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DIFFERENCES IN TOWNSEND'S CHIPMUNK POPULATIONS BETWEEN SECOND- AND OLD-GROWTH FORESTS IN WESTERN OREGON

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Abstract: Because Townsend's chipmunks (*Tomias townsendii*) may be important in maintaining natural ecosystem processes in forests in the central Oregon Cascade Range, we compared their population characteristics in young second-growth and old-growth forests. We live-trapped Townsend's chipmunks in 5 young (30–60 yr old) second-growth and 5 old-growth (>400 yr old) Douglas-fir (*Pseudotsuga menziesii*) stands during spring and autumn 1987–90 in western Oregon. We tested the null hypothesis of no difference in characteristics of chipmunk populations in these 2 stand age-classes. Densities ranged from 0.4 to 10.3 chipmunks/ha and were greater ($P < 0.05$) in old-growth ($\bar{x} \pm$ SE, 5.1 ± 0.4) than in second-growth (2.8 ± 0.3) stands. Chipmunk densities were related to large (≥50 cm diam at breast height [dbh]) snags in old-growth ($P = 0.002$) but not in second-growth ($P = 0.6$) stands. Chipmunks in old-growth stands moved shorter ($P = 0.03$) distances in autumn and had a greater proportion of young-of-the-year ($P = 0.007$) than those in second-growth stands. These differences suggest that old-growth stands provide better habitat for Townsend's chipmunks than young second-growth stands, and may reflect important functional differences in food chains and energy flow between the different stand age-classes.

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Timber harvesting in the Pacific Northwest has changed much of the landscape from old-growth coniferous forests to young, second-growth forests; <13% of old-growth forests remains (Booth 1991). Short logging rotations (e.g., removal of timber at <80 yr) and even-aged management practices do not allow these forests to attain ecological characteristics of older forests. Old-growth forests provide unique habitat for a variety of wildlife species (Meslow et al. 1981, Ruggiero et al. 1991) and also may provide optimum habitat for species that are of particular ecological importance. For example, several species of small mammals are believed to be important dispersers of mycorrhizal fungi (Maser et al. 1978), and some of these species may attain greater densities in old than young forests (Corn and Bury 1991, Gilbert and Allwine 1991, West 1991). Previous investigators (Nelson 1989, Buchanan et al. 1990, Corn and Bury 1991, Gilbert and Allwine 1991, West 1991) compared wildlife populations in old-growth coniferous forests with those in naturally regenerated (i.e., after wildfire), unmanaged young stands (<80 yr old), but few have investigated populations in managed second-growth stands after canopy closure, despite the fact that these stands increasingly dominate forested landscapes in this region.

One of the most prevalent small mammal species in old-growth forests in the Pacific Northwest is Townsend's chipmunk. The abundance and population dynamics of Townsend's chipmunks may be important in maintaining natural ecosystem processes. In coniferous forests of the central Oregon Cascade Range, Townsend's chipmunks often compose the largest proportion of small-mammal biomass (Doyle 1990) and are prey for both mammalian and avian predators (Maser 1981:150, Reynolds and Meslow 1984, Toweill and Anthony 1988). In this paper, we report differences in demographic characteristics between Townsend's chipmunk populations in young second-growth and old-growth coniferous forests in the central Oregon Cascades.

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Table 1. Stand characteristics of second- and old-growth Douglas-fir stands used for trapping Townsend's chipmunks, Willamette National Forest, Oregon, 1988.

	Second-growth ($n = 5$)			Old-growth ($n = 5$)		
Characteristic	$\bar{x}$[a]	SE	Range	$\bar{x}$	SE	Range
Coarse woody debris[b]	71	8.3	50–98	86	10.4	58–118
Small snags[c]	61	27.5	16–167	24	5.5	11–38
Large snags[d]	7	4.6	1–26	17	3.1	10–25
Small conifer trees[c]	516	71.6	346–778	196	20.5	130–241
Large conifer trees[d]	10	4.0	1–25	66	6.2	54–85
Small deciduous trees[c]	70	24.8	6–132	15	4.9	2–31
Large deciduous trees[d]	1	0.3	0–2	0	0.2	0–1

[a] Computed from mean of subsamples ($n = 33$) within each stand.
[b] Debris ≥25 cm diameter; m^3/ha.
[c] 10–49 cm dbh; no./ha.
[d] ≥50 cm dbh; no./ha.

