Response of northwestern chipmunks (*Tamias amoenus*) to variable habitat structure in young lodgepole pine forest

Thomas P. Sullivan and Walt Klenner

Abstract: This study was designed to test the hypothesis that large-scale habitat alteration by stand thinning over a range of densities would increase the abundance and related population dynamics of northwestern chipmunks (*Tamias amoenus*) in young lodgepole pine (*Pinus contorta*) forest. Replicate study areas were located near Penticton, Kamloops, and Prince George in south-central British Columbia, Canada. Each study area had three stands thinned to densities of ≈500 (low), 1000 (medium), and 2000 (high) stems/ha, with an unthinned young pine stand and an old-growth pine stand for comparison. Chipmunk populations were sampled intensively in thinned stands from 1989 to 1991 and in the unthinned and old-growth stands from 1990 to 1991. Habitat structure was sampled in all stands in 1990. For herbs and shrubs, the crown volume index values were similar among stands; for trees, this index was lowest for the low-density stands, with the index for all three thinned stands being lower than that for the unthinned stands. Species diversity and the structural diversity of vegetation were similar among stands. The abundance of chipmunks was significantly higher in low-density than in high-density thinned stands at Penticton (1.3–1.9 times higher) and Prince George (2.4–3.8 times higher) but not at Kamloops. Chipmunks were less abundant in old-growth stands than in the other four treatment stands. Breeding performance and recruitment followed the same pattern as abundance. Chipmunk survival was generally similar among stands. There were heavier chipmunks in the low-density stands in some years at Penticton. Northwestern chipmunks appear to prefer "open" habitats generated by heavy thinning of young lodgepole pine stands. This result was achieved in three different forest ecological zones and may enhance the overall forest ecosystem.

Résumé : Cette étude a été entreprise dans le but d'éprouver l'hypothèse selon laquelle une modification à grande échelle de l'habitat par éclaircissement des boisés jusqu'à des densités données pourrait augmenter l'abondance et les variables de la dynamique de la population chez le Tamia amène (*Tamias amoenus*) dans une jeune forêt de pins vrillés (*Pinus contorta*). Les stations où nous avons procédé à des tests répétés étaient situées près de Penticton, de Kamloops et de Prince George dans le centre sud de la Colombie-Britannique, Canada. À chaque site, nous avons procédé à une coupe jusqu'à des densités approximatives de ≈500 (faible), 1000 (moyenne) et 2000 (élevée) pins/ha; une jeune forêt et une vieille forêt intactes ont servi de témoins. Les populations de tamias ont été échantillonnées intensément de 1989 à 1991 dans les forêts clairsemées et en 1990 et 1991 dans les forêts témoins. La structure de l'habitat a été examinée à chaque site en 1990. Le coefficient du volume de la couronne des arbustes et des herbes était semblable dans tous les boisés, mais celui des arbres était minimum dans le boisé de faible densité et plus faible dans les trois boisés soumis à la coupe que dans les boisés intacts. La diversité des espèces et la diversité structurale de la végétation étaient semblables dans tous les boisés. L'abondance des tamias était significativement plus élevée (1,3–1,9 fois à Penticton et 2,4–3,8 fois à Prince George) dans les boisés coupés à haute densité, sauf à Kamloops. Les tamias étaient moins abondants dans les vieux boisés que dans les quatre autres boisés traités. La performance reproductrice et le recrutement suivaient le même pattern. La survie des tamias était généralement la même partout. Certaines années, nous avons trouvé des tamias plus lourds dans les boisés de faible densité à Penticton. Les Tamias amènes semblent préférer les habitats ouverts créés par une importante coupe au sein des jeunes forêts de pin vrillés. Ce résultat a été obtenu en trois zones écologiques forestières différentes et pourrait éventuellement mener à une amélioration générale de l'écosystème forestier.

[Traduit par la Rédaction]

Received May 10, 1999. Accepted September 15, 1999.

T.P. Sullivan.[1] Applied Mammal Research Institute, 11010 Mitchell Avenue, R.R. 3, Site 46, Compartment 18, Summerland, BC V0H 1Z0, Canada.
W. Klenner. Ministry of Forests, 515 Columbia Street, Kamloops, BC V2C 2T7, Canada.

[1] Author to whom all correspondence should be addressed (e-mail: sullivan@telus.net).

Can. J. Zool. **78**: 283–293 (2000)

© 2000 NRC Canada

Introduction

The northwestern or yellow-pine chipmunk (*Tamias amoenus*) is distributed throughout inland areas of the Pacific Northwest of North America (Banfield 1974; Sutton 1992). This sciurid usually occupies shrub-covered habitats associated with coniferous forests, particularly those areas with fruit- and seed-producing shrubs and trees. The northwestern chipmunk occurs within the range of lodgepole pine (*Pinus contorta*), a major tree and timber species covering much of the interior areas of the Pacific Northwest. Chipmunks are important prey species for a variety of avian and terrestrial predators and help disperse mycorrhizal fungal spores in forest ecosystems (Craighead and Craighead 1956; Maser et al. 1978; Maser 1981; McIntire 1984).

In terms of the influence of forest structure on their population dynamics, the habitat associations of the northwestern chipmunk are poorly known. Townsend's chipmunk (*Tamias townsendii*) appeared to be more abundant (1.7–2.0 times) in old forests than in young managed forests in studies in Washington, Oregon, and California (Raphael 1984; Carey 1991; West 1991; Rosenberg and Anthony 1993). Conversely, Anthony et al. (1987) reported Townsend's chipmunks to be 2–5 times more abundant in young than in older stands in riparian zones. Similarly, Hayes et al. (1995) concluded that *T. townsendii* was a generalist with respect to the stand age and seral stage of coastal forests in Oregon. Forest-stand structure appeared to play a major role in determining habitat quality for this species (Carey 1995; Hayes et al. 1995).

Rosenberg and Anthony (1993) suggest that generalist species of chipmunks (such as *T. amoenus*), which are usually abundant in many forest types, may be considerably reduced in numbers in managed second-growth forests. This prediction is based on the supposition that managed stands are structurally simple compared with natural stands. In this regard, Hayes et al. (1995) hypothesized that silvicultural activities that promote development of understory vegetation, such as the thinning of densely stocked stands, should enhance habitat structure for chipmunks.

There is a dearth of studies using experimental manipulations to measure the responses of chipmunks (and other small mammals) to alteration of habitat structure in young managed forests. Thus, the ambiguity in the results of studies to date is, perhaps, not surprising. This study was designed to test the hypothesis that large-scale habitat alteration, by stand thinning over a range of densities, would increase the abundance and related population parameters of northwestern chipmunks in young lodgepole pine forest compared with unthinned and old-growth pine forests.

Materials and methods

Study areas

All study areas were selected on the basis of having several thousand hectares of young lodgepole pine stands. Candidate stands within each of the three study areas had relatively uniform tree cover and comparable diameter, height, and density of lodgepole pine trees prior to stand thinning. The location, proximity (boundaries), and size (19–39 ha) of candidate stands were determined on the basis of a balance between adequate interspersion of experimental units (Hurlbert 1984) and operational feasibility in terms of road access and logistics for crews to conduct the thinning.

