Small-mammal response to group-selection silvicultural systems in Engelmann spruce – subalpine fir forests 14 years postharvest

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Abstract: Concerns about the impacts of clear-cut harvesting on ecosystem components in subalpine forests have generated a variety of alternative silvicultural systems in high-elevation forests in western North America. We examined responses of forest-floor small mammals, 14 years posttreatment, in four replicate units, uncut forest, a 1.0 ha group-selection cut, a large (>30 ha) clearcut, and the edge between the group-selection cut and uncut forest, in the Engelmann Spruce (*Picea engelmannii* Parry ex Engelm.) – Subalpine Fir (*Abies lasiocarpa* (Hook.) Nutt.) biogeoclimatic zone in south-central British Columbia, Canada. Populations of small mammals were livetrapped during five sessions from June to September 2006. The mean abundance of southern red-backed voles (*Myodes gapperi* Vigors) was significantly lower on large clearcuts than in uncut old-growth forests, with intermediate numbers in 1 ha cuts. The opposite trend was found for dusky shrews (*Sorex monticolus* Merriam), while there was no significant difference in mean abundance of deer mice (*Peromyscus maniculatus* Wagner) among treatments. Trappability, proportion of adult females breeding, and rate of survival of red-backed voles and deer mice were similar among treatments. Our results suggest that group-selection silviculture conducted in subalpine forests may have fewer negative impacts on the small-mammal community than large clearcuts.

Résumé : Les préoccupations d'ordre écologique au sujet des impacts de la coupe à blanc sur les composantes des écosystèmes en forêt subalpine ont favorisé le développement d'une variété de systèmes sylvicoles alternatifs dans les forêts de haute altitude de l'ouest de l'Amérique du Nord. Nous avons examiné les réponses des petits mammifères du parterre forestier dans quatre unités répétées de forêts non coupées, de coupes de jardinage par groupe de 1,0 ha, de grandes coupes à blanc (>30 ha) et de limites entre des coupes de jardinage par groupe et des forêts non coupées, 14 ans après les traitements, dans une forêt d'épinette d'Engelmann (*Picea engelmannii* Parry ex Engelm.) et de sapin subalpin (*Abies lasiocarpa* (Hook.) Nutt.), dans le centre-sud de la Colombie-Britannique, au Canada. Les populations de petits mammifères ont fait l'objet de cinq sessions de piégeage vivant de juin à septembre 2006. L'abondance moyenne du campagnol à dos roux de Gapper (*Myodes gapperi* Vigors) était significativement plus faible dans les grandes coupes à blanc que dans les forêts non coupées et atteignait des valeurs intermédiaires dans les coupes de 1 ha. La tendance inverse a été observée chez la musaraigne sombre (*Sorex monticolus* Merriam), tandis qu'il n'y avait pas de différence significative entre les traitements dans le cas de la souris sylvestre (*Peromyscus maniculatus* Wagner). Il n'y avait pas de différences entre les traitements dans le cas de la susceptibilité à la capture, de la proportion de femelles adultes reproductrices et de la survie du campagnol à dos roux de Gapper et de la souris sylvestre. Nos résultats indiquent qu'une approche sylvicole basée sur le jardinage par groupe, lorsqu'elle est appliquée en forêt subalpine, peut avoir moins d'impacts négatifs sur les petits mammifères que la coupe à blanc.

[Traduit par la Rédaction]

Introduction

Meeting biodiversity and sustainability objectives is important in directing forest-management activities across a wide range of ecosystems in North America (Hansen et al. 1991; Carey and Curtis 1996). In British Columbia (BC), high-elevation forestry is relatively new, and many questions arise relating to the sustainability of management practices (Farnden 1994). The Engelmann Spruce (*Picea engelmannii* Parry) – Subalpine Fir (*Abies lasiocarpa* (Hook.) Nutt.) (ESSF) biogeoclimatic zone extends from northern BC to New Mexico. This zone is the uppermost forested zone in BC, situated below the Alpine Tundra zone, and constitutes approximately 14% of BC's 95 × 10^6 ha total area (Meidinger and Pojar 1991). Our current understanding of the influence of forestry operations on these high-elevation forests, and their unique assemblage of animal species

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adapted to a snow-dominated climate, is limited (Vyse 1997). Consequently, the ecological sustainability and economic feasibility of managing these forests have been questioned (Farnden 1994; Vyse 1997). However, in light of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemic, pressure to harvest these forests will increase. However, clear-cutting these high-elevation stands has led to concerns about negative long-term impacts on wildlife habitat, biodiversity, and sustainability.

To address these concerns, group-selection silvicultural trials were established throughout BC in the 1990s to examine alternative harvesting techniques in the ESSF zone. In these trials, the effect of different opening sizes, ranging from single-tree harvest to 10 ha clearcuts, on various ecological parameters was examined.

Population and community parameters for forest-floor small mammals can be used as bio-indicators of sustainable forest management (Pearce and Venier 2005). Bio-indicator species that are particularly associated with mature late-succession forest types, such as the southern red-backed vole (*Myodes gapperi* Vigors), help determine the effect of structural changes resulting from forest-management practices (Klenner and Sullivan 2003; Pearce and Venier 2005). As a microtine that commonly inhabits late-successional coniferous and deciduous forests across temperate North America (Merritt 1981), the red-backed vole is an important indicator species of “old forest conditions” (Raphael 1988; Nordyke and Buskirk 1991).

Klenner and Sullivan (2003) examined the population dynamics of small mammals across five treatments: uncut forest, single-tree selection, 0.1 ha patch cut, 1.0 ha patch cut, and 10 ha clearcut. They found that during 4 posttreatment years, abundance, survival rates, and reproduction rates of southern red-backed voles, the dominant species on their sites, did not differ significantly among uncut forest, single-tree selection, and patch cuts. However, red-backed vole populations declined to extirpation on 10 ha clearcuts. In contrast, long-tailed voles (*Microtus longicaudus* Merriam) attained their highest abundance in 10 ha clearcuts and were absent in uncut forests (Klenner and Sullivan 2003). Those authors also reported that there was no difference in abundance of red-backed voles between 1.0 ha patch cuts and edges between uncut forest and 10.0 ha clearcuts.