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STUDY AREA AND METHODS

Study Sites

We selected 5 second-growth (30–60 yr old) and 5 old-growth (>400 yr old) Douglas-fir (*Pseudotsuga menziesii*) stands on the western slope of the Cascade Range in the Blue River or McKenzie Ranger districts, Willamette National Forest, near the towns of Blue River and McKenzie Bridge, Lane County, Oregon. We selected stands based on their being dominated by Douglas-fir within the age-classes stated above, size large enough to accommodate a 13-ha grid with a 50-m buffer, and accessibility by road. Climate was characterized by mild, wet winters and warm, dry summers (Franklin and Dyrness 1973:38). Selected stands were between 375- and 900-m elevation, and slope ranged from 10 to 60% (Appendix). They were dominated by Douglas-fir and western hemlock (*Tsuga heterophylla*). Western redcedar (*Thuja plicata*) and incense cedar (*Libocedrus decurrens*) were common canopy species in old- and second-growth stands, respectively. The understory (2–4 m in height) was dominated by vine maple (*Acer circinatum*), Pacific dogwood (*Cornus nuttallii*), California hazel (*Corylus cornuta*), and western hemlock. The lower-understory (<2 m in height) included Oregon grape (*Berberis nervosa*), salal (*Gaultheria shallon*), sword fern (*Polystichum munitum*), *Vaccinium* spp., and Pacific rhododendron (*Rhododendron macrophyllum*). Herbaceous vegetation was diverse, but twin-flower (*Linnaea borealis*), Oregon oxalis (*Oxalis oregana*), and gold-thread (*Coptis laciniata*) were most common.

At least 3 of the 5 second-growth stands were planted after clear-cutting, 1 stand was naturally regenerated after an extensive wildfire in 1918 (Teensma 1987), and the fifth stand was regenerated after clear-cutting, but whether it was planted is unknown. Silvicultural treatments varied from intensive clear-cuttings with no residual large trees to those with some large trees retained (1.2 trees >79 cm dbh/ha). The 3 young stands that were regenerated after clear-cutting were broadcast-burned and planted with Douglas-fir seedlings (Appendix). The 5 old-growth stands were not previously logged, except for small areas where a few individual trees were salvaged; in all cases <5% basal area was removed. Vegetative characteristics were highly variable both within and between stand age-classes. Second-growth stands had greater densities of coniferous and deciduous trees and small-diameter (<50 cm dbh) snags than old-growth stands. Densities of large (>50 cm dbh) trees and large snags were greater in old- than second-growth stands, and in some second-growth stands these components were rare or absent (Table 1; Rosenberg and Anthony 1992).

Habitat Characteristics

We used nested, circular plots modified from Spies et al. (1988) to sample vegetation on the grids at every third trapping station; stations were spaced at 40-m intervals. Large ($\geq$50 cm diam) trees, snags, down-wood, and stumps (<1.5 m tall) were recorded in 0.12-ha (20-m radius) plots centered at the trap station. Smaller trees ($\geq$5–49 cm dbh), snags ($\geq$10–49 cm dbh), and fallen trees (down-wood, $\geq$25–49 cm diam) were measured in 0.05-ha (12.6-m radius) plots. We recorded the species and dbh for live trees and recorded the diameter and condition (percent limbs remaining) for snags ($\geq$1.5 m tall) and down-wood. Vegetation was measured from July through September 1988.

To facilitate habitat comparisons, we established categories of tree, snag, and down-wood size. Live trees were grouped into 5–10, >10–49, and $\geq$50-cm dbh classes, snags into 10–49 and $\geq$50-cm dbh classes and condition categories (soft with $\leq$2% limbs remaining, and hard with >2% limbs), and down-wood volume (m^3) was computed for 25–49 and $\geq$50-cm-diameter classes. We computed the coefficient of variation (CV) of tree diameters as a measure of tree-size diversity.