The Penticton Creek study area was located in south-central British Columbia, Canada, 15 km northeast of Penticton (49°34′N, 119°27′W). This region is within the Interior Douglas-fir ($\mathrm{IDF_{dk}}$) biogeoclimatic zone (Meidinger and Pojar 1991). Topography in the area is hilly, with a southeast aspect and an average slope of 10%; the soil is a sandy loam, and the elevation is 1340–1500 m asl. The climate is characterized by warm dry summers and cool winters. The average temperature is below 0°C for 2–5 months and above 10°C for 3–5 months and the mean annual precipitation ranges from 30 to 75 cm. Open to closed mature forests of Douglas-fir (*Pseudotsuga menziesii*) cover much of this zone, with even-aged postfire lodgepole pine stands at higher elevations. This area (several thousand hectares) was burned by wildfire in 1970, salvage-logged in 1971, and planted with lodgepole pine in 1972. Natural regeneration increased the density of pine to a range of 18 500 – 30 000 stems/ha. Minor components of the stands included Douglas-fir, Engelmann spruce (*Picea engelmannii*), western larch (*Larix occidentalis*), willow (*Salix* spp.), Sitka alder (*Alnus sinuata*), and trembling aspen (*Populus tremuloides*).

Precommercial thinning was conducted in 1978, leaving ca. 1000–2000 stems/ha. Additional ingress of pine during the 10-year post-thinning period (up to 1988) resulted in the need to conduct further thinning. In 1988, dbh (diameter at breast height, 1.3 m above the soil surface) ranged from 8.0 ± 0.2 (mean ± 1 SE) to 8.5 ± 0.1 cm and mean age was 17 years. Height within stands ranged from 5.1 ± 0.1 to 5.8 ± 0.1 m (Table 1). Stands were 0.2–0.5 km apart.

The Kamloops study area was located 30 km south of Kamloops, British Columbia (50°28′N, 120°32′W), within the Montane Spruce ($\mathrm{MS_{dm}}$) biogeoclimatic zone (Meidinger and Pojar 1991). Engelmann and hybrid spruce (*Picea engelmannii* × *Picea glauca*) and various amounts of subalpine fir (*Abies lasiocarpa*) are the characteristic tree species. Owing to past wildfires, successional forests of lodgepole pine, Douglas-fir, and trembling aspen are common. This zone has a cool continental climate characterized by cold winters and moderately short warm summers. The mean temperature is below 0°C for 5 months and above 10°C for 2–4 months and the mean annual precipitation ranges from 38 to 90 cm. The topography is hilly, with northerly aspects, and the elevation is 1400–1500 m asl. This area (~15 000 ha) was burned by wildfire in 1960 and regenerated naturally with lodgepole pine to a mean density of 20 000 stems/ha. Minor components of the stands included Engelmann spruce, subalpine fir, willow, Sitka alder, and trembling aspen.

Precommercial thinning was conducted from 1975 to 1978, leaving 1100–1600 stems/ha over ~200 ha. However, additional ingress of pine up to 1989 suggested that further thinning was warranted. In 1989, the mean diameter and height within stands ranged from 8.6 ± 0.1 to 11.6 ± 0.2 cm and from 8.2 ± 0.1 to 8.6 ± 0.1 m, respectively (Table 1). The area of stands ranged from 15.3 to 21.5 ha. These stands were 0.5–5.0 km apart.

The Prince George study area was located 60 km west of Prince George, British Columbia (53°52′N, 123°32′W), in the Sub-boreal Spruce ($\mathrm{SBS_{dw}}$) biogeoclimatic zone (Meidinger and Pojar 1991). The general topography is gently rolling, with variable aspects, and the elevation is 800 m asl. In mature stands, hybrid Engelmann × white spruce (*Picea glauca*) and subalpine fir are mixed with extensive stands of lodgepole pine, which regenerated after wildfires. Stands of young lodgepole pine covered ~1000 ha. This area was harvested during 1966–1972 and left to regenerate naturally with pine. Stand densities ranged from 2700 to 4700 stems/ha. Minor components of the stands included white spruce, black spruce (*Picea mariana*), Douglas-fir, willow, alder, and aspen. In 1988, the mean diameter and height within stands ranged from 8.8 ± 0.3 to 11.1 ± 0.2 cm and from 7.0 ± 0.2 to 8.8 ± 0.2 m, respectively. The age of the trees ranged from 15 to 20 years (Table 1). Stand

Table 1. Characteristics of lodgepole pine stands at the Penticton, Kamloops, and Prince George study areas, British Columbia.

							Old growth characteristics			
							Relative abundance			
Study area	Stand[a]	Area (ha)	Density (no. of stems/ha)	Mean age (years)	dbh (cm) 1988[b]	Height (m) 1988[b]	Species	%	Understory dbh ≤15 cm	Overstory dbh >15 cm
Penticton	A	20	480	17	8.0±0.2	5.1±0.1	Lodgepole pine	61.0	12.2±0.3	19.8±0.5
	B	20	1170	17	8.5±0.1	5.6±0.1	Spruce	21.0	11.5±0.7	27.9±0.6
	C	20	1490	17	8.4±0.1	5.8±0.1	Subalpine fir	17.0	12.9±0.5	20.6±0.8
	D	100+	5000	17	—	—				
	E	1000+	2170	160–250	—	—				
Kamloops	A	22	500	24	11.6±0.2	8.2±0.1	Lodgepole pine	12.5	11.8±2.8	26.1±0.5
	B	15	900	23	11.6±0.2	8.6±0.1	Spruce	12.5	11.1±0.9	27.4±2.1
	C	15	1614	23	8.6±0.1	8.4±0.2	Subalpine fir	75.0	10.2±0.3	22.2±0.6
	D	100+	6000	27	—	—				
	E	1000+	1860	160–250	—	—				
Prince George	A	39	460	20	11.1±0.2	8.8±0.2	Lodgepole pine	53.5	11.8±0.5	24.1±0.8
	B	32	944	19	11.0±0.3	8.5±0.2	Spruce	46.5	10.4±0.3	23.9±1.2
	C	30	1900	15–20	8.8±0.3	7.0±0.2	Subalpine fir	0.0		
	D	41	4700	20	—	—				
	E	1000+	1980	160–250	—	—				

Note: Values for dbh, height, understory dbh, and overstory dbh are given as the mean ± 1 SE.

[a] Stand designation: A, low density, 500 stems/ha; B, medium density, 1000 stems/ha; C, high density, 2000 stems/ha; D, unthinned, >2000 stems/ha; E, old growth.

[b] Values given for the Kamloops study area are for 1989.

area ranged from 30.3 to 38.5 ha. These stands were 0.5–1.7 km apart.

Experimental design

The usual prescription (>90% of stands) for precommercial thinning of lodgepole pine in British Columbia is 1600–2000 stems/ha after thinning; variations from this range tend to be higher rather than lower, based on local site conditions and silvicultural programs. Thus, we included stands of low, medium, and high density in our experimental design. In addition, unthinned young and old-growth lodgepole pine stands were included at each study area in the following design: stand A, low density, target 500 stems/ha; stand B, medium density, target 1000 stems/ha; stand C, high density, target 2000 stems/ha; stand D, unthinned, >2000 stems/ha; stand E, old growth. This range of stand densities, after thinning, was considered large enough to allow detection of changes in the habitat structure and population dynamics of northwestern chipmunks. Treatments were assigned to stands in a randomized block design. Each of the three study areas was considered a regional replicate (block).