Waterhouse et al. (2004) examined the population dynamics of small mammals across four treatments: uncut forest and 0.03, 0.13, and 1.0 ha group-selection cuts. The results paralleled those of Klenner and Sullivan (2003) in that the dominant species on treatment sites was the red-backed vole, and the former authors failed to detect significant differences in its abundance among uncut forest and patch cuts for 2 years posttreatment. However, red-backed voles used the harvested openings less than the surrounding forest within each treatment (Waterhouse et al. 2004). Common shrews (*Sorex cinereus* Kerr) showed some preference for unharvested treatments and 1 ha group-selection cuts (Waterhouse et al. 2004). In both studies (Klenner and Sullivan 2003; Waterhouse et al. 2004), deer mice (*Peromyscus maniculatus* Wagner) were present in low abundance on all sites.

Hayward et al. (1999) also studied the response of red-backed voles to high-elevation patch cuts (mean area 1.8 ha; range 0.6–3.9 ha) in southern Wyoming for 2 years postharvest and found that they did not strongly avoid the interior of patch cuts or edge habitats. This microtine used the interior of patch cuts less than edge habitats in both posttreatment years and less than forest habitat in 1 posttreatment year. This result contrasts with that of Mills (1995), who reported that California red-backed voles (*Myodes californicus* Merriam) avoided edges of small (0.6–2.5 ha) remnant forest patches in a matrix of heavily fragmented forest. The high-elevation forests studied by Hayward et al. (1999) in Wyoming and Klenner and Sullivan (2003) and Waterhouse et al. (2004) in BC represent “perforated” forest landscapes, where fragmentation is much less than at lower elevations, and uncut old-growth forest represents the matrix.

Those studies documented the immediate and short-term responses of small mammals to group-selection cuts in high-elevation forests. However, populations of red-backed voles may persist in treatments immediately following harvest, then decline in subsequent years (Hayward et al. 1999; Sullivan and Sullivan 2001). Thus, long-term studies are needed to adequately determine the influence of group-selection harvest on forest-floor small mammals. Consequently, we revisited the study described by Waterhouse et al. (2004) to reexamine the population dynamics of small mammals in high-elevation forests in response to 1.0 ha group-selection cuts, large clearcuts, and uncut forest 14 years postharvest. This periodic sample was taken after a period of time that was presumably sufficient for vegetative succession and regeneration of conifers to substantially alter habitat conditions for small mammals.

We tested three predictive hypotheses. Firstly, group-selection cuts (1 ha openings) and clearcuts would supply suboptimal habitat for red-backed voles compared with uncut forest. We based this prediction on the observations that red-backed voles used the interior of patch cuts less than edge habitats and uncut forests (Hayward et al. 1999). Secondly, red-backed voles would respond to the edge habitat between a 1 ha opening and uncut forest, as reported by Hayward et al. (1999) and Mills (1995) for perforated (no avoidance) and fragmented (avoidance) forests, respectively. Thirdly, deer mice and dusky shrews (*Sorex monticolus* Merriam), being habitat generalists, would be equally abundant on all treatments, based upon the observations of Klenner and Sullivan (2003) and Waterhouse et al. (2004).

Study areas and methods

Study areas

Four replicate study areas were located 12–28 km east of Likely in south-central BC. Two sites, Upper and Lower Grain Creek (52°41′29″N, 121°12′02″W, and 52°40′45″N, 121°10′52″W, respectively), were located within the Grain Creek watershed. The remaining two sites, Upper and Lower Blackbear Creek, were located in the Blackbear Creek watershed (52°36′37″N, 121°24′30″W, and 52°36′57″N, 121°24′30″W). All study sites were submesic to mesic and within the ESSF wet, cold biogeoclimatic subzone variant ($\mathrm{ESSF}_{\mathrm{wc3}}$; Meidinger and Pojar 1991). The ESSF zone is the uppermost forested zone in the southern interior of BC, and is characterized by a relatively cold, moist climate with short cool summers and long cold winters. Mean annual temperatures range from –2 to 2 °C and mean monthly temperatures are below 0 °C for 5–7 months and above 10 °C for only 2 months (Meidinger and Pojar 1991). Most precipitation (50%–70%) occurs as snow. Sites extended from 1440 to 1690 m elevation; above this elevation the forest becomes subalpine parkland. Slopes were similar at all sites, ranging from 15% to 40%, while aspect was northeast at Blackbear Creek, northwest at Lower Grain Creek, and west at Upper Grain Creek (Steen et al. 2005).

The original study (Waterhouse et al. 2004) included a randomized complete block design with four 10 ha treatment units randomly assigned within each site: one old-growth and three group-selection treatments varying in opening size (0.03 ha (small), 0.13 ha (medium), and 1.0 ha (large)). In the present study, only the old-growth (C; Fig. 1) and 1.0 ha group-selection treatments (B and D; Fig. 1) were used. In addition to the original study design, two large (>30 ha) clearcuts were sampled (A; Fig. 1), each constituting two experimental units, resulting in sacrificial pseudoreplication (Hurlbert 1984).