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

Population Characteristics

We established live-trapping grids in each stand. During autumn (Oct to early Dec), grids (approx 13 ha) consisted of 96–100 trap stations spaced 40 m apart. Grids varied from 10 × 10 to 16 × 6 arrays of trap stations, depending on the size and shape of each stand (Appendix). The grids that tended towards a rectangular shape were both in second-growth stands. A larger perimeter-to-area ratio in these grids could allow greater movement of animals from outside the grids to inside the grids (edge effect, White et al. 1982:120, Bondrup-Nielsen 1983), possibly inflating estimated densities. Tomahawk #201 live-traps (41 × 13 × 13 cm) were placed at each station. One trap was nailed approximately 1.5 m high on the largest tree within 5 m of the trap station; the second was placed on the ground within 2 m of this trap. During spring (Apr–Jun), grids (approx 3.2 ha) consisted of 100 trap stations spaced 20 m apart in a 10 × 10 array, and were placed within the autumn-season grids. One Sherman live-trap (7.6 × 7.6 × 25.4 cm) was placed at each station. Traps were baited with a mixture of peanut butter, whole oats, molasses, and high (>30%) protein pellets during autumn and with whole oats and peanut butter during spring. Animals were eartagged with #1 monel tags (Nat. Band and Tag Co., Newport, Ky.), or toeclipped for individual recognition. Body mass and sex were recorded at first capture for each season and year.

Chipmunks were trapped in autumn 1987–89 and in spring 1988–90. In autumn 1987, traps were set from October to early December on 2 grids (1 second- and 1 old-growth) simultaneously for 8 consecutive nights, with a different set of grids in each of 5 trapping sessions. In autumn 1988 and 1989, traps were operated from October to November on 5 grids simultaneously during 2 sessions for 10 and 21 days, respectively. New animals were marked for only the first 10 days of trapping. Consequently, all analyses except for those of movements are based only on data from the first 10 days of each trapping session. During spring for all 3 years, traps were set from April to June for 8 consecutive days on 2 grids (1 second- and 1 old-growth) simultaneously for 5 trapping sessions.

We estimated chipmunk densities on each grid for each season and year. Animals that died before the last trap day of each session were omitted from mark–recapture analyses but were added to population estimates (White et al. 1982). Program CAPTURE (Otis et al. 1978) was used to analyze mark–recapture data. Capture probabilities were most affected by heterogeneity (Otis et al. 1978:33), so the first-order jackknife estimator (Burnham and Overton 1979) was used to estimate population size ($\hat{N}$). We estimated the area effectively trapped ($\hat{A}$) by adding one-half of the mean maximum distance moved (MMDM) to the grid's perimeter (Wilson and Anderson 1985) for each grid with males and females combined. We estimated density as $\hat{D} = \hat{N}/\hat{A}$.

Statistical Analyses

We compared densities, *s*, MMDM, sex-ratios, and body mass between stand age-classes, seasons, sexes, and years when appropriate with a split-plot analysis of variance (Sokal and Rohlf 1981:394). A split-plot design was used because

Table 2. Number of Townsend's chipmunks captured and resultant density estimates (no./ha)[a] in second- and old-growth Douglas-fir stands, Willamette National Forest, Oregon, 1987–90.

	Second-growth ($n = 5$)				Old-growth ($n = 5$)			
	n[b]		Density		n		Density	
Year	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Autumn								
1987	28.8	12.6	2.3	1.0	65.8	15.5	4.7	1.1
1988	29.2	8.0	1.9	0.6	56.4	13.1	3.6	0.8
1989	47.2	10.5	2.5	0.5	91.4	11.8	5.3	0.8
All years	35.1	6.1	2.2	0.4	71.2	8.2	4.5	0.5
Spring								
1988	26.6	5.0	4.6	1.1	41.8	5.1	7.7	0.9
1989	15.0	3.5	1.9	0.7	25.2	3.2	4.8	0.5
1990	17.0	2.5	3.4	0.5	24.4	2.2	4.7	0.7
All years	19.5	2.4	3.3	0.5	30.5	2.9	5.7	0.5

[a] Numerator: population estimate derived from the first-order jackknife estimator (Burnham and Overton 1979). Denominator: grid area + area in a strip around the grid perimeter, with width = one-half mean-maximum-distance-moved (Wilson and Anderson 1985). Densities differed between stand age-classes in both autumn ($F_{1,8} = 6.5$, $P = 0.03$) and spring ($F_{1,8} = 7.7$, $P = 0.02$).

