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Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest. I. Population dynamics of northern flying squirrels and red squirrels

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Abstract

A new paradigm in forest management is managing second-growth forests to accelerate development of structural characteristics associated with late-seral forests. A key uncertainty is whether those wildlife species associated with these structural characteristics will respond positively to their development in thinned young seral forests. This study was designed to test the hypothesis that population dynamics (abundance, breeding condition, and survival) of northern flying squirrels (*Glaucomys sabrinus*) and red squirrels (*Tamiasciurus hudsonicus*) would be maintained at levels recorded in old-growth forests by large-scale pre-commercial thinning of young (17–27 years old) lodgepole pine (*Pinus contorta*) forests. Replicated study areas were located near Penticton, Kamloops, and Prince George in south-central British Columbia, Canada. Each study area had three young pine stands thinned to densities of ~500 (low), ~1000 (medium), and ~2000 (high) stems/ha, with unthinned (4300–7600 stems/ha) and old-growth stands for comparison. Populations of *G. sabrinus* and *T. hudsonicus* were sampled intensively from 2000 to 2002 corresponding to 12–14 years after thinning.

Abundance of *G. sabrinus* was significantly higher in the high-density stand and lowest in the low-density and unthinned stands. Intermediate densities were found in the medium-density and old-growth stands. Adult male body mass was significantly greater in old-growth than high-density stands. We failed to detect significant differences among treatments for recruitment, movement, and survival for *G. sabrinus* and all parameters measured for *T. hudsonicus.* Survival increased significantly in 2002 from previous years for *G. sabrinus,* while survival decreased significantly for *T. hudsonicus* during this period. Our results support the hypothesis that population dynamics of *G. sabrinus* and *T. hudsonicus* would be maintained at levels recorded in old-growth forests by large-scale pre-commercial thinning of young lodgepole pine forests. Abundance of *G. sabrinus* in high-density stands exceeded levels recorded in old-growth stands.

Keywords: *Glaucomys sabrinus*; *Tamiasciurus hudsonicus*; Population dynamics; Pre-commercial thinning; Lodgepole pine; Old-growth attributes

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1. Introduction

Much of the biodiversity in British Columbia and the Pacific Northwest is associated with early and late-seral forests (Harris, 1984; Mackinnon, 1998). However, abundance of late-seral forests has been greatly reduced throughout this region owing to forest harvesting and other human-induced disturbances. Consequently, to maintain or restore biodiversity, changes to forest management practices are required (Harris, 1984; Hunter, 1990).

The rich wildlife diversities of early and late-seral forests are more likely attributable to their ecological characteristics than their age (Hayes et al., 1997). For example, the northern spotted owl (*Strix occidentalis caurina*) is apparently the most renowned old-growth dependent species throughout the Pacific Northwest and requires old-growth forests for its survival (Thomas et al., 1990). However, most authorities agree that forest structure is more important in determining habitat suitability for owls than tree age (Thomas et al., 1990). Current research is determining whether we can manage second-growth forests to provide structural characteristics that closely approximate those found in late-seral forests. These structural characteristics include a multilayered and relatively dense canopy, mixed species composition dominated by large trees, numerous large logs and other woody debris on the ground, large diameter snags, and vertical and horizontal heterogeneity in these structural features (reviewed by Hayes et al., 1997).

Thinning (pre-commercial and commercial) might be used to accelerate development of old-growth characteristics in young, second-growth stands (McComb et al., 1993; Carey and Johnson, 1995; Carey and Curtis, 1996; Hayes et al., 1997; Sullivan et al., 2001; Lindgren et al., unpublished). Thinning can increase species diversity, volume, and diameter growth of trees; crown volume; understory development; and total vertical structural diversity of even-aged stands (reviewed by Carey and Wilson, 2001; Sullivan et al., 2001; Suzuki and Hayes, 2003). A key uncertainty is whether those wildlife species associated with structural characteristics of late-seral forests respond positively to their development in thinned, second-growth stands.

Carey (2000) suggested that management strategies designed to accelerate late-seral forest conditions could be evaluated by comparing the population dynamics of sciurids between late-seral forests and thinned stands. Sciurids fulfill an important ecological role. Northern flying squirrels (*Glaucomys sabrinus*) consume primarily the fruiting bodies of ectomycorrhizal fungi (McKeever, 1960; Fogel and Trappe, 1978; Maser et al., 1978; Maser and Maser, 1988; Hall, 1991; Waters and Zabel, 1995; Colgan, 1997; Aubry et al., 2003; Smith et al., 2003). Red squirrels (*Tamiasciurus hudsonicus*) consume these fruiting bodies as well but are less dependent upon them than *G. sabrinus* (Smith, 1970, 1981; Currah et al., 2000). Ectomycorrhizal fungi have developed a mutualistic symbiotic relationship essential to growth and health of all species in the economically important Pinaceae family (*Abies*, *Larix, Picea, Pinus, Pseudotsuga*, and *Tsuga*; Maser et al., 1978; Maser and Maser, 1988; Molina et al., 1999). These sciurids play an important role in dispersing spores of ectomycorrhizal fungi when they defecate. This process forms new mycorrhizal colonies enhancing growth and health of trees (Maser et al., 1986; Maser and Maser, 1988; Cazares et al., 1999). This dispersal is especially important for young tree growth in early seral stages (Molina et al., 1999). The abundance of *G. sabrinus* is limited primarily by abundance of food (Ransome and Sullivan, 1997, 2004). In turn, *G. sabrinus* is the primary prey of spotted owls (Carey et al., 1992; Forsman et al., 1977, 1984). Recent studies have found a strong relationship between prey abundance and reproductive success of *S. occidentalis* (White, 1996; Thome et al., 1999), their home range size and habitat use (Zabel et al., 1995), and their survival during natal dispersal (Miller et al., 1997). Consequently, squirrels might prove to be a vital link between critical belowground processes in a forest and higher trophic levels, especially in late-seral forests.