The dominant climax coniferous species in old-growth stands was subalpine fir (Steen et al. 2005). The oldest trees were spruces ranging in age from 290 to 310 years on the Blackbear Creek sites and from 460 to 480 years on the Grain Creek sites. However, old-growth stands were multi-aged and multi-layered as a result of single-tree and group-tree mortality due to insect attack, disease, and windthrow. Tree density in old-growth stands ranged from 283 to 474 trees/ha and snag densities ranged from 68 to 262 stems/ha (Waterhouse et al. 2004). Volume of coarse woody debris (≥7.5 cm dbh) ranged from 317 m^3/ha on the Blackbear Creek sites to 354 m^3/ha on the Grain Creek sites. Understory ground cover in old-growth stands included a dense shrub layer dominated by white-flowered rhododendron (*Rhododendron albiflorum* Hook.) (45%) and a well-developed moss layer (primarily *Brachythecium* spp.) (40%) with a minor component of black huckleberry (*Vaccinium membranaceum* Dougl. ex Hook.) (5%), oak fern (*Gymnocarpium dryopteris* (L.) Newm.) (6.0%), and Sitka valerian (*Valeriana sitchensis* Bong.) (7.5%) (Waterhouse 2005).

All group-selection cuts and clearcuts were harvested with feller-bunchers, while hand-falling was used for the largest spruce. Skidding was ground-based, using tracked and rubber-tired skidders. Harvesting took place from December 1992 to January 1993 at the Grain Creek and Upper Blackbear Creek sites. Harvesting was done on a snowpack of 0.5–1.5 m depth to minimize forest-floor disturbance. Harvesting at the Lower Blackbear Creek sites was done during summer 1992.

The large (34.8 ha) clearcut at Grain Creek (A; Fig. 1) was harvested in the winter of 1993 and planted with Engelmann spruce and lodgepole pine (*Pinus contorta* Dougl. ex Loud.). The large (30.5 ha) clearcut at Blackbear Creek was harvested in the fall of 1992 and also planted with Engelmann spruce and lodgepole pine. Clearcuts were harvested using both ground-based skidding and highlead yarding. Both clearcuts were dominated by white-flowered rhododendron and black huckleberry with a minor component of fireweed (*Epilobium angustifolium* L.).