[b] Number of individual chipmunks captured.

the same stands were used in each year. Stand nested within stand age-class was used as the error term in all split-plot analyses, along with the interaction of year, season, and sex when these variables were included as factors. We analyzed density and MMDM for autumn and spring separately because different grid sizes and trap intervals were used, which may have influenced these estimates (Stickel 1954, White et al. 1982:120). Only stands in which we captured ≥2 chipmunks >1 time for a given sex and sampling period were included in analyses of movement data. We did not estimate chipmunk density on 1 grid (second-growth) in autumn 1987 because few chipmunks were captured and none were recaptured; these data were not included in our analyses. This stand tended to have the lowest densities during subsequent sampling periods. The relative stability of density through time was compared between stand age-classes and seasons (spring and autumn) by computing *s* (Connell and Sousa 1983, Ostfeld 1988), the standard deviation of the logarithms of each density estimate for each stand. Season was not a significant factor in this ANOVA model ($P = 0.9$), so we pooled seasons and completed the analysis with a 1-way split-plot ANOVA. We compared body mass for chipmunks ≥60 g. Minimum body mass of chipmunks that were known to be ≥1 year old from trap records was 61 g, so animals <60 g were considered young-of-the-year. Most young-of-the-year attain adult mass by autumn (Gashwiler 1976), so some individuals ≥60 g could have been young-of-the-year. The proportion of animals <60 g was compared between stand age-classes with Chi-square goodness-of-fit tests.

Relationships of chipmunk density to habitat characteristics were evaluated with linear regression analyses. We used the autumn 1989 density estimates rather than other sampling periods because (1) selection of trap stations to measure habitat characteristics was made within the autumn-season grids, and (2) we believed the density estimates in autumn 1989 were least affected by hibernation. We selected variables related ($P < 0.05$) to 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 differences in chipmunk density between second- and old-growth stands.

RESULTS

Population Characteristics

We captured 2,344 Townsend's chipmunks during 1987–90 and captured each individual an average of 3.6 times. Estimated densities (seasons pooled) ranged from 0.4 to 10.3/ha and were almost twice as high in old- ($\bar{x}$ ± SE, 5.1 ± 0.4) as in second-growth (2.8 ± 0.3) stands in both autumn ($F_{1,8} = 6.5$, $P = 0.03$) and spring ($F_{1,8} = 7.7$, $P = 0.02$; Table 2). Estimated densities often fluctuated within particular stands among years, although some stands were relatively stable. Temporal variability, *s*, ranged

Table 3. Mean maximum distance moved (MMDM)[a] (m) for Townsend's chipmunks captured in second- and old-growth Douglas-fir stands, Willamette National Forest, Oregon, 1987–90.

	Second-growth ($n = 5$)				Old-growth ($n = 5$)			
	Males		Females		Males		Females	
Year	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Autumn[b]								
1987	109.8[c]	20.8	76.3[c]	8.5	65.6	6.8	62.9	4.0
1988	81.4	11.4	86.2	7.9	73.7	9.1	82.0	6.1
1989	122.9	6.4	109.1	10.1	97.0	6.1	76.6	5.8
All years	104.3	8.5	91.6	6.1	78.8	5.3	73.8	3.6
Spring								
1988	96.4	9.8	72.3[c]	8.2	79.7	7.1	52.2	4.4
1989	122.2[c]	21.9	48.6[d]	2.9	83.5	5.1	50.4	1.8
1990	100.1	13.9	70.6	7.3	79.3	11.4	45.9	5.5
All years	102.2	8.1	64.7	5.1	80.8	4.5	49.5	2.3