We examined population dynamics of *G. sabrinus* and *T. hudsonicus* among lodgepole pine (*Pinus contorta*) stands pre-commercially thinned to three densities, 12–14 years post-thinning, and in unthinned and old-growth stands. This study was designed to test the hypothesis that population dynamics (abundance, breeding condition, and survival) of *G. sabrinus* and *T. hudsonicus* would be maintained at levels recorded in old-growth forests by large-scale thinning of young lodgepole pine stands. Two concurrent studies examined the response in abundance and diversity of vegetation (Lindgren et al., unpublished) and forest floor small mammals (Sullivan et al., 2004) to these treatments.

2. Methods

2.1. Study areas

Five lodgepole pine stands were located in each of three replicate study areas in British Columbia, Canada: Penticton Creek, Kamloops, and Prince George. Each replicate had an old-growth lodgepole pine stand (age range of 160–250 years) and four second-growth lodgepole pine stands (age range of 17–27 years); three of which were pre-commercially thinned to low (~500 stems/ha), medium (~1000 stems/ha) or high (~2000 stems/ha) density. Second-growth stands within each of the three replicates had relatively uniform tree cover and comparable diameter, height, and density of trees prior to stand thinning (Sullivan et al., 2001). Very few remnant trees and snags remained from previous stands (Sullivan et al., 2001).

The Penticton Creek study area was located in south-central British Columbia, Canada, 15 km northeast of Penticton (49°34′ N; 119°27′ W). All stands were located in the Interior Douglas-fir (IDF_{dk}) biogeoclimatic zone (Meidinger and Pojar, 1991). Elevation of stands ranged from 1340 to 1500 m. Topography in the area is hilly with sandy loam soil, southeast aspect, and an average slope of 10%. This area (several thousand ha) was burned by wildfire in 1970, salvage logged in 1971, and planted with lodgepole pine in 1972. Density of pine from natural regeneration ranged from 18,500–30,000 stems/ha. Dominant coniferous species in stands include lodgepole pine with a minor component of Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and western larch (*Larix occidentalis*). Dominant ground cover included willow (*Salix* spp.), Sitka alder (*Alnus sinuata*), and grouseberry (*Vaccinium scoparium*), fireweed (*Epilobium angustifolium*), grasses, and Arctic lupine (*Lupinus arcticus*).

Stands were pre-commercially thinned in 1978 to ca. 1000–2000 stems/ha. Density of pine, 10-year post-thinning, exceeded 4000 stems/ha from additional ingress of pine. Three treatment stands were pre-commercially thinned again in 1988 to low, medium, and high densities. At time of treatment, mean stand diameter (dbh, diameter at breast height, 1.3 m above the soil surface) ranged from 7.7 ± 0.1 cm (mean ± 1 S.E.) to 8.5 ± 0.1 cm (Sullivan et al., 2001). Stand height ranged from 5.1 ± 0.1 to 5.6 ± 0.1 m. In 1998, mean stand dbh ranged from 12.7 ± 0.2 to 14.8 ± 0.2 cm and mean stand height ranged from 8.9 ± 0.1 to 9.8 ± 0.1 m (Sullivan et al., 2001). All stands were 0.2–2.3 km apart and ranged in area from 20 (each of the thinned stands) to 100+ ha (unthinned stand).

The Kamloops study area was located 30 km south of Kamloops, British Columbia (50°28′ N; 120°32′ W). All stands were located in the Montane Spruce (MSdm) biogeoclimatic zone (Meidinger and Pojar, 1991) and ranged in elevation from 1400 to 1500 m. Topography is hilly with a northerly aspect. This area (ca. 15,000 ha) was burned by wildfire in 1960 and regenerated naturally to lodgepole pine to a density of 20,000 stems/ha. Dominant coniferous species in stands include lodgepole pine with a minor component of subalpine fir (*Abies lasiocarpa*) and hybrid spruce (*P. engelmannii* × *P. glauca*). Dominant ground cover included Sitka alder, twinflower (*Linnaea borealis*), willow, fireweed, grasses, and Arctic lupine.

Two-hundred hectar were pre-commercially thinned from 1975 to 1978 to ca. 1100–1600 stems/ha. Density of pine, 10-year post-thinning, exceeded 7000 stems/ha from additional ingress of pine. Three treatment stands were pre-commercially thinned again in 1989 to low, medium, and high densities. At time of treatment, mean stand diameter of pine ranged from 8.7 ± 0.1 cm (mean ± 1 S.E.) to 11.7 ± 0.1 cm (Sullivan et al., 2001). Stand height ranged from 8.2 ± 0.1 to 8.6 ± 0.1 m. In 1998, mean stand dbh and height ranged from 12.2 ± 0.2 cm to 16.5 ± 0.2 and 11.0 ± 0.1 to 12.5 ± 0.1 m, respectively (Sullivan et al., 2001). All stands were 0.5–5.0 km apart and ranged in area from 15 to 22 ha (thinned stands) to 100+ ha (unthinned stand).