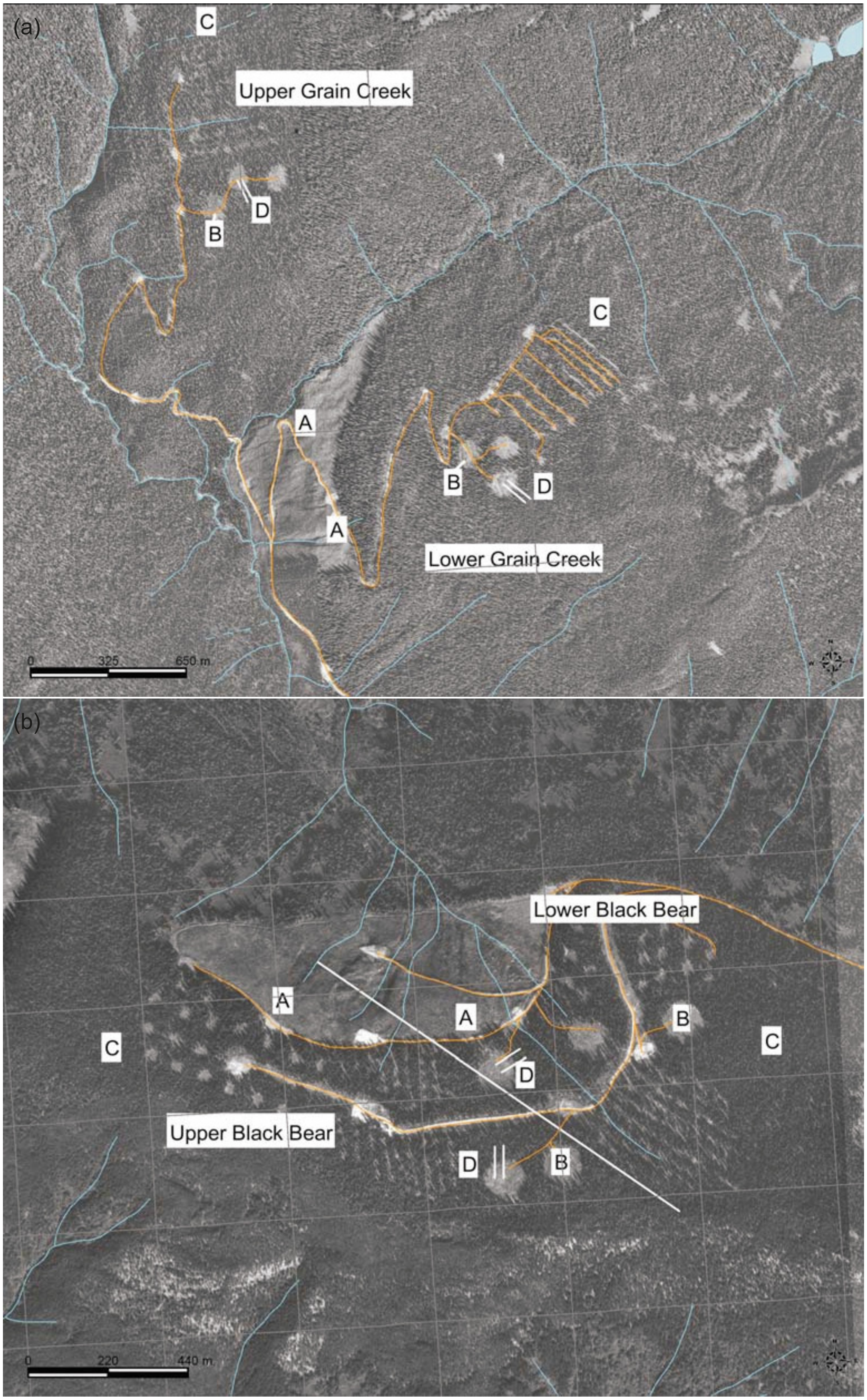
Livetrapping and demographic analysis

Populations of small mammals were livetrapped every 3 weeks from June to October 2006 (five sessions). For the main experiment (hypotheses 1 and 3), a 1 ha livetrapping grid with 49 stations (7 × 7) at 14.3 m intervals was established in large clearcuts, 1 ha group-selection cuts, and old-growth stands in all study sites (A, B, and C, respectively, in Fig. 1). For the edge experiment (hypothesis 2), two transects, each nine stations long, were established 14.3 m apart in a second 1 ha group-selection cut (D in Fig. 1). Each transect had nine stations at 14.3 m intervals, centred (station 5) on the canopy drip line, and four stations extending into the forest and the 1 ha opening. Stations 1–3 were classified as clearcut habitat, with station 1 in the centre of the opening. Stations 4–6 were classified as edge habitat. Stations 7–9 were classified as old-growth habitat. Each of the stations on grids and transects contained one Longworth-type live trap baited with whole oats and carrot (for moisture) and was supplied with coarse brown cotton for insulation. Traps were set in the evening on day 1 and checked in the morning of days 2 and 3, then closed until the next trapping session. Traps were closed in the morning of day 2 and reset that evening if the daytime temperature had exceeded 25 °C.

All small mammals captured were identified with individually numbered ear tags and released at point of capture. For each animal captured, ear-tag number, location, body mass, gender, and breeding condition were recorded. Females were categorized as "nonbreeding" (small mammaries) or "breeding" (large mammaries). The breeding condition of males was evaluated by palpating the testes and they were categorized as nonbreeding (testes abdominal) or breeding (testes scrotal; Krebs et al. 1969).

For the main experiment (large clearcut, 1 ha group-selection cut, and old-growth stands), trappability, population size, percentage and number of individuals in breeding condition, and rate of survival of red-backed voles and deer mice were estimated. These parameters were compared among treatments to evaluate the influence of harvesting method on these two species. Jolly trappability is the probability that an individual that is present in the population will be captured in that particular trapping session (Krebs and Boonstra 1984). Because the number of captures of deer mice in the old-growth stand at Lower Grain Creek was low, trappability estimates for this study site were not included in the analysis. Population size was estimated for each trapping session using the Jolly–Seber (J–S) stochastic model (Seber 1982). The reliability of J–S estimates decreases when few tagged animals are captured (Krebs et al. 1986). Therefore, the minimum number of animals known to be alive (MNA; Krebs 1966) was also calculated as a precautionary measure and to indicate the lower limits of the J–S estimates. MNA estimates were used for the first and last trapping sessions for all study sites and for all estimates of deer mouse population size on the Lower Grain Creek study sites. The J–S model did not estimate population size for these sessions. All statistical tests were based on J–S estimates (including MNA substitutions) for the reasons indicated by Jolly and Dickson (1983). Abundance of shrews was based on total captures (live and dead individuals) per

Fig. 1. Locations of the (*a*) Upper and Lower Grain Creek and (*b*) Upper and Lower Blackbear Creek study sites in the southern interior of British Columbia. Each study site contained four treatments: one large clearcut (A), two 1 ha group-selection cuts (B and D), and an old-growth stand (C).



trapping session, averaged across five sessions for each study site.

Jolly survival was calculated for each trapping session (Nichols and Pollock 1983) for red-backed voles in all study sites, and for deer mice in all sites except Lower Grain Creek. Jolly survival does not distinguish between mortality and emigration. For deer mice on the Lower Grain Creek sites, minimum survival estimates were substituted for Jolly survival (Krebs 1966). Comparison of reproductive performance among treatments was based upon the number of successful pregnancies calculated for each trapping session (Klenner and Sullivan 2003; Sullivan et al. 2005). Each record of a lactating female was considered an independent successful pregnancy, based upon a 3-week nursing period within our 3-week trapping interval (Klenner and Sullivan 2003). The percentage of adult females in breeding condition was estimated by dividing the number of successful pregnancies by the total number of adult females captured during each trapping session. Body mass of red-backed voles and deer mice was used to classify individuals as adult (≥19 g) or non-adult (<19 g; i.e., subadults and juveniles; Klenner and Sullivan 2003; Sullivan et al. 2005).

Experimental design and statistical analysis

The main experiment (large clearcut, 1 ha group-selection cut, and old-growth stands) was a randomized complete block design with three treatments and four blocks: Upper Grain Creek, Lower Grain Creek, Upper Blackbear Creek, and Lower Blackbear Creek. The Blackbear Creek sites varied in their time of harvesting (summer or winter), potentially causing variation in the degree of soil compaction and amount of understory development, and so were kept as two distinct blocks. Similarly, the Grain Creek sites varied in aspect; were associated with different drainage systems (Fig. 1), and varied 3-fold in seedling density and 1.5-fold in volume of coarse woody debris in decay classes 4 and 5 (Steen et al. 2005). Consequently, these sites were treated as independent blocks. Differences in trappability, population size, survival rate, and reproduction rate for red-backed voles and deer mice among treatments were evaluated by a two-way ANOVA (Zar 1999). These parameters were estimated for each trapping session and averaged across all trapping sessions for each grid, prior to performing ANOVAs. When distributions deviated significantly from normality, survival rate and proportion of adult females breeding were arcsine-transformed and number of successful pregnancies was square-root-transformed before performing ANOVAs to better approximate a normal distribution. Bonferroni's post-hoc multiple-comparison tests were used to determine significant differences in parameters among treatments.

The edge experiment was a randomized complete block design with three treatments (opening, edge, and old growth) and four blocks: Upper Grain Creek, Lower Grain Creek, Upper Blackbear Creek, and Lower Blackbear Creek. Differences in the number of individual red-backed voles or deer mice captured among treatments were evaluated by a two-way ANOVA (Zar 1999). Counts were square-root-transformed before performing ANOVAs to better approximate a normal distribution. For all comparisons, differences were considered significant if $P \leq 0.05$.