[a] Computed from stand means.
[b] MMDM differed between stand age-classes in autumn ($F_{1,8} = 7.2$, $P = 0.03$).
[c] $n = 4$ stands.
[d] $n = 3$ stands.

from 0.01 to 0.42 and tended to be greater in second- (0.25 ± 0.05, $n = 9$) than in old-growth (0.15 ± 0.02, $n = 10$) stands ($F_{1,8} = 3.0$, $P = 0.12$). Densities were almost twice as high in spring 1988 as in spring 1989 and 1990 ($F_{2,16} = 12.1$, $P = 0.0006$), and in autumn tended to be lowest in 1988 ($F_{2,16} = 2.1$, $P = 0.15$; Table 2).

MMDM was greater in second- than in old-growth stands in autumn ($F_{1,8} = 7.2$, $P = 0.03$) but not in spring ($F_{1,8} = 0.6$, $P = 0.5$). This difference was more consistent for males than for females (Table 3). Males tended to have greater MMDM than females with significant differences during spring ($F_{1,24} = 7.5$, $P = 0.01$) but not during autumn ($F_{1,24} = 0.4$, $P = 0.5$). MMDM differed among years in autumn ($F_{2,16} = 9.7$, $P = 0.002$) but not in spring ($F_{2,16} = 1.9$, $P = 0.2$) despite the greater densities in spring 1988, which suggested that MMDM was not simply a function of density. MMDM was highest during autumn 1989, probably due to the greater number of trapping days and more recaptures.

Sex ratios of captured chipmunks were skewed in favor of males, particularly so in second-growth stands in spring (Table 4), although the pooled difference between stand age-classes was not significant ($F_{1,8} = 1.0$, $P = 0.3$). A greater proportion of males tended to be captured in spring than in autumn ($F_{1,16} = 2.6$, $P = 0.12$), and this relationship was most evident in second-growth stands ($F_{1,16} = 2.8$, $P = 0.11$; Table 4). Sex ratios varied among years ($F_{3,24} = 2.5$, $P = 0.08$); more than a 2-fold difference in sex ratio between stand age-classes was found in spring 1988 and 1989 (Table 4).

Body mass of chipmunks did not differ between second- and old-growth stands ($F_{1,8} = 0.3$, $P = 0.6$), years ($F_{3,24} = 1.1$, $P = 0.4$), or seasons ($F_{1,16} = 0.2$, $P = 0.6$), but differed between sexes ($F_{1,48} = 67.2$, $P = 0.0001$; Table 5). Females averaged about 5% heavier than males.

Few young-of-the-year were distinguishable from adults. Twenty-four chipmunks <60 g (range = 36–59 g) were captured, all during autumn, and most in 1989 ($n = 18$, 75%). More were captured in old- ($n = 22$) than second-growth ($n = 2$) stands ($\chi^2 = 7.3$, 1 df, $P = 0.007$).

Table 4. Sex ratios (males : females) of Townsend's chipmunk populations in second- and old-growth Douglas-fir stands, Willamette National Forest, Oregon, 1987–90.

	Second-growth ($n = 5$)			Old-growth ($n = 5$)		
	Sex ratio[a]			Sex ratio[a]		
Year	$\bar{x}$	SE	n[b]	$\bar{x}$	SE	n[b]
Autumn						
1987	1.2	0.2	130	1.2	0.2	309
1988	2.2	1.1	154	1.7	0.6	273
1989	1.4	0.3	23	1.2	0.1	452
Spring						
1988	2.9	0.4	120	1.3	0.1	197
1989	3.6	1.3	75	1.6	0.3	131
1990	3.8	1.3	85	3.4	0.7	122

[a] No differences ($P > 0.05$) occurred in sex ratios due to the main effect of stand age.
[b] Number of chipmunks.

Table 5. Body mass (g) of Townsend's chipmunks[a] in second- and old-growth Douglas-fir stands, Willamette National Forest, Oregon, 1987–90.