The Prince George study area was located 60 km west of Prince George, British Columbia (53°52′N; 123°32′W). All stands were located in the Sub-boreal Spruce (SBSdw) biogeoclimatic zone (Meidinger and Pojar, 1991). General topography is gently rolling, at 800 m elevation and variable aspects. This area (ca. 1000 ha) was harvested from 1966 to 1972 and regenerated naturally to lodgepole pine to a density of

2700–4700 stems/ha. Dominant coniferous species in stands include lodgepole pine with a minor component of subalpine fir and hybrid spruce. Dominant ground cover included willow, Sitka alder, fireweed, grasses, and Arctic lupine.

Three treatment stands were pre-commercially thinned in 1988 to low, medium, and high densities. At time of treatment, mean stand dbh ranged from 8.8 ± 0.3 cm (mean ± 1 S.E.) to 11.3 ± 0.3 cm (Sullivan et al., 2001). Stand height ranged from 7.0 ± 0.2 to 8.7 ± 0.2 m. In 1998, mean stand dbh ranged from 13.5 ± 0.3 to 17.8 ± 0.3 cm and mean stand height ranged from 11.3 ± 0.2 to 13.0 ± 0.2 m (Sullivan et al., 2001). All stands were 0.5–1.7 km apart and ranged in area from 30 to 39 ha (thinned stands) and 41 ha (unthinned stand).

Operational thinning was conducted after the growing season in fall of 1988 at the Penticton and Prince George study areas, and in fall of 1989 at the Kamloops study area. Trees in low-density stands were pruned to a 2.8 m lift (above ground level) at Penticton (October 1992), Kamloops (September 1992), and Prince George (November 1991). Densities of pine (stems/ha) in unthinned stands were 5000 at Penticton, 6000 at Kamloops, and 4700 at Prince George in 1988. These densities were 4755, 7665, and 4300 respectively, in 1998.

The Penticton old-growth stand was dominated by lodgepole pine with a relative abundance of 64.6% followed by spruce (14.6%) and subalpine fir (20.8%) for overstory trees (Sullivan et al., 2001). The Kamloops stand was dominated by subalpine fir (68.4%) with lesser proportions of somewhat larger diameter pine and hybrid spruce. The Prince George old-growth stand had similar abundance of lodgepole pine (57.5%) and hybrid spruce (42.5%). Heights of overstory trees ranged from 19.5 to 23.9 m and were similar in all stands. Overall stand density in stems/ha was 2330 (Penticton), 1930 (Kamloops), and 1960 (Prince George) (Sullivan et al., 2001). Overstory snag densities ranged from 90/ha at Penticton and Prince George to 140/ha at Kamloops.

2.2. Live trapping and demographic analysis

Populations of *G. sabrinus* and *T. hudsonicus* were live-trapped at 4-week intervals from May to October 2000 and 2001, and at 8-week intervals in 2002. Each stand had a 9 ha trapping grid with100 (10 × 10 or 6 × 16 + 4) stations at 30 m intervals with one Tomahawk live-trap (Model 201, Tomahawk Live Trap Company, Tomahawk, Wisconsin) equipped with a nest box (1 L plastic jar with coarse brown cotton) at every other station, resulting in ~5 traps/ha. Traps were baited with sunflower seeds (*Helianthus annuus*) and set in the evening on day 1 and checked in the morning and afternoon of day 2 and morning of day 3. Traps were closed in the morning of day two and reset that evening when day-time temperatures exceeded 25 °C.

All squirrels captured were identified with individually numbered ear tags. For each capture, ear tag number, location, mass, gender, and breeding condition were recorded. Breeding condition of females was evaluated by palpation of the mammaries and females were classified as "non-breeding" (small mammaries) or "breeding" (large mammaries). Breeding condition of males was evaluated by palpating the testes and males were classified as either non-breeding (testes abdominal) or breeding (testes scrotal; Krebs et al., 1969; McCravy and Rose, 1992).

Trappability, movement, population size, percentage of squirrels in breeding condition, mass, recruitment, and survival were estimated. Comparisons of these parameters between treatments were used to evaluate influence of stand thinning on *G. sabrinus* and *T. hudsonicus*. Trappability, as defined by Jolly (1965) and Jolly and Dickson (1983), is the probability that an individual present in the population will be included in that particular sample (Krebs and Boonstra, 1984; Efford, 1992). Population size was estimated for each trap session using the Jolly–Seber stochastic model (Seber, 1982). Reliability of Jolly–Seber estimates declines when few tagged animals are captured (Krebs et al., 1986). Therefore, minimum number of animals know to be alive (MNA—Krebs, 1966) was also calculated as a precautionary measure and to indicate lower limits of the Jolly–Seber estimates. MNA estimates were used for first and last trap sessions. The Jolly–Seber model does not estimate population sizes for these sessions. All statistical tests were based on Jolly–Seber estimates (including MNA estimates for first and last trap sessions) for the reasons indicated by Jolly and Dickson (1983). Movement was calculated as mean distance moved between points of first capture on consecutive trapping sessions. Recruits were classified as new squirrels captured at least twice. Distinguishing recruits from resident individuals during initial trap sessions is difficult. Therefore, recruitment was not calculated for 2000.

Jolly survival was calculated for each trap session (Nichols and Pollock, 1983). Mass at sexual maturity, coupled with the lowest mass attained by any known adult was used to determine age categories. *T. hudsonicus* and *G. sabrinus* weighing <165 and <100 g, respectively, were never sexually mature and were classified as juveniles. No known adults weighed less than these values. Comparisons of mass between treatments were based on mean mass of each adult male averaged for each year of the study.