Results

In the main experiment we captured 1641 individuals belonging to 10 forest-floor small-mammal species, with captures totalling 2751 (Table 1). The most abundant small-mammal species was the red-backed vole (43.9% of all small mammals captured), followed by the dusky shrew (24.6%), deer mouse (18.4%), and common shrew (5.8%). In total, these four species accounted for 92.7% of small mammals captured in all treatments and blocks. Captures of all other species varied among treatments and blocks (Table 1). Trappability of red-backed voles was high, averaging 93% across all blocks and treatments (Table 2). Estimates of abundance of red-backed voles did not differ significantly between J–S (18.6 individuals) and MNA (17.8 individuals; t_{35} = 0.06) methods. Mean abundance of red-backed voles was significantly higher in old-growth stands than in large clearcuts (Fig. 2A, Table 2). Mean abundance in 1 ha group-selection cuts was intermediate between, but not significantly different from, abundances in large clearcuts and old-growth stands. Similarly, the number of successful pregnancies was significantly higher in old-growth stands than in large clearcuts. In contrast, proportions of adult females with successful pregnancies and survival rates of adult red-back voles were similar among treatments.

Total captures of dusky shrews differed significantly among treatments, with large clearcuts having the greatest abundance and old-growth stands the lowest (Table 2). In contrast, abundance of common shrews was low in all sites and abundances were similar among treatments (Table 2).

Trappability of deer mice was similar among treatments and averaged 88% across all sites (Table 2). J–S estimates of mean abundance of deer mice (12.1 individuals) was 8% higher than MNA estimates (11.2 individuals; t_{35} = 0.002). There were no significant differences in mean abundance of deer mice among treatments (Fig. 2B, Table 2). Similarly, we failed to detect significant differences in the number of successful pregnancies, proportion of adult females with successful pregnancies, and rates of survival of deer mice among treatments (Table 2). Captures of the remaining six species varied among treatments and blocks, with most occurring in harvested sites: 97.3% for meadow voles (*Microtus pennsylvanicus* Ord), 93.8% for western jumping mice (*Zapus princeps* J. A. Allen), and 100% for northwestern chipmunks (*Tamias amoenus* J. A. Allen), long-tailed voles, and short-tailed weasels (*Mustela erminea* L.).

In the edge experiment we captured 278 individuals belonging to nine forest-floor small-mammal species, with captures totalling 395 (Table 3). The most abundant species was the red-backed vole, with a total of 137 individuals captured. Only 11 individuals were captured in more than one treatment: 8 individuals were captured in both old-growth and edge habitat and 3 in all three treatments. Of the 62 deer mice captured, only 8 were found in more than one treatment: 4 in both edge habitat and old growth, and 3 in group-selection cuts and edge habitat. We failed to detect significant differences in number of captures among treatments for either red-back voles or deer mice (Table 3). However, total captures of all species were significantly greater in group-selection cuts and edge habitat than in old growth (Fig. 3, Table 3). Shrews were captured in all treat-

Table 1. Numbers of individual small mammals captured in three treatments in four replicate study blocks in the southern interior of British Columbia in 2006.

	Upper Grain Creek			Lower Grain Creek			Upper Blackbear Creek			Lower Blackbear Creek		
Species	A	B	C	A	B	C	A	B	C	A	B	C
Red-backed vole	14	78	94	22	68	83	52	55	90	45	52	68
Deer mouse	21	15	18	30	19	5	58	36	12	28	27	33
Long-tailed vole	—	1	—	—	—	—	—	—	—	2	1	—
Meadow vole	3	17	—	—	—	—	—	—	—	—	25	3
Northwestern chipmunk	3	—	—	8	—	—	—	1	—	—	2	—
Heather vole	1	3	2	2	—	—	2	—	1	2	1	4
Western jumping mouse	3	7	2	7	3	—	7	3	—	—	—	—
Dusky shrew	42	42	17	41	26	21	52	36	23	42	32	29
Common shrew	7	2	17	10	14	6	3	2	7	8	11	8
Short-tailed weasel	—	—	—	—	—	—	1	2	—	1	—	—
Total	94	165	150	120	130	115	175	135	133	128	151	145

Note: A, large clearcut; B, 1 ha group-selection cut; C, old-growth stand.

Table 2. Estimates (mean ± SE (n = 4 blocks) of trappability, abundance (Jolly–Seber population estimates), reproduction rates (number of successful pregnancies and proportion of adult females with successful pregnancies), and survival rates for red-backed voles and deer mice in large clearcuts, 1 ha group-selection cuts, and old-growth stands in the southern interior of British Columbia in 2006.

				Treatment	
	Large clear-cut	1 ha group-selection cut	Old-growth stand	$F_{[2,6]}$	p
Red-backed vole					
Trappability	0.91±0.08	0.92±0.03	0.97±0.01	0.29	0.76
Abundance	8.4±1.9a	19.0±2.3ab	27.3±3.1b	9.30	0.02
Reproduction rate					
Number	5.8±2.9a	21.5±2.0ab	37.0±5.2b	15.00	0.005
Proportion	0.77±0.16	0.78±0.02	0.87±0.01	0.32	0.74
Survival rate	0.60±0.09	0.60±0.06	0.64±0.04	0.18*	0.84
Deer mouse					
Trappability	0.82±0.07	0.96±0.02	0.85±0.09	0.81*	0.47
Abundance	11.6±2.0	9.6±1.4	6.6±1.2	1.13	0.49
Reproduction rate					
Number	9.3±2.4	6.5±2.9	5.0±1.8	1.35	0.33
Proportion	0.73±0.04	0.53±0.21	0.63±0.22	0.33	0.73
Survival rate	0.60±0.07	0.70±0.04	0.74±0.07	1.07*	0.43
Dusky shrew					
Abundance	44.3±2.6a	34.0±3.4ab	22.5±2.5b	13.9	0.005
Common shrew					
Abundance	7.0±1.5	7.3±3.1	9.5±2.5	0.40	0.69

Note: Values followed by the same letter are not significantly different as indicated by ANOVA and Bonferroni's post-hoc multiple-comparison tests.