Operational thinning was conducted after the growing season in the fall of 1988 at the Penticton and Prince George study areas and after the growing season in the fall of 1989 at the Kamloops study area. The unthinned and old-growth stands (Table 1) were added to the design at each study area in 1990, primarily to compare stand-structure attributes and chipmunk populations between thinned and unthinned stands of young pine and old-growth pine. Densities of pine in the unthinned stands were 5000 and 4700 stems/ha at Penticton and Prince George, respectively, in 1988 and 6000 stems/ha at Kamloops in 1989.

Habitat structure

Three 25-m transects, consisting of five 5 × 5 m plots, were randomly located in each of the five stands at each of the study areas. Each plot contained three sizes of nested subplots: the 5 × 5 m plot for sampling trees, a 3 × 3 m subplot for sampling shrubs, and a 1 × 1 m subplot for sampling herbaceous species. Tree, shrub, and herb layers were subdivided into height classes: 0–0.25, 0.25–0.5, 0.5–1.0, 1.0–2.0, 2.0–3.0, and 3.0–5.0 m (Walmsley et al. 1980). A visual estimate of percent cover of the ground was made for each species – height class combination within the appropriate nested subplot. The total percent cover for each layer was also estimated for each subplot. These data were then used to calculate a crown volume index (m^3/0.01 ha) for each plant species (Stickney 1980, 1985). The product of percent cover and representative height gives the volume of a cylindroid that represents the space occupied by the plant in the community. Crown volume index values were then averaged by species for each plot size and converted to a 0.01-ha base, to produce the values given for each species and layer (mosses, herbs, shrubs, and trees). Sampling was done in July–August 1990. Plant species were identified in accordance with Hitchcock and Cronquist (1973). Grasses were not identified to species. Species richness, species diversity, and structural diversity (foliage height diversity; MacArthur and MacArthur 1961) were calculated for these stand-structure data.

Chipmunk populations

Chipmunk populations were sampled on a 9-ha livetrapping grid located in each of the five (A, B, C, D, E) stands at each study area. Each grid had either 96 (6 × 16) or 100 (10 × 10) stations at 30-m intervals, with one Tomahawk live trap (Model 201, Tomahawk Live Trap Company, Tomahawk, Wis.) located permanently at every other station, resulting in ~5 traps/ha. Traps were baited with sunflower seeds (10 g); they were set shortly after dawn and checked 4–6 h later on 2 consecutive days in a given trapping period. Traps were closed and left permanently in the field between trapping periods. Livetrapping was conducted every 2 weeks from May to August 1989, 1990, and 1991 at Penticton and Prince George and from May to August 1990 and 1991 at Kamloops.

All chipmunks captured were ear-tagged with individually numbered tags; breeding condition was noted, as indicated by the size of testes in males and mammaries in females (Krebs et al. 1969). Animals were weighed with Pesola spring balances, and the point of capture was recorded. Animals captured for the first time on a

© 2000 NRC Canada

Table 2. Mean (n = 3) values for stand-structure attributes for the five treatment stands in 1990.

	Stand					Analysis	
Parameter	A	B	C	D	E	$F_{[4,8]}$	P
Crown volume index (m^3/0.01 ha)							
Herbs	7.10	10.59	8.14	5.44	4.82	1.42	0.33
Shrubs	27.68	17.74	32.65	44.92	15.52	1.62	0.26
Trees	36.66*a*	73.26*ab*	80.13*ab*	133.18*c*	95.93*bc*	5.07	0.02
Mosses	1.90*a*	2.55*a*	2.66*a*	3.84*a*	11.73*b*	5.34	0.02
Species richness							
Herbs	9.33	9.44	10.44	7.11	8.00	0.69	0.63
Shrubs	8.11	7.78	7.22	7.22	6.55	0.86	0.53
Trees	2.78	3.00	2.33	3.11	2.22	0.63	0.66
Total	31.00	28.33	29.67	25.67	27.00	0.45	>0.75
Species diversity							
Herbs	2.00	1.98	2.26	1.63	1.83	0.80	0.57
Shrubs	2.05	1.98	1.72	1.50	1.62	0.19	>0.75
Trees	0.42	0.56	0.22	0.37	0.66	0.67	0.64
Total	2.86	2.38	2.02	1.84	2.15	2.28	0.17
Structural richness							
Herbs	2.89	2.67	2.78	2.55	2.00	0.91	0.50
Shrubs	4.33*ab*	4.33*ab*	4.78*a*	5.11*a*	3.78*b*	3.73	0.06
Trees	4.55	4.56	3.44	4.11	5.56	1.98	0.21
Total	5.67	5.45	5.67	5.78	6.00	1.04	0.46
Structural diversity							
Herbs	1.28	0.93	1.21	1.13	0.63	1.39	0.34
Shrubs	1.89	1.75	1.79	1.79	1.48	0.93	0.49
Trees	0.63	0.40	0.15	0.70	0.59	0.84	0.54
Total	2.03	1.52	1.58	1.29	1.26	1.71	0.24

Note: Stand designations are as follows: A, low density, 500 stems/ha; B, medium density, 1000 stems/ha; C, high density, 2000 stems/ha; D, unthinned, >2000 stems/ha; E, old growth. Diversity measurements are represented by the Shannon–Wiener function. Within a parameter, mean values followed by different letters are significantly different according to Duncan's multiple-range test.

grid were called recruits. All handling of animals was in accordance with the principles of The University of British Columbia Animal Care Committee.

Demographic parameters

To assess the effects of variable habitat structure on population dynamics, we measured trappability, population density, number of successful pregnancies, recruitment, survival, and body mass of chipmunks in each of the stands. Jolly trappability was calculated according to the trappability estimate discussed by Krebs and Boonstra (1984). Population density was estimated using the Jolly–Seber mark–recapture estimate of population size (Seber 1982). For reproduction, a pregnancy was considered successful if a female chipmunk was lactating during the period following the estimated time of birth of a litter (Sullivan 1990). Mean survival for the May–August (summer) period and September–April (winter) period each year was estimated using the Jolly–Seber model. Mean body mass was calculated for males and females for each year and was used as an index of condition within chipmunk populations.

Statistical analysis

The randomized block design incorporated both spatial and temporal replication. Therefore, a randomized block ANOVA (Zar 1984), which assumes no interaction between the blocks and the levels of treatment, was conducted to test differences in mean crown volume index of herbs, shrubs, and trees and mean species richness and diversity of these layers. Mean structural diversity of the herb, shrub, and tree layers was also compared using this ANOVA model.

The mean number of chipmunks, the number of successful pregnancies, and the number of recruits were compared among treatments with this same model. An initial ANOVA compared parameters among the three stand densities in 1989–1991. A second ANOVA compared these same parameters among all five treatment stands in 1990–1991. For these analyses, a single estimate of the given parameter for each year and treatment was derived, to use the variability among years and blocks to test for differences among levels of the treatment. We also calculated the mean number of chipmunks and its 95% confidence limits for each summer in each stand. Mean Jolly–Seber survival rates and 95% confidence limits were calculated for all male and female chipmunks in each population for summer and winter periods. Mean body mass and 95% confidence limits were calculated for all male and female chipmunks in each population for summer periods. Duncan's multiple-range test (DMRT) was used to compare mean values. In all analyses, the level of significance was at least $P = 0.05$.