2.3. Experimental design and statistical analysis

The experimental design was a randomized-complete block design with five treatments: low density, medium density, high density, and unthinned young lodgepole pine stands; and an old-growth lodgepole pine stand. Thinning treatments were randomly assigned to young lodgepole pine stands. Each of the three study areas was considered a regional replicate (block).

A repeated measures analysis of variance (RM-ANOVA) was used to evaluate the effect of thinning on mean (averaged for each year of the study: 2000, 2001, 2002) abundance, trappability, survival, and breeding condition. Mauchly's *W* test statistic was used to test for sphericity (independence of parameters estimated for each year of the study; Kuehl, 1994) prior to examining differences among years. For parameters found to be correlated among years, the Huynh–Feldt (H–F) correction (Huynh and Feldt, 1976) was used to adjust the degrees of freedom of the within-subjects *F*-ratio. Differences in movement, mass, and recruitment among treatments were evaluated by a one-way ANOVA (Sokal and Rohlf, 1981). Survival and breeding condition were arcsine transformed and recruitment was square-root transformed before performing ANOVAs to better approximate a normal distribution. Duncan's multiple range test (DMRT) was used to determine significant differences in parameters among treatments. Differences were considered significant if $P < 0.05$ for all comparisons.

3. Results

3.1. Population dynamics of G. sabrinus

We captured 187 *G. sabrinus* 375 times. Majority of captures (80.1%) for *G. sabrinus* occurred in the fall (August–October) with a mean (±S.E.) trappability for this period of 60.2% (±4.1). We failed to detect significant treatment effects for trappability for *G. sabrinus* (Table 1); however, trappability was, in general, lowest in low-density stands. We calculated mean abundance of *G. sabrinus* across all trap sessions

Table 1
Mean ($n = 3$ replicate stands) ± S.E. trappability of *G. sabrinus* and *T. hudsonicus* for the five treatments during 2000–2002 and results of RM-ANOVA

Species and year	Low density	Medium density	High density	Unthinned	Old growth	Treatment		Time		Treatment × time	
						$F_{4,8}$	P	$F_{2,20}$	P	$F_{8,20}$	P
G. sabrinus											
2000	13.3 ± 9.1	59.9 ± 12.2	60.6 ± 11.5	67.3 ± 10.5	45.3 ± 11.6						
2001	40.6 ± 11.1	40.2 ± 9.2	36.7 ± 9.4	48.6 ± 11.5	47.1 ± 10.1						
2002	22.2 ± 16.4	45.3 ± 18.8	21.9 ± 8.3	66.7 ± 21.1	44.1 ± 15.9						
Mean	27.3 ± 6.9	48.6 ± 6.9	43.6 ± 6.6	58.6 ± 7.4	45.9 ± 6.7	1.91	0.20	2.24	0.13	1.91	0.12
T. hudsonicus											
2000	55.1 ± 6.1	66.8 ± 5.7	60.4 ± 9.7	43.4 ± 8.1	58.1 ± 2.7						
2001	70.9 ± 5.9	66.9 ± 7.3	68.0 ± 7.7	55.3 ± 8.7	74.6 ± 3.8						
2002	75.3 ± 9.5	61.6 ± 15.3	57.7 ± 19.6	59.6 ± 19.4	90.3 ± 5.1						
Mean	65.5 ± 4.0	66.0 ± 4.5	63.5 ± 5.8	51.4 ± 5.8	70.6 ± 2.8	0.22	0.92	2.90	0.08	0.67	0.71

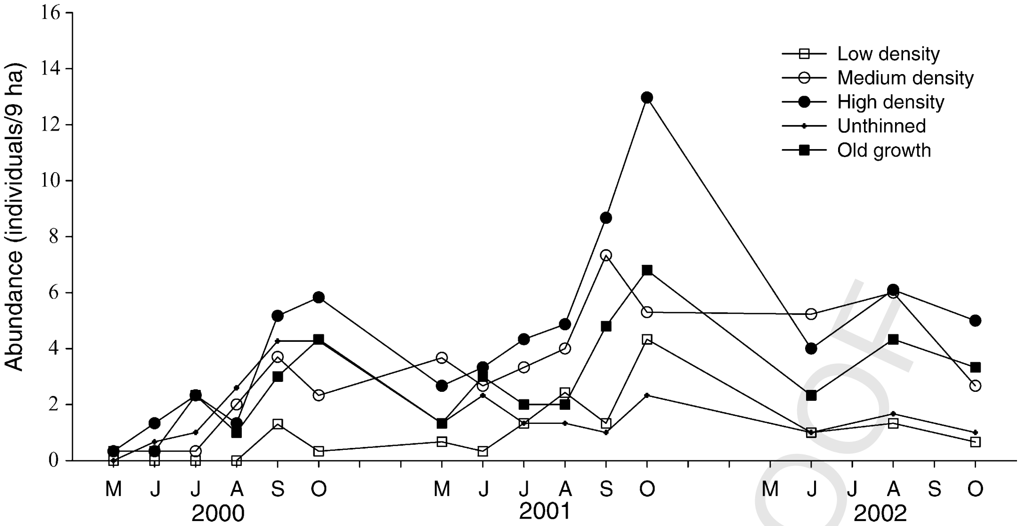

Fig. 1. Mean ($n = 3$ replicate stands) total abundance/9 ha of northern flying squirrels (*G. sabrinus*) for the five treatments and 3 years 2000–2002.

and for fall trap sessions only when 80% of captures occurred (Fig. 1; Table 2). Abundance of *G. sabrinus* was significantly higher in high-density stands than in other treatments for all sessions. Abundance of *G. sabrinus* in medium-density and old-growth stands was not significantly different; while low-density and unthinned stands maintained a significantly lower abundance of *G. sabrinus* than other treatments. The same trend was maintained for mean abundance when only fall trap sessions were examined. Abundance of *G. sabrinus* was significantly higher in 2001 than in 2000 and 2002 (Table 2; Fig. 1).