	Second-growth[b]						Old-growth[b]					
	Males			Females			Males			Females		
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
Autumn	77.2	0.4	294	79.2	0.6	220	76.4	0.3	545	80.6	0.4	463
Spring	77.6	0.4	193	84.4	1.0	80	76.6	0.4	281	83.3	0.7	150
Pooled	77.3	0.3	487	80.6	0.5	300	76.5	0.2	826	81.2	0.4	613

[a] Chipmunks believed to be young-of-the-year (i.e., <60 g, $n = 24$) were not included.

[b] No differences ($P > 0.05$) occurred in body mass due to the main effect of stand age.

Habitat Characteristics

Density of large snags (≥50 cm dbh) was the only habitat variable that was related ($P < 0.05$) to 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 explained most of the variability in the data set ($R^2 = 95.8$, $P < 0.001$, $n = 10$; Fig. 1). Stand age-class was significant in the model ($t = 5.8$, $P = 0.0004$). In old-growth stands, chipmunk densities were strongly and positively related to densities of large, hard snags ($R^2 = 0.96$, $n = 5$, $P = 0.002$); however, in second-growth stands, no relationship was observed with large snags ($R^2 = 0.12$, $n = 5$, $P = 0.6$) or with any other snag class.

DISCUSSION

The differences between chipmunk populations suggest that old-growth forests can support higher densities of Townsend's chipmunks than young second-growth forests due to higher quality habitat. These data contrast with the phenomenon described by Van Horne (1983) where density appeared to be a poor indicator of habitat quality. The demographic data support our interpretation. In old-growth stands, chipmunks moved shorter distances, and the proportion of females and young-of-the-year tended to be greater, whereas body mass was similar between stand age-classes.

Chipmunks occur at high densities in a wide range of forest types, such as early regeneration clear-cuttings (Tevis 1956, Anthony and Morrison 1985), mature (Hooven and Black 1976) and old-growth forests (Gashwiler 1959, this study), and riparian areas in second-growth coniferous forests (Anthony et al. 1987). This suggests that population size of chipmunks may not be limited directly by structural characteristics of their habitat. In our study, chipmunk density was related to density of large snags in old- but not in second-growth stands. The number of large snags in second-growth stands varied little, but chipmunk densities varied substantially among these stands.

Townsend's chipmunk populations may be limited by food supply rather than structural characteristics of their habitat. Experimental work supports this speculation. For example, characteristics of an experimentally fed population of Townsend's chipmunks tended to have higher densities, survival and growth rates, and smaller home-range size than unfed populations (Sullivan et al. 1983). Experimental work on eastern chipmunks (*Tamias striatus*) suggested that home-range size was a function of food supply rather than density (Mares et al. 1982), despite the expected negative correlation of home-range size with density (Lacki et al. 1984). Home-range size is considered a measure of the productivity of the habitat (Lindstedt et al. 1986), so the difference in movement patterns that we observed between stand types may be related to differences in food availability.

The potential importance of Townsend's chipmunks in the forest ecosystem results from their broad diet (Tevis 1952, 1953; Gunther et al. 1983), which includes the fruiting bodies (sporocarps) of mycorrhizal fungi that form symbiotic relationships with many plant species. Townsend's chipmunks may be important dispersers of these fungi (Maser et al. 1978). Townsend's chipmunks also are prey of numerous species of mammalian and avian predators (Maser 1981) and are a major component in the diet of some species in western Oregon (e.g., Cooper's hawk [*Accipiter cooperii*], Reynolds and Meslow 1984).