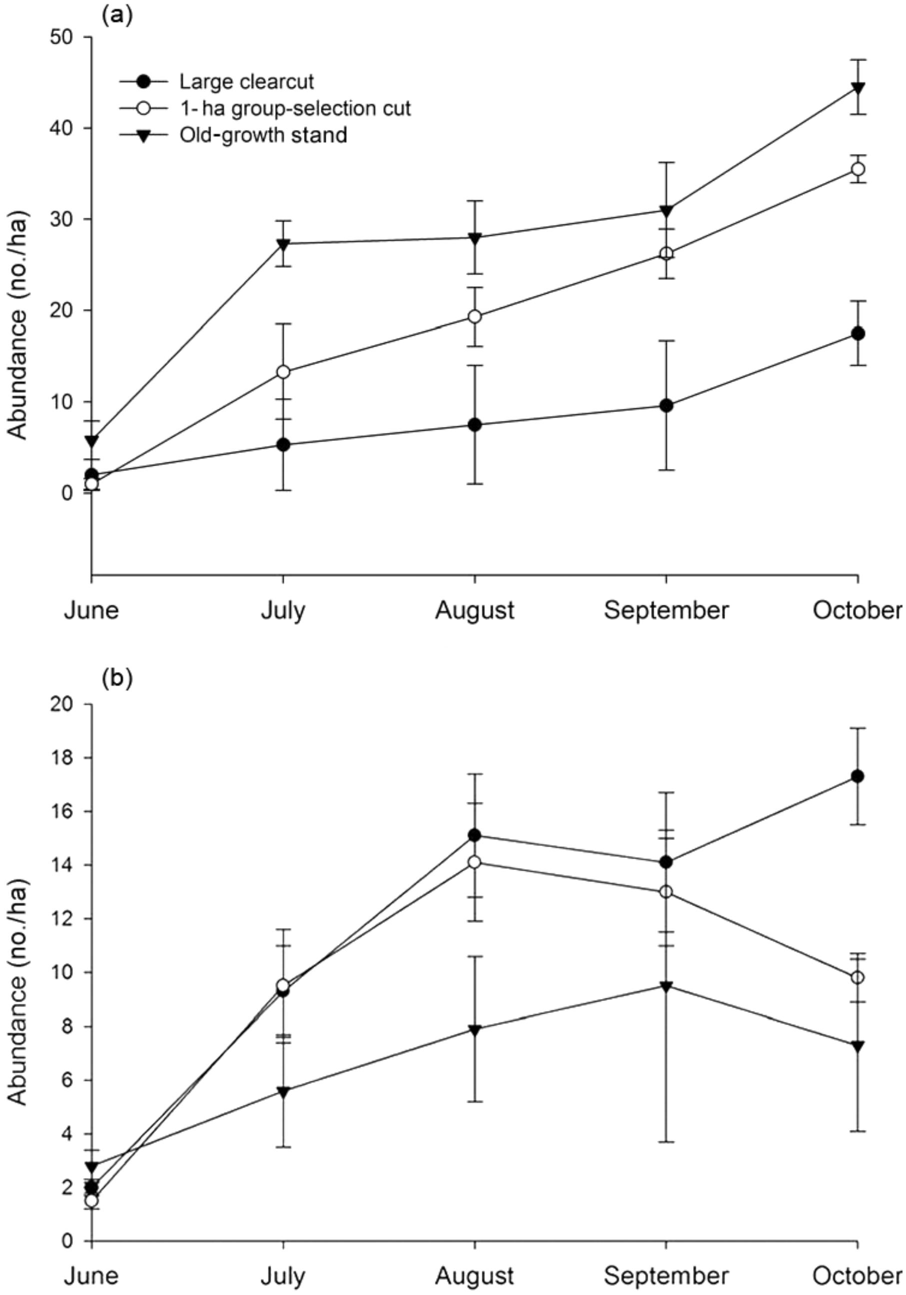
*2,4 degrees of freedom for treatment.

ments, while the remaining five species (northwestern chipmunk, *Microtus* spp., heather vole (*Phenacomys intermedius* Merriam), and western jumping mice) were captured only in group-selection cuts and edge habitat.

Discussion

The pattern of abundance of small mammals among treatments paralleled patterns in other studies performed in the ESSF zone (Klenner and Sullivan 2003; Waterhouse et al. 2004). The community was dominated primarily by red-backed voles and deer mice. Overall trappability for red-backed voles (93%) and deer mice (88%) was high and among the highest for these species in BC (Sullivan and Sullivan 2001; Sullivan et al. 2005). Consequently, estimated demographics (abundance, reproduction rate, and survival rate) accurately reflect those of the trappable population and provide reliable parameters for evaluating the influence of treatment effects on these species. Proportions of females in breeding condition and rates of survival

Fig. 2. Jolly–Seber estimates (mean ± SE; *n* = 4 blocks) of abundance of red-backed voles (*a*) and deer mice (*b*) in 1 ha group-selection cuts, large clearcuts, and old-growth stands in the southern interior of British Columbia in 2006.



of red-backed voles and deer mice did not differ significantly among treatments. Therefore, evaluating treatment effects on habitat quality for these species could presumably be based on abundance alone (Van Horne 1983).

The question of whether a single year of abundance data can be used for species that potentially exhibit multi-annual fluctuations in numbers needs to be addressed. The population dynamics of species in the genus *Clethrionomys/Myodes* appear to be highly variable, ranging from regular 3 to 4 year cycles to irregular fluctuations in Europe and Asia, but numbers being relatively stable in North America (Fuller 1985; Henttonen et al. 1985; Gilbert and Krebs 1991). However, as noted by Klenner and Sullivan (2009), there is a dearth of relatively long-term population data for *M. gapperi* in temperate and boreal forests of North America, and hence patterns of population fluctuations are not clear. In this connection, winter irruptions of owls in the boreal forest of eastern North America may be related to fluctuations in populations of small mammals, particularly *M. gapperi* (Cheveau et al. 2004).