Table 2
Mean ($n = 3$ replicate stands) ± S.E. estimates of abundance (individuals/9 ha) for *G. sabrinus* and *T.hudsonicus*, and breeding condition for *T. hudsonicus* for the five treatments during 2000–2002

Species and year	Low density	Medium density	High density	Unthinned	Old growth	Treatment		Time		Treatment × time	
						$F_{4,8}$	P	$F_{2,20}$	P	$F_{8,20}$	P
G. sabrinus											
Abundance	1.3 ± 0.3 c	3.3 ± 0.5 b	4.6 ± 0.6 a	1.8 ± 0.2 c	2.8 ± 0.4 b	3.84	0.05	8.21	<0.01	1.66	0.17
Fall only	1.5 ± 0.5 c	4.2 ± 0.7 b	6.3 ± 0.8 a	2.3 ± 0.3 c	3.7 ± 0.7 b	4.35	0.04	5.55	0.01	2.07	0.09
Fall mean overall	2000: 2.8 ± 0.4		2001: 4.6 ± 0.7	2002: 3.2 ± 0.5							
T. hudsonicus											
Abundance	13.5 ± 1.4	9.7 ± 1.0	10.8 ± 1.2	11.3 ± 1.3	15.0 ± 0.9	1.04	0.44	3.31	0.06	0.95	0.50
Mean overall	2000: 12.1 ± 0.8		2001: 13.0 ± 0.9	2002: 9.9 ± 1.1							
Breeding condition											
2000	0.94 ± 0.1	1.0 ± 0.0	0.82 ± 0.1	0.88 ± 0.0	0.83 ± 0.1						
2001	0.94 ± 0.1	1.0 ± 0.0	0.96 ± 0.1	1.0 ± 0.0	0.66 ± 0.2						
2002	0.67 ± 0.3	1.0 ± 0.0	0.84 ± 0.2	1.0 ± 0.0	1.0 ± 0.0						
Mean	0.85 ± 0.1	1.0 ± 0.0	0.87 ± 0.1	0.95 ± 0.0	0.90 ± 0.1	2.34[a]	0.22	1.36[a]	0.30	0.91[a]	0.54

Means followed by the same letter were not different as indicated by RM-ANOVA and Duncan's multiple range test.

[a] Degrees of freedom for treatment 4,4; time 2,10, and time × treatment 8,10.

Table 3
Mean ($n = 3$ replicate stands) ± S.E. estimates of adult body mass (g), recruitment (individuals/trap session), and movement (m) for *G. sabrinus* and *T. hudsonicus* for the five treatments during 2000–2002

Parameter	Low density	Medium density	High density	Unthinned	Old growth	Treatment	
						$F_{4,8}$	P
G. sabrinus							
Mass	126.5 ± 3.4 ab	126.8 ± 2.6 ab	125.5 ± 1.9 a	127.5 ± 2.8 ab	136.4 ± 2.8 b	3.99	0.05
Recruitment	0.15 ± 0.09	0.41 ± 0.10	0.67 ± 0.33	0.15 ± 0.07	0.52 ± 0.17	2.50	0.13
Movement	59.1 ± 28.0	82.2 ± 10.1	89.4 ± 11.2	81.8 ± 12.5	67.2 ± 14.7	0.47[a]	0.76
T. hudsonicus							
Mass	225.6 ± 4.7	220.4 ± 4.6	226.5 ± 4.7	225.9 ± 4.5	218.1 ± 4.7	3.38	0.07
Recruitment	1.22 ± 0.33	1.10 ± 0.29	1.52 ± 0.34	0.74 ± 0.19	1.30 ± 0.28	1.38	0.32
Movement	54.6 ± 3.4	63.6 ± 3.9	50.0 ± 3.2	63.9 ± 4.3	63.0 ± 3.1	0.23	0.92

Means followed by the same letter were not different as indicated by ANOVA and Duncan multiple range test.
[a] Degrees of freedom for treatment was 4,6.

Too few individuals were captured in spring to evaluate effects of thinning on breeding condition of *G. sabrinus*. Adult body mass for male *G. sabrinus* was not significantly different among young stands (range 125.5–127.5 g; Table 3); however, mass in old-growth stands (136.4 g) was significantly greater than that in high-density stands. We failed to detect significant treatment effects for recruitment for *G. sabrinus* (Table 3). However, recruitment followed the same pattern as abundance with low-density and unthinned stands generally having low recruitment and high-density and old-growth stands having high recruitment. Recruitment varied four-fold from low-density to high-density stands and might represent a biologically significant trend. We failed to detect significant differences among treatments for movement of *G. sabrinus* (Table 3). Survival of *G. sabrinus* was similar among treatments (range: 0.76–0.87; Table 4). However, survival of *G. sabrinus* increased significantly in 2002 from previous years. *G. sabrinus* were significantly heavier in Prince George than in Kamloops or Penticton (Table 5). Recruitment of *G. sabrinus* was significantly lower in Kamloops than in the other two study areas (Table 5).

3.2. Population dynamics of *T. hudsonicus*

We captured 587 *T. hudsonicus* 2429 times. We failed to detect significant differences among treatments for trappability (Table 1). Average trappability among years ranged from 51.4% in unthinned stands to 70.6% in old-growth stands.