Results

Habitat structure

The mean total crown volume index values of herbs and shrubs were similar among treatment stands (Table 2). Prominent herbaceous species in these stands included several species of grasses, fireweed (*Epilobium angustifolium*), wild strawberry (*Fragaria virginiana*), Arctic lupine (*Lupinus arcticus*), white-flowered hawkweed (*Hieracium albiflorum*), one-sided wintergreen (*Orthilia secunda*), bunchberry (*Cornus* *canadensis*), heart-leaved arnica (*Arnica cordifolia*), showy aster (*Aster conspicuus*), yarrow (*Achillea millefolium*), and cow-wheat (*Melampyrum lineare*). Common shrubs included Sitka alder (*Alnus sinuata*), twinflower (*Linnaea borealis*), willow (*Salix* sp.), prickly rose (*Rosa acicularis*), black twinberry (*Lonicera involucrata*), and various species of *Vaccinium*. The mean total crown volume index of trees was significantly different ($F_{[4,8]}$ = 5.07, P = 0.02) among treatments. All three thinned stands had significantly lower (DMRT, P = 0.05) crown volume index values of trees than the unthinned stands (Table 2). Prominent tree species found in addition to lodgepole pine included interior spruce, subalpine fir, and trembling aspen. The mean total crown volume index of mosses was also significantly different ($F_{[4,8]}$ = 5.34, P = 0.02) among stands. The volumes of mosses among the four young stands of pine were similar and significantly less (DMRT, P = 0.05) than those in the old-growth stands (Table 2).

The mean total richness of plant species was similar among treatment stands, ranging from 25.67 in the unthinned stands to 31.00 in the low-density stands. Mean species richness and diversity of herbs, shrubs, and trees also followed this pattern (Table 2). The mean structural diversity, in terms of richness of the vegetation layers, was similar among treatment stands for herbs, trees, and total vegetation, but approached significance ($F_{[4,8]}$ = 3.73, P = 0.06) across stands for shrubs (Table 2). The structural richness of shrubs was similar in the four stands of young lodgepole pine, but this parameter was significantly higher (DMRT, P = 0.05) in the high-density and unthinned stands than in the old-growth stands. Structural diversity based on the Shannon–Wiener index indicated no difference among treatment stands for any of the vegetation components (Table 2).

Chipmunk populations

Estimates of trappability averaged 53.6–79.2% (low density), 41.6–73.5% (medium density), and 43.3–79.0% (high density) at Penticton; 37.8–60.3% (low density), 54.8–66.4% (medium density), and 45.9–68.4% (high density) at Kamloops; and 56.4–61.8% (low density), 79.8–84.8% (medium density), and 50.0–68.5% (high density) at Prince George (Table 3). The trappability of chipmunks in the unthinned stands ranged from 56.2 to 89.6% at Penticton, from 49.0 to 70.4% at Kamloops, and from 75.0 to 80.1% at Prince George; in the old-growth stands, these values ranged from 68.0 to 94.2% at Penticton, from 44.1 to 71.9% at Kamloops, and from 18.8 to 68.8% at Prince George. Since these trappability estimates were often less than 70%, density estimates based on the minimum number of animals alive (Krebs 1966) would likely be low (Hilborn et al. 1976). Therefore, for reasons outlined in Jolly and Dickson (1983), Jolly–Seber population estimates (Seber 1982) were used for this study.

The abundance of chipmunks was significantly different ($F_{[2,14]}$ = 4.90, P = 0.02) among the three stand densities (Fig. 1, Table 4). There were significantly more (DMRT, P = 0.05) chipmunks in low- than in high-density stands, with no difference between the medium- and either the low- or high-density stands. This pattern was particularly evident at Penticton and Prince George, where there were 1.3–1.9 and 2.4–3.8 times as many chipmunks in low- than in high-density stands, respectively. When compared, the numbers of

Table 3. Jolly trappability (%) estimates (mean values, with 95% confidence limits in parentheses) for northwestern chipmunks during summer periods (May–August) in the thinned stands at each study area.

	Penticton				Kamloops				Prince George			
Year	*n*	A	B	C	*n*	A	B	C	*n*	A	B	C
1989	8	79.2	73.5	67.3	—	—	—	—	8	61.8	84.8	50.0
		(70.9–87.6)	(63.1–83.9)	(47.1–87.4)						(51.7–71.8)	(65.0–104.5)	(5.3–94.7)
1990	9	69.9	70.0	79.0	8	60.3	54.8	68.4	9	56.4	79.8	68.1
		(60.7–79.1)	(65.2–74.8)	(71.1–86.9)		(41.2–79.3)	(28.3–81.2)	(52.8–84.0)		(41.9–71.0)	(69.0–90.5)	(51.3–84.9)
1991	8	53.6	41.6	43.3	8	37.8	66.4	45.9	8	57.1	80.0	68.5
		(39.6–67.6)	(31.4–51.8)	(22.5–64.0)		(20.4–55.1)	(33.2–99.6)	(34.5–57.3)		(42.0–72.2)	(70.4–89.6)	(44.9–92.1)
Total	25	67.7	62.0	63.8	16	49.0	60.6	57.1	25	58.4	81.4	62.4

Note: The sample size (*n*) is number of trapping periods. Stand designations are as follows: A, low density, 500 stems/ha; B, medium density, 1000 stems/ha; C, high density, 2000 stems/ha.

Fig. 1. Population density (number/9 ha) of northwestern chipmunks in the three thinned stands of lodgepole pine at each study area during May–August 1989–1991. Stand densities are as follows: low, 500 stems/ha; medium, 1000 stems/ha; high, 2000 stems/ha.