Microtus spp. (long-tailed voles and meadow voles) were captured in low numbers and in only 5 of the 12 study sites. These species exhibit cyclic fluctuations in abundance every 3–5 years (Krebs and Myers 1974; Krebs 1996) and appear synchronous across geographic areas (Taitt and Krebs 1985). The low abundance of *Microtus* spp. may have been associ-

Table 3. Numbers of individual small mammals captured in three treatments on four replicate study blocks in the southern interior of British Columbia in 2006.

	Upper Grain Creek			Lower Grain Creek			Upper Blackbear Creek			Lower Blackbear Creek			Treatment	
	GSC	E	OG	GSC	E	OG	GSC	E	OG	GSC	E	OG	$F_{[2,6]}$	*P*
Red-backed vole	10	11	14	6	9	19	11	16	11	4	10	16	0.86	0.47
Deer mouse	5	8	3	7	7	1	7	5	1	7	5	6	2.11	0.20
Long-tailed vole	—	—	—	1	4	—	—	—	—	—	1	—	—	—
Meadow vole	—	—	—	—	—	—	—	—	—	5	5	—	—	—
Northwestern chipmunk	—	—	—	1	1	—	2	1	—	1	—	—	—	—
Heather vole	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Western jumping mouse	2	1	—	—	—	—	—	—	—	1	1	—	—	—
Sorex spp.	7	7	1	5	1	4	8	3	7	4	4	—	—	—
Total	24	27	18	20	22	24	28	25	19	23	26	22	6.70	0.03

Note: GSC, 1 ha group-selection cut; E, edge; OG, old-growth stands.

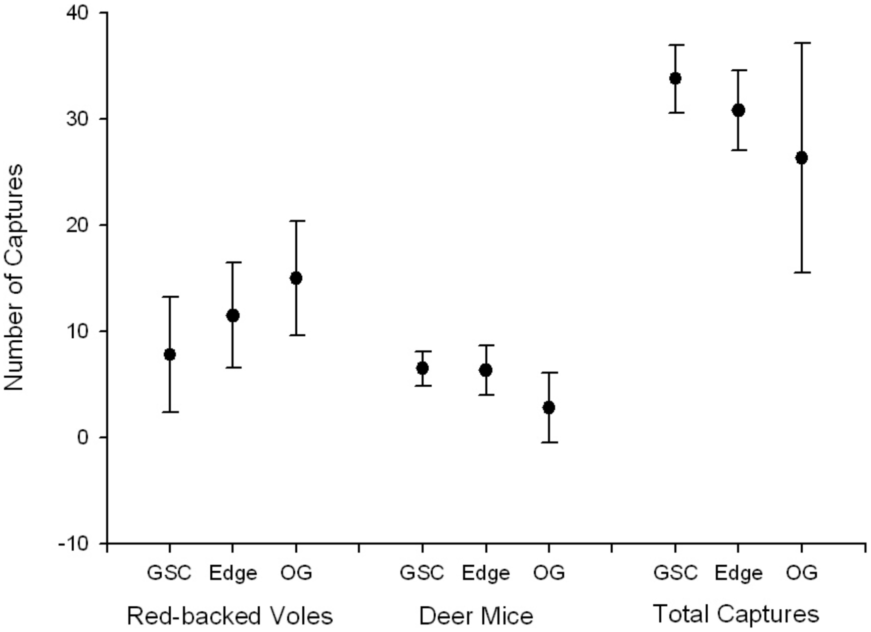
ated with the low phase of their population cycle. Therefore, a more accurate assessment of the effects of group-selection cuts on *Microtus* spp. would require multiyear sampling.

Large clearcuts maintained significantly fewer red-backed voles than did old-growth stands. Thus, our hypothesis 1, that 1 ha group-selection cuts and clearcuts supply suboptimal habitat for red-backed voles compared with uncut forests, was only partially supported. Mean abundance of red-backed voles on 1 ha group-selection cuts was intermediate between, but not significantly different from, their low abundance on large clearcuts and high abundance in old-growth stands. These results are similar to those of other studies in which no differences were reported in the responses of red-backed voles to openings of various sizes (<1–4 ha) in high-elevation (Hayward et al. 1999; Klenner and Sullivan 2003) and low- to mid-elevation forests (Steventon et al. 1998; Gitzen and West 2002). However, their abundance was significantly lower on large clearcuts than in small openings (Klenner and Sullivan 2003; this study).

Many authors have reported that red-backed voles declined to near extirpation on clearcuts in western North America (Sullivan et al. 1999; Sullivan and Sullivan 2001). It appears that small (<4 ha) clearcuts and group-selection silvicultural systems create sufficient habitat to support healthy populations of red-back voles; although their abundance appears to be lower, though not consistently and significantly, than in old-growth forests. This is supported by the observation that red-backed voles tend to use the interior of group-selection cuts less than edge habitat (Hayward et al. 1999), though not consistently (Klenner and Sullivan 2003; this study). Thus, the prediction of hypothesis 2, that red-backed voles will not avoid edges in perforated forest, seemed to be supported for our study sites in the perforated ESSF landscape, at least for 1 ha openings, 14 years postharvest. Keinath and Hayward (2003) reported similar findings for edge use by red-backed voles in regenerating stands in Wyoming, where voles would cross edges into older (20–30 years postharvest) cuts.