MANAGEMENT AND RESEARCH IMPLICATIONS

Our results suggest that Townsend's chipmunks, usually considered a generalist species

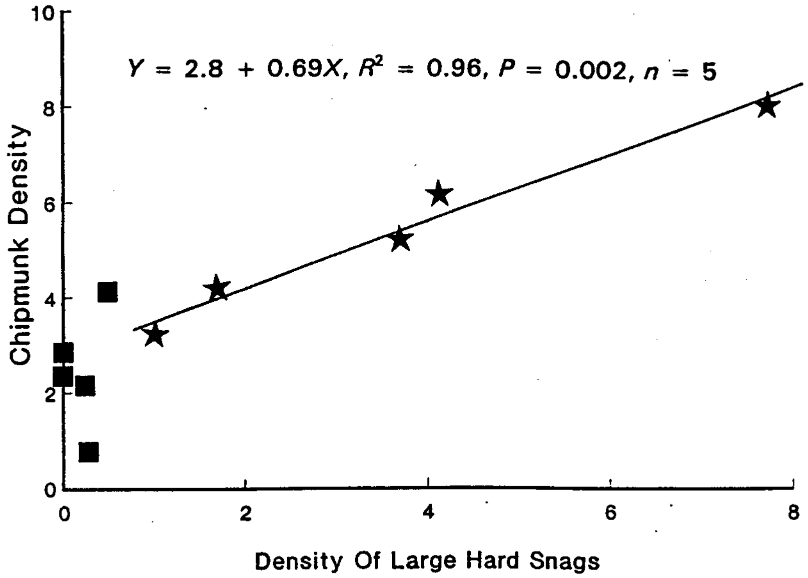

Fig. 1. Relationship of densities (no./ha) of chipmunks to large (≥50 cm dbh) hard snags (snags with >2% limbs remaining), Willamette National Forest, Oregon, autumn 1989. Each point (■ = second-growth, ★ = old-growth) represents the densities in a stand ($n = 10$). The regression line includes only data from old-growth stands; there was no relationship ($P = 0.6$) within second-growth stands.

(Maser 1981) that is abundant in many forest types, may be considerably reduced in numbers by forest management practices that harvest stands in relatively early seral stages (30–60 yr). Although the stands we sampled were young second-growth stands, most still had residual components of old-growth, such as large sizes of woody debris, snags, and trees (Rosenberg and Anthony 1992). Without this additional structure in intensively managed stands, the differences we found between chipmunk populations in second-growth and old-growth forests may be even more pronounced. The relationship of chipmunk densities to densities of large snags warrants further investigation. Rather than directly affecting chipmunk density, large snags may be related to other attributes of the forest affecting chipmunks.

Because Townsend's chipmunks represent a high proportion of the biomass of the small-mammal community in coniferous forests, they are probably important to food chains and energy flow. The potentially high number of carnivore species in old-growth Douglas-fir forests was speculated by Harris and Maser (1984:50) to result from the complex food chains that occur in these forests. Because of their broad diet and their high densities, chipmunks may provide important, functional roles in coniferous forests. Supplemental feeding of chipmunk populations could be done to test the hypothesis that food abundance limits population size of chipmunks in young second-growth stands. The actual roles they play in natural and managed forests will require further investigation.

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Appendix. Stand and silvicultural characteristics of trapping sites for Townsend's chipmunks, Willamette National Forest, Oregon, 1988.

Stand[a]	Size (ha)	Age (yr)	Elevation (m)	Aspect	Slope (%)	Stand history
1107-86	55	60	900	NW	35	WF[b], RIC[c]
1303-33	28	30	600	E	25	SPC[d], SFL[e], REF[f], FBR[g], HCC[h]
7115-16	59	30	800	S	25	SFL, SPC, REF, FBR, HCC
7115-31	52	40	500	SW	10	SFL, REF, FBR, HCC
7115-83	36	40	450	S	20	RIC
1109-43	97	>400	850	N	55	NPC[i]
1109-84	82	>400	500	NW	60	NPC
1110-90	48	>400	800	SW	20	NPC
1111-44	110	>400	900	SW	40	NPC
7116-08	23	>400	375	NW	20	SC[j]

[a] Numbers represent USDA Forest Service compartment number followed by stand number (last 2 digits).
[b] Stand originated from wildfire.
[c] Forest Service records incomplete.
[d] Precommercial thinning.
[e] Fertilization.
[f] Reforestation by planting.
[g] Broadcast or spot burn.
[h] Harvest clear-cut.
[i] No previous cutting; small amounts of salvage cutting may have occurred.
[j] Selective cutting; not extensive.