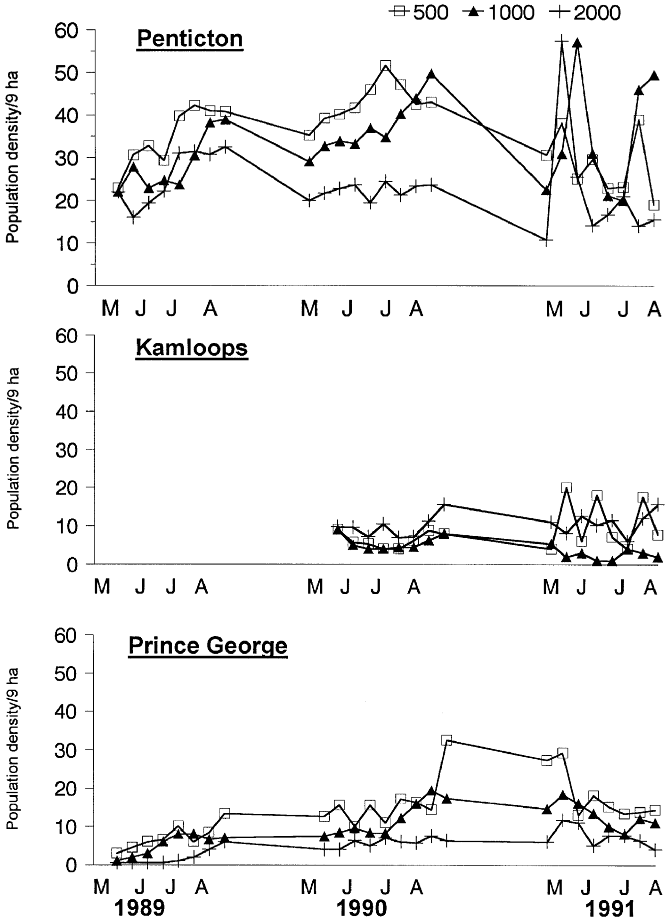
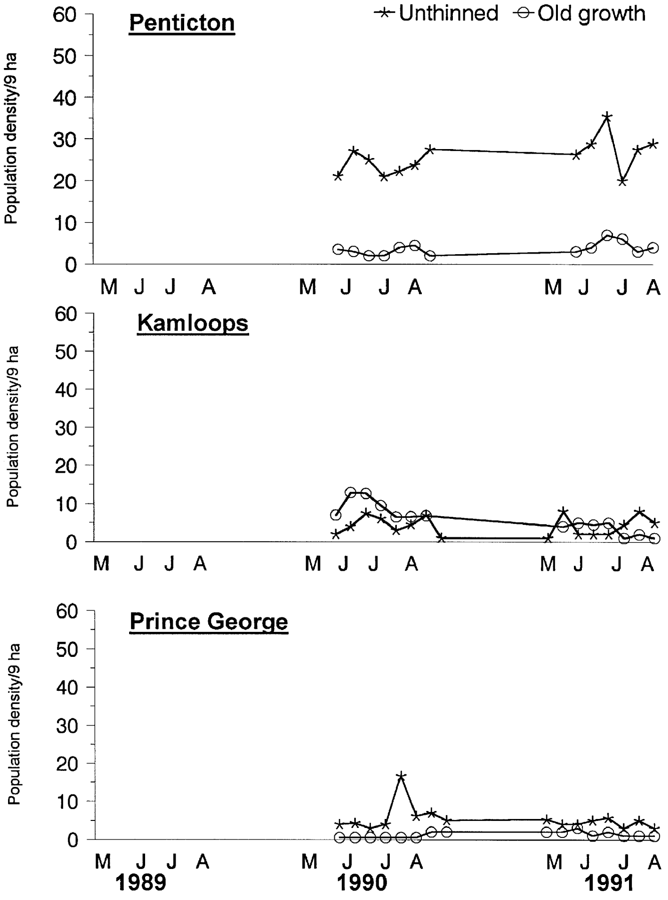


Fig. 2. Population density (number/9 ha) of northwestern chipmunks in the unthinned and old-growth stands of lodgepole pine at each study area during May–August 1990–1991.



chipmunks over all five stands in 1990–1991 were also significantly different ($F_{[4,20]}$ = 5.34, P < 0.01), the population in the old-growth stands being significantly less (DMRT, P = 0.05) dense than those in any of the other four stands (Fig. 2, Table 4). Although not significant by DMRT, the average abundance of chipmunks was higher (non-overlapping 95% confidence limits) in the low-density than in the unthinned stands at Penticton in 1990 and at Prince George in both years (Table 4). Conversely, in 1990 and 1991, the high-density stand at Kamloops had a higher average density of chipmunks than the unthinned stand, based on 95% confidence limits.

Demographic parameters

In comparisons, the mean number of successful pregnancies for chipmunks in the three thinned stands approached significance ($F_{[2,14]}$ = 3.36, P = 0.07). This measure of breeding performance tended to be higher in low- than in high-density stands, and hence followed the pattern for abundance (Table 5). There was a significant difference ($F_{[4,20]}$ = 3.04, P = 0.04) among the five treatment stands in 1990–1991. Chipmunk populations in low- and medium-density stands had significantly more (DMRT, P = 0.05) successful pregnancies than those in old-growth stands, but there were no differences when other stands were compared.

The recruitment of chipmunks followed the same pattern as reproductive success, with the low-density stands having significantly more ($F_{[2,14]}$ = 3.78, P = 0.05) (DMRT, P = 0.05) recruits than the high-density stands (Table 6). A comparison of recruitment over the five stands for 1990–1991 was also significant ($F_{[4,20]}$ = 4.35, P = 0.01), with the old-growth stands having significantly fewer (DMRT, P = 0.05) recruits than any of the other stands.

Estimates of Jolly survival for summer and winter periods were similar among thinned stands at all three study areas (Fig. 3). Survival rates were generally similar in the unthinned and old-growth stands compared with the thinned stands in all study areas.

At Penticton, the mean body mass of chipmunks was significantly higher in low- and medium-density than in high-density stands in 1989 and, for females, higher in low- than in medium- (1990) or high-density (1991) stands (Fig. 4). At Kamloops, there were no differences in mean body mass of chipmunks between stands (Fig. 5). This similarity in body mass was also recorded at Prince George, except that male chipmunks were heavier in the low- and high-density stands than in the medium-density stand in 1989 (Fig. 6). Mean body masses of chipmunks in the unthinned and old-growth stands were similar to those in the thinned stands at Kam-

Table 4. Mean number (with 95% confidence limits in parentheses) of northwestern chipmunks during each summer in the five stands at each study area for Jolly–Seber population estimates.

Study area	Year	A	B	C	D	E
Penticton	1989	34.90 (29.02–40.78)	28.59 (22.96–34.22)	25.65 (20.26–31.04)	—	—
	1990	42.94 (39.24–46.64)	37.14 (32.17–42.11)	22.29 (20.90–23.60)	23.99 (21.52–26.46)	3.00 (2.04–3.96)
	1991	28.43 (22.38–34.48)	34.76 (22.83–46.69)	21.90 (9.32–34.48)	27.82 (22.62–33.02)	4.52 (2.78–6.26)
Kamloops	1990	6.36 (4.69–8.03)	5.64 (4.04–7.24)	9.74 (7.33–12.15)	4.86 (2.96–6.76)	8.86 (6.20–11.52)
	1991	10.54 (4.89–16.19)	2.66 (1.42–3.90)	10.88 (8.46–13.30)	4.50 (2.02–6.98)	3.21 (1.53–4.89)
Prince George	1989	7.23 (4.49–9.97)	5.20 (2.88–7.52)	1.88 (0.15–3.61)	—	—
	1990	16.13 (11.05–21.21)	11.88 (8.34–15.42)	5.76 (4.82–6.70)	6.28 (2.60–9.96)	0.88 (0.30–1.46)
	1991	18.08 (12.62–23.54)	12.95 (10.11–15.79)	7.40 (5.12–9.68)	4.38 (3.52–5.24)	1.63 (1.01–2.25)

Note: Stand designations are as follows: A, low density, 500 stems/ha; B, medium density, 1000 stems/ha; C, high density, 2000 stems/ha; D, unthinned, >2000 stems/ha; E, old growth.

Table 5. Numbers of successful pregnancies for northwestern chipmunks in the five treatment stands at the Penticton, Kamloops, and Prince George study areas in 1989–1991.