Which features differ sufficiently between 1 ha group-selection cuts and large clearcuts that the larger openings provide only suboptimal habitat for red-backed voles is a key question. Potentially, red-backed voles were moving through group-selection cuts rather than being resident within them. Gillis and Nams (1998) suggested that when distances between patches of old-growth forest were small, red-backed voles readily crossed suboptimal openings to reach old-growth stands, treating the openings as part of their home range. However, if distances become too great (>20 m), they may no longer cross these unfavourable openings. It is unlikely this behavioural mechanism can explain their use of 1 ha group-selection cuts in our study. Trappability of red-backed voles was high, indicating that individuals were using 1 ha openings regularly rather than just passing through them. In addition, Jolly survival does not distinguish between mortality and emigration. The consistency of this parameter among treatments indicated that individuals were behaving similarly with respect to emigration. If voles were primarily moving through openings to gain access to old-growth forests, a lower survival rate would have been documented for 1 ha group-selection cuts than for old-growth forests. Finally, of 121 voles cap-

Fig. 3. Total captures (mean ± SE; *n* = 4 blocks) of red-backed voles, deer mice, and all species in 1 ha group-selection cuts (GSC), edge, and old-growth stands (OG) in the southern interior of British Columbia in 2006.



tured on transects, only 2.5% were captured in both the old-growth and the interior of 1 ha group-selection cuts. The majority of voles were captured within one habitat or two adjacent habitats. Thus, red-backed voles appeared to be residents of 1 ha openings rather than just moving through them.

Coarse woody debris (CWD), fungal sporocarps, a moisture gradient, and understory cover have all been identified as important habitat features for red-backed voles (Merritt 1981). Tallmon and Mills (1994) found that 98% of relocations of California red-backed voles in southwestern Oregon coincided with the presence of CWD. In contrast, Sullivan and Sullivan (2001) found no relationship between abundance of southern red-backed voles and dispersed CWD in BC. Fruiting bodies of hypogeous fungi are a major food item for red-backed voles (Fogel and Trappe 1978; Ure and Maser 1982). Total dry mass of hypogeous fungi in CWD exceeded that in soil more than 10-fold in mature forests in California (Amaranthus et al. 1994). Potentially, the association between red-backed voles and CWD noted by Tallmon and Mills (1994) may have been due more to abundance of food than to physical structure supplied by CWD.

Subalpine fir was the dominant tree species in old-growth stands, and its root system can extend up to 13 m from the trunk (Stone and Kalisz 1991), potentially reaching 70% of a 1 ha opening. Hagerman et al. (1999) found that the number of fine roots and the diversity of ectomycorrhizae in clearcuts decreased significantly with distance from the forest edge in ESSF patch cuts in BC. Consequently, production of fruiting bodies of ectomycorrhizal fungi would be greater in openings adjacent to old growth than in the centre of openings. This pattern of production of ectomycorrhizal fungi may explain why red-backed voles tended to use edge habitat more than the interior of patch-cut openings (Hayward et al. 1999). This influence of edge would decrease as the size of clearcuts increased, a possible causal factor for the decreased abundance of red-back voles in large clearcuts.

In this study, shrub cover was reduced from 57% (preharvest) to 21% in 1 ha openings 2 years postharvest, but increased to 40% by 2004 (Waterhouse 2005). In contrast, percent cover of herbs in 2004 was much higher (47%–66%) than preharvest levels (33%–46%). Potentially, the trend toward lower abundance of red-backed voles (though not significant) between 1 ha group-selection cuts and old-growth forests may reflect the variation in vegetation cover noted by Waterhouse (2005). This change may be associated with the actual change in amount of vegetation cover (security and food source) or may occur through modification of the microclimate. Vegetation was not monitored in large clearcuts in Waterhouse (2005), therefore direct comparisons among all treatments could not be made.

Deer mice were captured in relatively low numbers in all sites and similar in abundance among treatments. This outcome supported part of hypothesis 3, that deer mice and dusky shrews, being habitat generalists, would be equally abundant on all treatments. These results are similar to those of other studies in which the responses of deer mouse populations to patch cuts were recorded (Steventon et al. 1998; Craig et al. 2006). Since deer mice are habitat generalists (Martell 1983), they are more adaptable to changes in their habitat than specialists such as red-backed voles.

We found that dusky shrews were twice as abundant in large clearcuts as in old-growth forests, thus partially refuting our hypothesis 3. These results are similar to those of studies in which a greater abundance of this soricid was found in clearcuts than in uncut forests (Doyle 1990; Steventon et al. 1998). In contrast, dusky shrews have been found in equal abundance in stands ranging in age, density, and opening size (Carey and Johnson 1995; Sullivan et al. 2005). Interestingly, common shrews were as abundant as dusky shrews immediately following treatments, but were more abundant on 1 ha group-selection cuts and in old-growth forests than in smaller group-selection cuts (Waterhouse et al. 2004). In our study, the abundances of common shrews were low and similar in all treatments.

Management implications

In this study the longer term impacts of 1 ha openings, within a group-selection (33% removal) silvicultural system, on the population dynamics of forest-floor small mammals were compared with those of a similar-aged clearcut (>30 ha) system. Our results, 14 years postharvest, indicate that openings of different sizes do not supply habitats of equal quality to small mammals in subalpine forests. Large clearcuts (>30 ha) provided suboptimal habitat for red-backed voles, but clearly provided better habitat than old-growth forests for many other species of small mammals, especially dusky shrews. The 1 ha group-selection cuts supplied habitats of intermediate quality for red-back voles, while maintaining most species of small mammals that were found in large clearcuts.

Since fruiting bodies of ectomycorrhizal fungi are a major food item for red-backed voles, this microtine may contribute significantly to spore dispersal and establishment of fungal communities. Reforestation of some sites in the ESSF will continue to challenge silviculturists because of poor performance of planted trees, and hence marginal reforestation success on clearcuts (Farnden 1994). Small group-selection cuts would enhance spore dissemination and establishment of ectomycorrhizal communities relative to large clearcuts, through the foraging activities of red-backed voles. This, in turn, may be of benefit in reforestation activities in these high-elevation sites.

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