Similarly, there were no significant differences among treatments for abundance (Fig. 2; Table 2)

Table 4
Mean ($n = 3$ replicate stands) ± S.E. estimates of Jolly–Seber 28-day survival for *G. sabrinus* and *T. hudsonicus* for the five treatments during 2000–2002 and results of RM-ANOVA

Species and year	Low density	Medium density	High density	Unthinned	Old growth	Mean	Treatment		Time		Treatment × time	
							$F_{4,8}$	P	$F_{2,20}$	P	$F_{8,20}$	P
G. sabrinus												
2000	0.91 ± 0.04	0.82 ± 0.06	0.75 ± 0.07	0.73 ± 0.07	0.71 ± 0.09	0.78 ± 0.03						
2001	0.78 ± 0.06	0.91 ± 0.04	0.85 ± 0.06	0.83 ± 0.07	0.77 ± 0.08	0.83 ± 0.02						
2002	1.00 ± 0.00	0.90 ± 0.10	0.89 ± 0.11	0.89 ± 0.11	1.00 ± 0.00	0.94 ± 0.03						
Mean	0.85 ± 0.04	0.87 ± 0.03	0.81 ± 0.04	0.79 ± 0.05	0.76 ± 0.06		0.48	0.75	6.52	0.01	1.24	0.33
T. hudsonicus												
2000	0.79 ± 0.06	0.83 ± 0.06	0.85 ± 0.04	0.91 ± 0.03	0.84 ± 0.04	0.85 ± 0.02						
2001	0.88 ± 0.04	0.86 ± 0.04	0.80 ± 0.05	0.85 ± 0.05	0.82 ± 0.05	0.84 ± 0.02						
2002	0.67 ± 0.19	0.56 ± 0.14	0.76 ± 0.12	0.79 ± 0.11	0.72 ± 0.11	0.70 ± 0.06						
Mean	0.82 ± 0.03	0.82 ± 0.04	0.82 ± 0.03	0.87 ± 0.03	0.82 ± 0.03		0.52	0.72	5.42	0.01	0.44	0.88

Table 5
Mean (n = 3 replicate stands) ± S.E. estimates of trappability, abundance (individuals/9 ha), survival, adult body mass (g), recruitment (individuals/trap session), and movement (m) for *G. sabrinus* and *T. hudsonicus* for the three replicate study areas (blocks) during 2000–2002

Species and parameter	Penticton	Kamloops	Prince George	Block effect	
				$F_{2,8}$	P
G. sabrinus					
Trappability	40.9 ± 5.5	40.5 ± 5.7	53.1 ± 5.0	0.91	0.50
Abundance	3.0 ± 0.3	1.7 ± 0.3	3.6 ± 0.4	3.51	0.08
Survival	0.82 ± 0.03	0.79 ± 0.09	0.81 ± 0.10	0.52	0.62
Mass	124.7 ± 1.6	128.6 ± 2.1	131.9 ± 2.4	4.38	0.05
Recruitment	0.42 ± 0.1	0.11 ± 0.06	0.58 ± 0.1	6.79	0.02
Movement	95.6 ± 14.9	80.0 ± 18.7	75.9 ± 6.1	0.39[a]	0.69
T. hudsonicus					
Trappability	62.0 ± 5.2	65.9 ± 2.4	62.4 ± 3.0	0.06	0.94
Abundance	3.7 ± 0.5	14.9 ± 0.6	17.6 ± 0.7	21.5	<0.01
Survival	0.80 ± 0.06	0.85 ± 0.01	0.82 ± 0.06	1.40	0.30
Mass	211.9 ± 4.5	234.2 ± 4.6	216.0 ± 4.1	80.7	<0.01
Recruitment	0.60 ± 0.1	1.64 ± 0.3	1.30 ± 0.2	10.5	0.01
Movement	62.2 ± 5.6	57.4 ± 2.5	59.4 ± 2.2	0.61	0.57

[a] Degrees of freedom for block was 2,6.

and breeding condition (Table 2); mass, recruitment, and movement (Table 3); or survival (Table 4) for *T. hudsonicus*. Survival of *T. hudsonicus* decreased significantly in 2002 from previous years (Table 4). Adult male *T. hudsonicus* were significantly heavier in Kamloops than in Prince George and Penticton; while abundance and recruitment were significantly lower in Penticton than in the other sites (Table 5).

4. Discussion

4.1. Population dynamics of *G. sabrinus*

Our study was the first manipulative experiment to examine population response of *G. sabrinus* to precommercial thinning with three stand densities. We found that the average abundance of *G. sabrinus* in