	Penticton					Kamloops					Prince George				
Year	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
1989	16	7	11	—	—	—	—	—	—	—	4	2	1	—	—
1990	18	14	13	11	3	3	3	4	1	1	10	8	5	6	1
1991	7	9	2	15	5	0	2	3	0	1	11	7	6	0	0
Mean	13.7	10.0	8.7	13.0	4.0	1.5	2.5	3.5	0.5	1.0	8.3	5.7	4.0	3.0	0.5

Note: Stand designations are as follows: A, low density, 500 stems/ha; B, medium density, 1000 stems/ha; C, high density, 2000 stems/ha; D, unthinned, >2000 stems/ha; E, old growth.

loops and Prince George. This was also generally true at Penticton, except that in 1990, males were heavier in the unthinned ($\bar{x}$ = 52.0 g) than in the medium-density ($\bar{x}$ = 49.2 g) stand and females were lighter in the unthinned ($\bar{x}$ = 41.9 g) than in all three thinned stands.

Discussion

Experimental design

This study had three areas that acted as regional replicates, and the experimental design incorporated units that were both true replicates (Hurlbert 1984) of, and as large as, typical forestry operations. Northwestern chipmunk populations were sampled on 9-ha livetrapping grids that provided reasonable population samples within the operational-size treatment stands. These stands provided essentially independent samples of chipmunks within a study area, since only 7 of 457 (Penticton), 2 of 140 (Kamloops), and 0 of 150 (Prince George) individual chipmunks were captured on more than one grid. Ideally, sampling of chipmunk populations should have been conducted in these stands prior to treatment, but this was not possible in this study. The initial similarity of young lodgepole pine stands within each block prior to treatment, in terms of stand density and tree diameters and heights (Table 1), may be used as a reasonable measure of pretreatment habitat conditions for chipmunks.

Inferences from this study represent the responses of chipmunks to variable habitat structure during the summer (May–August) months only. Because chipmunks (*Tamias* spp.) hibernate during winter months (approximately October–April), additional sampling in September and October would have supplemented the population data but likely would not have altered the pattern of results. It is important to note that the recruitment of young commenced in July each year and was essentially completed by the end of trapping in late summer. In addition, the study did cover 3 years at Penticton and Prince George and 2 years at Kamloops. Over-winter survival and changes in the abundance of chipmunks from one year to the next seemed to be consistent for the winter periods, when data were not available. Because of this consistency in chipmunk response to treatments, the years of data were considered temporal replicates in addition to the spatial replicates.

Chipmunk populations and habitat structure

Chipmunks were more abundant in low-density than in high-density stands. In addition, chipmunk numbers were lowest in all old-growth stands, and the low-density pine stands tended to have higher numbers than the unthinned stands.

Fig. 3. Mean Jolly survival ± 95% confidence limits for northwestern chipmunk populations in the thinned stands (A, low density; B, medium density; C, high density) during each year at the three study areas.

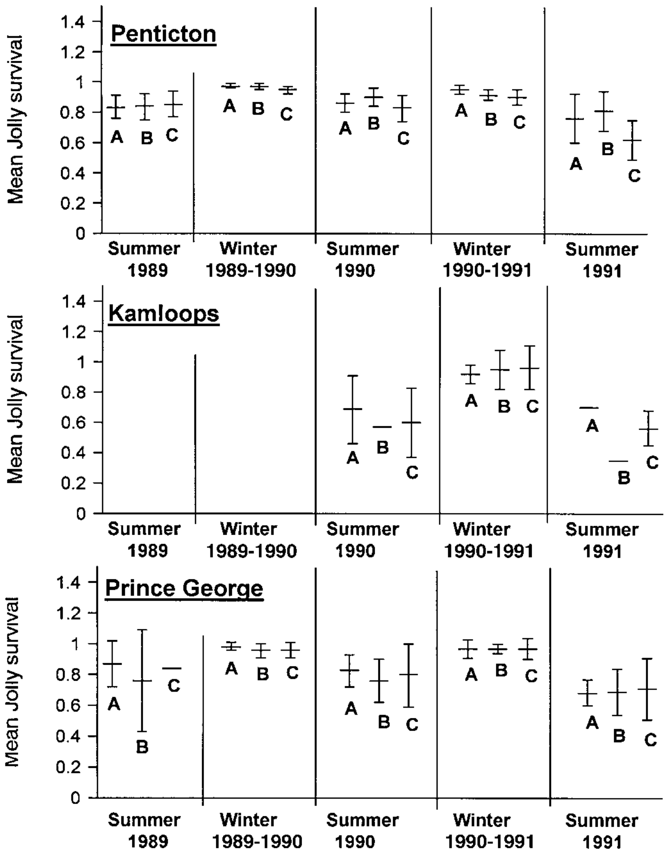


Fig. 4. Mean body mass (g) ± 95% confidence limits for northwestern chipmunk populations in the thinned stands (A, low density; B, medium density; C, high density) during each year at the Penticton study area. Numbers above the upper confidence limit are sample sizes.

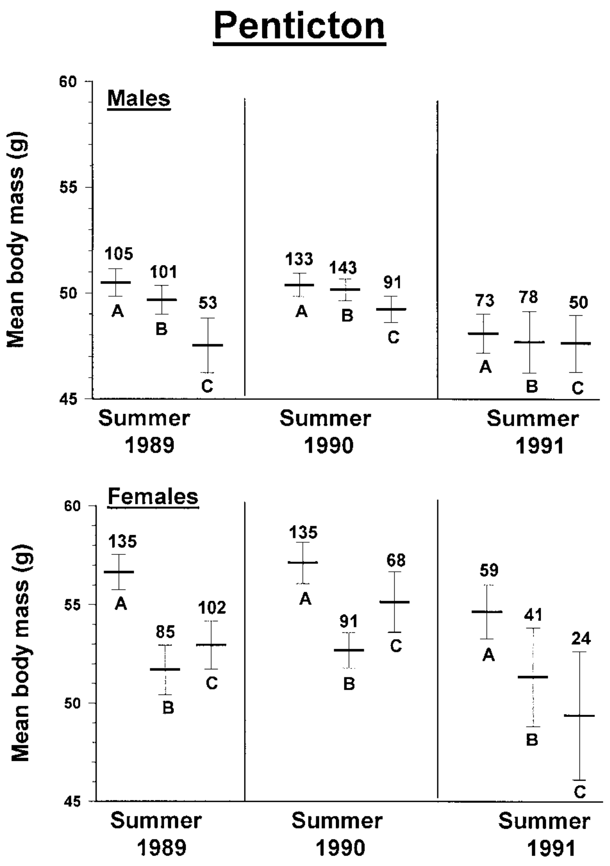


Table 6. Numbers of northwestern chipmunk recruits appearing in the five stands at the Penticton, Kamloops, and Prince George study areas.

	Penticton					Kamloops					Prince George				
Year	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
1989	44	40	34	—	—	—	—	—	—	—	12	14	6	—	—
1990	32	32	20	32	5	13	9	17	7	16	19	20	8	14	2
1991	31	34	34	48	12	18	9	15	16	4	23	17	7	4	2
Mean	35.7	35.3	29.3	40.0	8.5	15.5	9.0	16.0	11.5	10.0	18.0	17.0	7.0	9.0	2.0

Note: Stand designations are as follows: A, low density, 500 stems/ha; B, medium density, 1000 stems/ha; C, high density, 2000 stems/ha; D, unthinned, >2000 stems/ha; E, old growth.

