stand age and seral stage. The structural characteristics of a forest stand are not closely associated with stand age in the Oregon Coast Range. We hypothesize that management activities which promote understory development, such as thinning densely stocked stands, would enhance chipmunk habitat in the Oregon Coast Range.

### Acknowledgements

Doug Bateman, Liz Dent, Steve Heibert, Kathleen Maas, Barbara Schrader, and Arne Skaugset provided assistance with various aspects of the study. Skye Etessami provided clerical support and generally helped to keep the project operational. Caryn Davis, Donald Smith, and an anonymous reviewer made helpful comments on an earlier draft of this paper. Financial support for this study was provided by the Coastal Oregon Productivity Enhancement (COPE) Program, College of Forestry, Oregon State University.

### References

- Anthony, R.G., Forsman, E.D., Green, G.A., Witmer, G., and Nelson, S.K. 1987. Small mammal populations

in riparian zones of different-aged coniferous forests. *Murrelet*, **68**: 94–102.

- Bonham, C.D. 1989. Measurements for terrestrial vegetation. John Wiley & Sons, New York.
- Burnham, K.P., and Overton, W.S. 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology*, **60**: 927–936.
- Carey, A.B. 1991. The biology of arboreal rodents in Douglas-fir forests. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. PNW-GTR-276.
- Carey, A.B., Biswell, B.L., and Witt, J.W. 1991. Methods for measuring populations of arboreal rodents. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. PNW-GTR-273.
- Doyle, A.T. 1990. Use of riparian and upland habitats by small mammals. *J. Mammal.* **71**: 14–23.
- Franklin, J.F., and Spies, T.A. 1991. Ecological definitions of Douglas-fir old-growth forests. *In* Wildlife and vegetation of unmanaged Douglas-fir forests. *Technical coordinators*: L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. PNW-GTR-285. pp. 61–69.
- Gashwiler, J.S. 1970. Plant and mammal changes on a clearcut in west-central Oregon. *Ecology*, **51**: 1018–1026.
- Hayes, J.P., Horvath, E.G., and Hounihan, P. 1994. Securing live traps to small-diameter trees for studies of arboreal mammals. *Northwest. Nat.* **75**: 31–33.
- Hooven, E.F., and Black, G.C. 1976. Effects of some clearcutting practices on small mammal populations in western Oregon. *Northwest Sci.* **50**: 189–208.
- Martin, A.C., Zim, H.S., and Nelson, A.L. 1951. American wildlife and plants: a guide to wildlife food habits. Dover Publications, Inc., New York.
- Maser, C. 1981. Land mammals. *In* Natural history of Oregon coast mammals. *Edited by* C. Maser, B.R. Mate, J.F. Franklin, and C.T. Dyrness. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. PNW-GTR-133. pp. 35–371.
- Maser, C., Trappe, J.M., and Nussbaum, R.A. 1978. Fungal – small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology*, **59**: 799–806.
- McIntire, P.W. 1984. Fungus consumption by the Siskiyou chipmunk within a variously treated forest. *Ecology*, **65**: 137–146.
- McIntire, P.W., and Carey, A.B. 1989. A microhistological technique for analysis of food habits of mycophagous rodents. U.S. Dep. Agric. For. Serv. Res. Pap. PNW-RP-404.
- Otis, D.L., Burnham, K.P., White, G.C., and Anderson, D.R. 1978. Statistical inference from capture data on closed animal populations. *Wildl. Monogr.* No. 62.
- Raphael, M.G. 1984. Wildlife populations in relation to stand age and area in Douglas-fir Forests of northwestern California. *In* Fish and Wildlife Relationships in Old-growth Forests: Proceedings of a Symposium, April 12–15, 1982, Juneau, Alaska. *Edited by* W.R. Meehan, T.R. Merrell, Jr., and T. Hanley. American Institute of Fishery Research Biologists, Morehead City, N.C. pp. 259–274.

- Rosenberg, D.K., and Anthony, R.G. 1993. Differences in Townsend's chipmunk populations between second- and old-growth forests in western Oregon. *J. Wildl. Manage.* **57**: 365–373.
- SAS Institute Inc. 1987. SAS/STAT guide for personal computers, version 6 ed. SAS Institute Inc., Cary, N.C.
- Sullivan, T.P., Sullivan, D.S., and Krebs, C.J. 1983. Demographic responses of a chipmunk (*Eutamias townsendii*) population with supplemental food. *J. Anim. Ecol.* **2**: 743–755.
- Tevis, L.L., Jr. 1956. Responses of small mammals to logging of Douglas-fir. *J. Mammal.* **37**: 189–196.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *J. Wildl. Manage.* **47**: 893–901.
- Woods, S.E., Jr. 1980. The squirrels of Canada. National Museums of Canada, Ottawa.
- Wilson, K.R., and Anderson, D.R. 1985. Evaluation of two density estimators of small mammal population size. *J. Mammal.* **66**: 13–21.