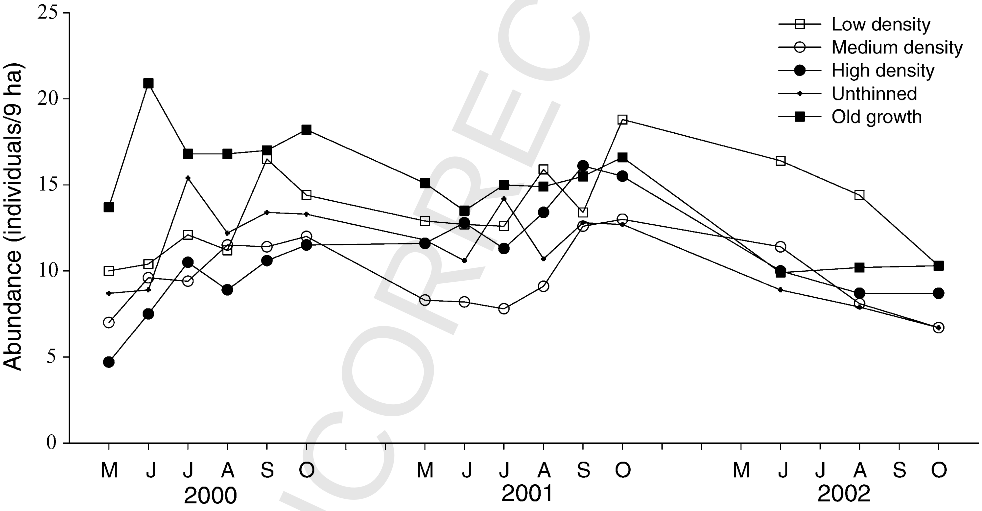

Fig. 2. Mean (n = 3 replicate stands) total abundance/9 ha of red squirrels (*T. hudsonicus*) for the five treatments and 3 years 2000–2002.

high-density stands (∼2000 stems/ha) were 70% higher than that in old-growth stands, while medium-density (∼1000 stems/ha) and old-growth stands maintained similar numbers. In addition, their abundance was significantly higher in medium- and high-density stands than unthinned stands. However, average mass of *G. sabrinus* was significantly heavier in old-growth than in high-density stands. Since abundance alone may be a misleading indicator (Van Horne, 1983; Wheatley et al., 2002), habitat quality should be evaluated in terms of breeding condition and survival attributes, as well as abundance of the species occupying the habitat. Since the majority of captures for *G. sabrinus* occurred in the fall, we could not evaluate their breeding response to thinning. However, there was no difference in mean survival of *G. sabrinus* among thinned and old-growth stands. Thus, the hypothesis that population dynamics of *G. sabrinus* would be maintained at levels recorded in old-growth forests by large-scale thinning of young stands was supported by our results. Medium- and high-density young lodgepole pine stands maintained an abundance of *G. sabrinus* significantly greater than that in unthinned young lodgepole pine stands and similar to, or greater than, that in old-growth stands.

All study sites within each block regenerated after similar disturbance events (wildfire or harvesting) and had relatively uniform tree cover, and comparable diameter, height, and density of lodgepole pine trees prior to thinning (Sullivan et al., 1996, 2001). There were no differences among stands in volume and abundance of downed wood within three diameter and five decay classes at 10 years post-thinning (Sullivan et al., 2001). Second-growth stands of lodgepole pine typically have few, if any, legacies (standing live or dead trees) from the original stand (Sullivan et al., 2001). Thus, study sites within each block were homogeneous prior to thinning. We are confident that the differences found in our study are directly attributable to stand development following pre-commercial thinning and not to inherent site differences.

Alternatively, in another study, long-tailed weasels (*Mustela frenata*) were captured more-often in unthinned than thinned stands while short-tailed weasels (*M. erminea*) favoured thinned stands (Wilson and Carey, 1996). The authors also noted that weasel predation on rodents, in general, was higher in old-growth than second-growth stands. Potentially, the significant difference in abundance of *G. sabrinus* among our stands might have resulted from differences in predation rates, rather than differences in stand quality. However, we failed to detect significant differences in survival of *G. sabrinus* and abundance of mustelid predators (Sullivan et al., 2004) among stand types. Thus, it is unlikely that variation in predation rates on *G. sabrinus* among stand types could explain the differences we observed.

G. sabrinus is primarily limited by abundance of its food (Waters and Zabel, 1995; Ransome and Sullivan, 1997, 2004) and functions as an indicator of ecological productivity (Carey and Harrington, 2001). *G. sabrinus* consume primarily the fruiting bodies of hypogeous fungi. In the short term, biomass of hypogeous fungi decreased following medium and heavy variable-density thinning (VDT) in Washington (Colgan et al., 1999). However, Colgan et al. (1999) found a shift in species dominance that resulted in a greater abundance of the more nutritious hypogeous fungi in VDT than in controls. The authors suggested that a greater abundance of hypogeous fungi might have been available in VDT stands than controls during periods of low food abundance. Similarly, long term, total relative frequency and biomass of hypogeous fungi did not vary significantly among heavily-and moderately-thinned stands, and in unthinned stands 10 and 17 years after commercial-thinning in California (Waters et al., 1994). Although we did not evaluate the response of hypogeous fungi to pre-commercial thinning, higher abundance of *G. sabrinus* in high-density stands might reflect a positive response of hypogeous fungi to thinning.

Alternatively, recent studies have found that in some habitats, *G. sabrinus* consume primarily vegetation and epigeous fungi, rather than hypogeous fungi, in southeast Alaska (Pyare et al., 2002) and southwestern British Columbia (Anderson, 2003). Our thinned stands had higher volumes of herbs and structural richness of shrubs than unthinned and old-growth stands (Sullivan et al., 2001; Lindgren et al., unpublished). Trends worth noting and possibly biologically significant were a higher volume of shrubs in thinned than old-growth stands and higher total structural diversity in thinned than unthinned and old-growth stands (Sullivan et al., 2001; Lindgren et al., unpublished). Abundance of *G. sabrinus* has been correlated with abundance of shrubs in Washington (Carey, 1995), Oregon (Rosenberg and Anthony, 1992), and the Sierra Nevada (Pyare and Longland, 2001). Potentially, changes in volume of herbs and shrubs induced by thinning might have improved the abundance of vegetative food items for *G. sabrinus,* resulting in their higher abundance in high-density than old-growth stands. Although the differences induced in these vegetative characteristics by thinning were similar among low-, medium-, and high-density stands, abundance of *G. sabrinus* was not. Canopy connectivity was significantly reduced in our low-density stands and this might have negatively impacted travel in these stands by *G. sabrinus.* In addition, to improve wood quality in low-density stands, crop trees were pruned resulting in all lower branches being removed (Fig. 1 in Sullivan et al., 2001). Actual or perceived security cover in low-density stands might have been negatively impacted, thereby resulting in a lower abundance of *G. sabrinus* than that permitted by the abundance of food.