Abundance alone may be a poor indicator of habitat quality for a given species (Van Horne 1983). Sullivan (1979) suggested that poor quality habitats may serve as dispersal or behavioural sinks during times of aggressive interactions. Therefore, demographic parameters also need to be evaluated and, in this study, chipmunk reproduction and recruitment followed the pattern of abundance; there were more successful pregnancies and more recruitment of new animals in the low-density than in the high-density pine stands. Mean body mass of chipmunks also tended in this direction, but survival was consistent among stand treatments. These results support the hypothesis that habitat alteration by stand thinning in young lodgepole pine forest increases abundance and related population parameters in northwestern chipmunk populations.

Based on the demographic responses, we should have expected enhanced stand structure attributes in the low-density stands. However, except for crown volume index of trees, there were no differences in habitat structure among the four lodgepole pine stand treatments. This lack of difference was likely due to the short post-treatment periods of 1 year at Kamloops and 2 years at Penticton and Prince

Fig. 5. Mean body mass (g) ± 95% confidence limits for northwestern chipmunk populations in the thinned stands (A, low density; B, medium density; C, high density) during each year at the Kamloops study area. Numbers above the upper confidence limit are sample sizes.

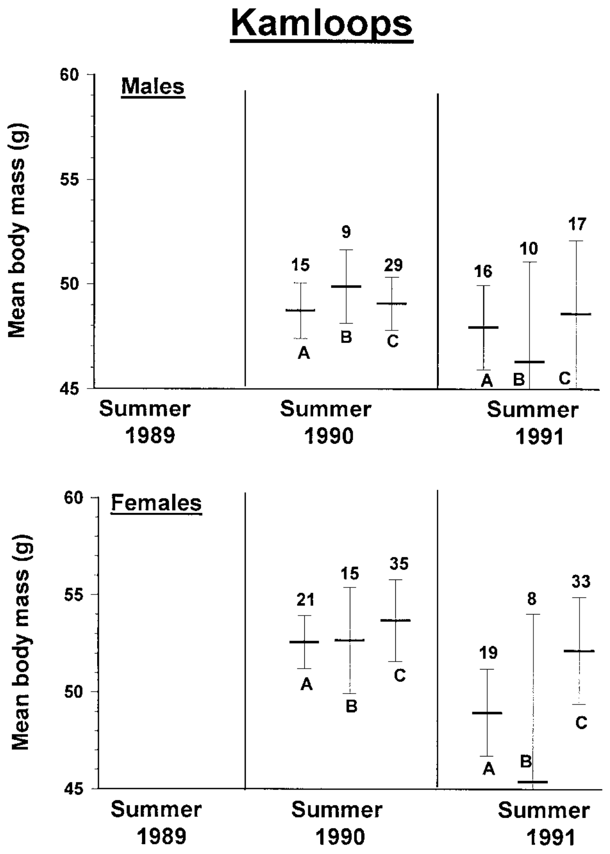
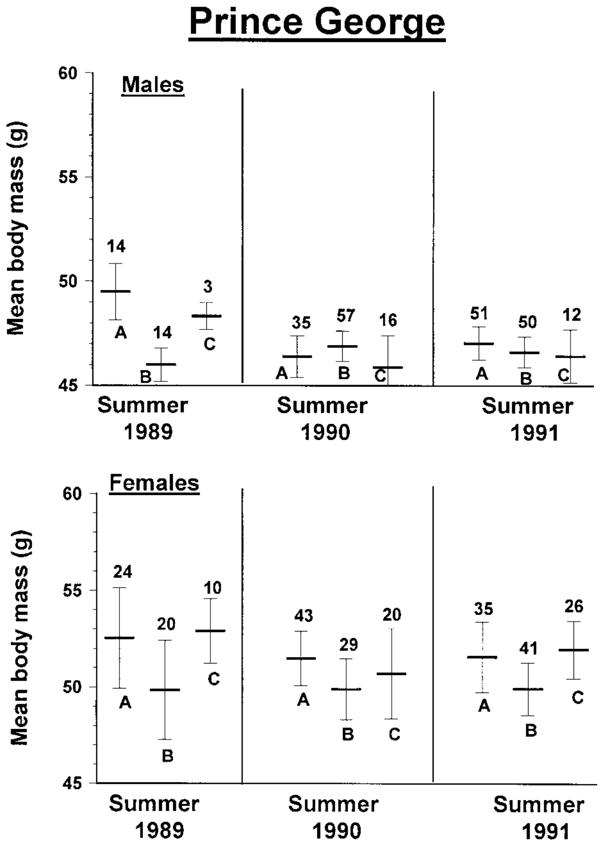


Fig. 6. Mean body mass (g) ± 95% confidence limits for northwestern chipmunk populations in the thinned stands (A, low density; B, medium density; C, high density) during each year at the Prince George study area. Numbers above the upper confidence limit are sample sizes.



George since the thinning for vegetative development in these thinned stands. Measurement of stand structure in subsequent years, (e.g., 5 and 10 years post thinning) would likely yield significant differences in stand-structure attributes among these stands.

As discussed by Banfield (1974) and Sutton (1992), the northwestern chipmunk prefers early successional stages of young forests and tends to be associated with relatively “open” habitats. Stand thinning did create more “open” conditions with respect to tree cover than were found in the unthinned young pine stands. Crown volume index of herbs in the three stands averaged 8.61 m^3/0.01 ha compared with 5.44 m^3/0.01 ha in the unthinned stands. Although not statistically significant, this increase in herbaceous biomass may have been sufficient to provide a somewhat continuous overlapping layer of security cover (Harestad 1991). Understory cover may partially explain the abundance of chipmunks in various habitats in other studies (Doyle 1990; Rosenberg and Anthony 1993; Carey 1995; Hayes et al. 1995).

We predict that mature and old-growth forests, which have poorly developed understory herb and shrub layers, are suboptimal habitat for the northwestern chipmunk. Our results (Table 4, Fig. 1) support this prediction, as do those of Sullivan et al. (2000) for northwestern chipmunk populations in seed-tree, young-pine, and old-growth stands. This pattern varies from that reported for the Townsend’s chipmunk in Oregon and California (Raphael 1984; Carey 1991; Rosenberg and Anthony 1993).

Competition among sciurids

Although not documented on an experimental basis, there was likely competition between northwestern chipmunks and red squirrels (*Tamiasciurus hudsonicus*), at least with respect to food resources, in our study. As the result of a pest-management strategy, the numbers of red squirrels were reduced significantly in the low-density thinned stands at both Penticton and Prince George, and tended to be reduced at Kamloops (Sullivan et al. 1996). It was hypothesized that predator effectiveness in capturing squirrels might be enhanced and (or) the perceived risk of predation might be increased for squirrels that fed in open microhabitats. It may also be that trees in lightly thinned stands of lodgepole pine have more cones for squirrels to feed on than heavily thinned stands. Therefore, chipmunks may have been responding positively to reduced numbers of red squirrels. This apparently reciprocal pattern of abundance was also recorded for the Townsend’s chipmunk and the Douglas squirrel (*Tamiasciurus douglasii*) in the North Cascades of Washington State (Carey 1995) and in a supplemental feeding study in south-coastal British Columbia (Sullivan and Sullivan

1982; Sullivan et al. 1983). As discussed by Carey (1995), tree squirrels may be at a competitive disadvantage when foraging for food resources in the presence of the omnivorous *Tamias* spp. (Sutton 1992, 1993). Carey (1991) reported a lack of large caches of cones typical of the genus *Tamiasciurus* in areas where the seed-eating Townsend's chipmunk could interfere with central-place storage of food. A similar pattern may have occurred in our study areas for the red squirrel and northwestern chipmunk, but *T. hudsonicus* is the only rodent capable of opening serotinous lodgepole pine cones, which would presumably safeguard caches of cones of this tree species (Smith 1968). Parapatric species of *Tamias* display interspecific agonism and habitat displacement (Meredith 1977). However, interspecific interactions between *Tamiasciurus* spp. and *Tamias* spp. are speculative. In another supplemental food study, elevated populations of red squirrels did not appear to adversely affect the abundance of chipmunks (Sullivan and Klenner 1993).

Conclusions

We conclude that northwestern chipmunks appear to prefer relatively "open" habitats, which may be produced by heavy thinning of young lodgepole pine stands. This is the first large-scale experimental manipulation of cover for the northwestern chipmunk. This result occurred in replicated study areas covering three different forest ecological zones within the range of *T. amoenus*. This rodent plays important roles both as prey for a variety of avian and terrestrial predators and as a disperser of mycorrhizal fungi. Thus, because of these interrelationships, stand management practices that benefit northwestern chipmunks should also help enhance the overall forest ecosystem, particularly when interspersed with other stand treatments across landscapes.

Acknowledgements

We thank the Silviculture Branch, British Columbia Ministry of Forests (MoF), Victoria, British Columbia, and the Canada – British Columbia Partnership Agreement on Forest Resource Development (FRDA II) for financial support. Operational treatments were conducted by the Silviculture sections of the Penticton, Kamloops, and Vanderhoof Forest Districts (MoF), for which we are most grateful. We thank C. Nowotny, R. Ostby, J. Craig, I. Teske, T. Friese, D. Pshebniski, B. Runciman, S. Kurta, W. Annas, C. Chapman, J. Hagen, S. Milne, and T. Taylor for assistance with the fieldwork.

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.

Banfield, A. 1974. Mammals of Canada. National Museum of Natural Sciences, National Museums of Canada, and University of Toronto Press, Toronto.

Carey, A.B. 1991. The biology of arboreal rodents in Douglas-fir forests. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-276.

Carey, A.B. 1995. Sciurids in Pacific Northwest managed and old-growth forests. Ecol. Appl. **5**: 648–661.

Craighead, F., and Craighead, J. 1956. Hawks, owls, and wildlife. Stackpole Books, Harrisburg, Pa.

Doyle, A.T. 1990. Use of riparian and upland habitats by small mammals. J. Mammal. **71**: 14–23.

Harestad, A. 1991. Spatial behaviour of Townsend's chipmunks and habitat structure. Acta Theriol. **36**: 247–254.

Hayes, J.P., Horvath, E.G., and Hounihan, P. 1995. Townsend's chipmunk populations in Douglas-fir plantations and mature forests in the Oregon Coast Range. Can. J. Zool. **73**: 67–73.

Hilborn, R., Redfeild, J.A., and Krebs, C.J. 1976. On the reliability of enumeration for mark and recapture census of voles. Can. J. Zool. **54**: 1019–1024

Hitchcock, C.L., and Cronquist, A. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle, Wash.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. **54**: 187–211.

Jolly, G.M., and Dickson, J.M. 1983. The problem of unequal catchability in mark-recapture estimation of small mammal populations. Can. J. Zool. **61**: 922–927.

Krebs, C.J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecol. Monogr. **36**: 239–273.

Krebs, C.J., and Boonstra, R. 1984. Trappability estimates for mark–recapture data. Can. J. Zool. **62**: 2440–2444.

Krebs, C.J., Keller, B.L., and Tamarin, R.H. 1969. *Microtus* biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. Ecology, **50**: 587–607.

MacArthur, R.H., and MacArthur, J.W. 1961. On bird species diversity. Ecology, **42**: 594–598.

Maser, C. 1981. Land mammals. USDA For. Serv. Gen. Tech. Rep. PNW-133.

Maser, C., Trappe, J.M., and Nussbaum, R.A. 1978. Fungal – small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology, **59**: 799–809.

McIntire, P.W. 1984. Fungus consumption by the Siskiyou chipmunk within a variously treated forest. Ecology, **65**: 137–146.

Meidinger, D., and Pojar, J. 1991. Ecosystems of British Columbia. B.C. Minist. For. Spec. Rep. Ser. No. 6.

Meredith, D.H. 1977. Interspecific agonism in two parapatric species of chipmunks (*Eutamias*). Ecology, **58**: 423–430.

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, 12–15 April 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. Manag. **57**: 365–373.

Seber, G.A. 1982. The estimation of animal abundance and related parameters. 2nd ed. Charles Griffin, London.

Smith, C.C. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. Ecol. Monogr. **38**: 31–63.

Stickney, P.F. 1980. Data base for post-fire succession, first 6 to 9 years, in Montana larch-fir forests. USDA For. Serv. Gen. Tech. Rep. INT-62.

Stickney, P.F. 1985. Data base for early postfire succession on the sundance burn, northern Idaho. USDA For. Serv. Gen. Tech. Rep. INT-189.

Sullivan, T.P. 1979. Demography of populations of deer mice in coastal forest and clear-cut (logged) habitats. Can. J. Zool. **57**: 1636–1648.

Sullivan, T.P. 1990. Influence of forest herbicide on deer mouse and Oregon vole population dynamics. J. Wildl. Manag. **54**: 566–576.

Sullivan, T.P., and Klenner, W. 1993. Influence of diversionary food on red squirrel populations and damage to crop trees in young lodgepole pine forest. Ecol. Appl. **3**: 708–718.

Sullivan, T.P., and Sullivan, D.S. 1982. Population dynamics and regulation of the Douglas squirrel (*Tamiasciurus douglasii*) with supplemental food. Oecologia (Berl.), **53**: 264–270.

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.

Sullivan, T.P., Klenner, W., and Diggle, P.K. 1996. Response of red squirrels and feeding damage to variable stand density in young lodgepole pine forest. Ecol. Appl. **6**: 1124–1134.

Sullivan, T.P., Sullivan, D.S., and Lindgren, P.M.F. 2000. Small mammals and stand structure in young pine, seed-tree, and old-growth forest in southern British Columbia. Ecol. Appl. **10.** In press.

Sutton, D.A. 1992. *Tamias amoenus*. Mamm. Species No. 390. pp. 1–8.

Sutton, D.A. 1993. *Tamias townsendii*. Mamm. Species No. 435. pp. 1–6.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manag. **47**: 893–901.

Walmsley, M.E., Utzig, G., Vold, T., and Van Barneveld, J. 1980. Describing ecosystems in the field. Land Management Rep. No. 7, British Columbia Ministry of the Environment and Ministry of Forests, Victoria.

West, S.D. 1991. Small mammal communities in the southern Washington Cascade Range. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285. pp. 269–284.

Zar, J.H. 1984. Biostatistical analysis. 2nd ed. Prentice Hall, Englewood Cliffs, N.J.