These results are consistent with those reported for commercially thinned stands in coastal coniferous forest (Ransome and Sullivan, 2002). The authors reported that commercial thinning had no negative short-term effects on population dynamics of *G. sabrinus.* In contrast, a retrospective analysis reported that *G. sabrinus* was twice as abundant in unthinned (legacy retention) than commercially thinned stands (Carey, 2000). In Carey (2000), unthinned stands had significantly more structural characteristics that closely approximated those found in late-seral forests than thinned stands. Consequently, the difference in abundance of *G. sabrinus* between thinned and unthinned stands in Carey (2000) might have resulted from differences in stand structure rather than to reduced densities of trees (Ransome and Sullivan, 2002). This observation, if true, adds additional support to the hypothesis that wildlife species associated with structural characteristics of late-seral forests respond positively to the development of these structural characteristics in second-growth stands.

4.2. *Population dynamics of T. hudsonicus*

Overall, pre-commercial thinning to three densities had no influence 12–14 years post-thinning on abundance, breeding condition, and survival of *T. hudsonicus* when compared to unthinned and old-growth stands. In contrast, these treatments had a significant influence on *T. hudsonicus* immediately following treatments (Sullivan et al., 1996). Shortly after thinning, abundance of *T. hudsonicus* was significantly reduced in low-density stands and was generally higher (1.6–18.3 times) in medium- (two of three replicates) and high-density stands (all three replicates) than unthinned stands. In general, abundance of *T. hudsonicus* in unthinned stands was similar to that in low-density stands while their abundance in old-growth stands was similar to (two replicates) or lower (one replicate) than that in high-density stands 3 years after thinning (Sullivan et al., 1996). Sullivan et al. (1996) concluded that low-density stands (heavily thinned) provided marginal habitat for red squirrels 1–3 years following thinning. However, in the current study, habitat quality assessment based on population dynamics of *T. hudsonicus* indicated that all stands appeared to supply habitat of equal quality for this species.

Population sizes of *T. hudsonicus* are determined by food supply during years of poor food abundance, modified through spacing behaviour (Rusch and Reeder, 1978; Sullivan, 1990; Klenner and Krebs, 1991; Smith et al., 2003). *T. hudsonicus* maintains well advertised, strongly defended territories, with limited flexibility in size (Klenner, 1991). Their over-winter survival is dependent on inhabiting a territory with adequate over-winter food caches of conifer cones (Smith, 1968; Kemp and Keith, 1970; Rusch and Reeder, 1978). Consequently, changes in population sizes of *T. hudsonicus* result primarily from changes in abundance of territories with suitable food resources. Initial changes in abundance of *T. hudsonicus* in low-density stands following thinning might be best explained by the significant reduction in cone-bearing trees, significantly reducing number of territories with an adequate overwinter food supply. Mean crown volumes of lodgepole pine trees in low- and medium-density stands were significantly larger (1.6–3.0 times larger in 1998 and 1.8–6.0 times larger in 2003) than those in high-density and unthinned stands (Sullivan et al., 2001; Lindgren et al., unpublished). As trees responded to pre-commercial thinning, the increase in crown volume 12–14 years post-thinning in low-density stands might have offset the initial reduction in abundance of cones resulting from reduced densities of crop trees in years immediately after thinning.

5. Management implications

A new paradigm in forest management is managing second-growth stands to accelerate development of structural characteristics associated with late-seral forests. A key uncertainty is whether those wildlife species associated with these structural characteristics will respond positively to their development in thinned, young seral forests. Our results showed that population dynamics of *G. sabrinus* and *T. hudsonicus* would be maintained in young thinned stands at levels recorded in old-growth forests. In fact, habitat quality for *G. sabrinus,* based on population dynamics, in high-density, pre-commercially thinned stands appeared to exceed that in old-growth stands. Furthermore, abundance of *G. sabrinus* in young lodgepole pine stands were maintained at higher levels in pre-commercially thinned stands than that in unthinned stands. Consequently, pre-commercial thinning may be used to enhance populations of *G. sabrinus* in young lodgepole pine stands.

Our knowledge of long-term responses to thinning is scant (Hayes et al., 1997). However, our study adds to the growing body of knowledge that indicates thinning can enhance habitat for species associated with late-seral conditions (Hayes et al., 1997; Carey and Wilson, 2001; Ransome and Sullivan, 2002; Suzuki and Hayes, 2003; Sullivan et al., 2004). With the exception of the latter two studies, and our study, stands were commercially thinned. Stands commercially thinned might be susceptible to extensive windthrow, as reported in Ransome and Sullivan (2002) and provide a lower economical yield over the long term (Hayes et al., 1997). Pre-commercial thinning in young stands might accelerate development of late-seral structural characteristics decades earlier, provide habitat for species associated with these structural features, and reduce the potential for windthrow occasionally associated with commercial thinning. In our study, pre-commercial thinning resulted in homogeneous stands with trees spaced evenly throughout. Our result might be enhanced further by thinning with variable spacing (variable-density thinning), coupled with legacy retention and management for decadence (Carey, 2000).

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