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Partial and clearcut harvesting of dry Douglas-fir forests: Implications for small mammal communities

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ABSTRACT

Dry Douglas-fir (*Pseudotsuga menziesii*) forests offer a wide range of timber and non-timber values, which may benefit from a balanced timber harvest by variable retention systems with conservation of biodiversity. A major component of biodiversity are forest floor small mammal communities whose abundance and diversity serve as ecological indicators of significant change in forest structure and function from harvesting activities. This study was designed to test the hypotheses that abundance, reproduction, and survival of (i) the southern red-backed vole (*Myodes gapperi*, formerly *Clethrionomys gapperi*), will decline; (ii) the deer mouse (*Peromyscus maniculatus*), will be similar; and (iii) the meadow vole (*Microtus pennsylvanicus*) and northwestern chipmunk (*Tamias amoenus*), will increase, with decreasing levels of tree retention. Small mammal populations were live-trapped from 1994 to 1997 in replicated sites of uncut forest, 20% and 50% volume removal by single tree selection, 20%, 35%, and 50% patch cuts based on openings of 0.1–1.6 ha, and small 1.6 ha clearcuts in Douglas-fir forest near Kamloops, British Columbia, Canada. *M. gapperi* dominated the small mammal community, starting with an abundance of 74–98 animals/ha with mean values ranging from 33 to 51 animals/ha. In the two post-harvest years, abundance, reproduction, and survival of *M. gapperi* populations were consistently similar among uncut forest and the various levels of tree retention. Thereafter, *M. gapperi* was seldom found on the small clearcuts. *M. pennsylvanicus, T. amoenus, and P. maniculatus* occurred predominantly in clearcut sites. As with other types of forest disturbance, responses to our treatments were species-specific. The most striking result was the high abundance and productivity of *M. gapperi* populations in a dry forest ecosystem, a novel result for this bio-indicator species of closed-canopy forest conditions. At least with respect to small mammals, the retention systems studied seem to enable timber extraction and maintenance of mature forest habitat in these dry fir ecosystems.

1. Introduction

Variable retention harvesting ("green-tree retention") is an alternative to clearcutting in forests of the Pacific Northwest (PNW) of North America (Franklin et al., 1997). Retention patterns, which may be dispersed or aggregated across harvest units, may help sustain plant and animal diversity within harvested landscapes. As discussed by Franklin et al. (1997, 2002), and others, silvicultural approaches need to integrate ecological and economic objectives by aligning harvesting systems with natural disturbance processes. Retention of biological legacies such as large live trees, snags, and logs provide attributes of mature forest habitat, increase structural diversity, and provide continuity in the regenerating forest (McComb et al., 1993; Franklin et al., 2002).

The relationship between stand structural development and green-tree retention is being studied in Douglas-fir (*Pseudotsuga menziesii*)-western hemlock (*Tsuga heterophylla*) forests in Washington and Oregon of the PNW (Aubry et al., 1999; Franklin et al., 2002). The influence of Douglas-fir retention on forest ecosystem attributes after harvest of mixed lodgepole pine (*Pinus contorta*)-Douglas-fir forests in south-central British Columbia (BC) was reported by Sullivan and Sullivan (2001) and Sullivan et al. (2008). The dry Douglas-fir forests of BC have been managed by stand-level partial cutting for 50–60 years. Various methods of tree marking and diameter-limiting harvest have been implemented during this period (Klenner and Vyse, 1998). However, timber and non-timber values increased dramatically in these dry forests in the 1990s. Consequently, various uneven-aged harvesting regimes have been proposed to maintain a balanced distribution of age classes for timber, range, biodiversity, and recreational objectives. Rather than implementing one general prescription applicable to a highly variable forest type occupying

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over one million ha, a long-term investigation of silvicultural options in dry Douglas-fir forests (Opax Mountain Silvicultural Systems Project) was initiated in 1993 (Klenner and Vyse, 1998).

A major component of biodiversity are forest floor small mammal communities that are widespread across temperate and boreal forest ecosystems, and their abundance and diversity may serve as ecological indicators of significant change in forest structure and function (Carey and Harrington, 2001). Functions of this group of vertebrates include prey for many predators (Martin, 1994), distribution of beneficial mycorrhizal fungi (Maser et al., 1978), and consumers of invertebrates (Buckner, 1966), and plants and plant products (Carey et al., 1999). Selecting bio-indicator species that are particularly associated with mature late succession forest types, such as the southern red-backed vole (*Myodes gapperi*, formerly *Clethrionomys gapperi*) may help determine the effect of structural changes resulting from forest management practices (Pearce and Venier, 2005). As a microtine that commonly inhabits late successional coniferous and deciduous forests across temperate North America (Merritt, 1981), *M. gapperi* is an important indicator species of "old forest conditions" (Nordyke and Buskirk, 1991).

The forest-floor small mammal community also includes major species such as the deer mouse (*Peromyscus maniculatus*) that occupies a wide variety and age of forested habitats (Martell, 1983). Another habitat generalist is the northwestern chipmunk (*Tamias amoenus*) that is found primarily in early successional harvested sites (Sutton, 1992). The meadow vole (*Microtus pennsylvanicus*) prefers an abundance of herbs and grasses that provide food and cover in early successional habitats that develop after natural or forest harvesting disturbances (Getz, 1985).

In several coniferous forest ecosystems, *M. gapperi* has persisted in forests subjected to selection, patch, and shelterwood harvesting (Martell, 1983; Steventon et al., 1998; Von Trebra et al., 1998; Sullivan and Sullivan, 2001), but not up to 3–8 years post-harvest in seed-tree systems of montane spruce forest (Sullivan et al., 2008). In subalpine spruce-fir forests, patch cutting and single-tree selection appeared to have little effect on abundance of *M. gapperi* (Hayward et al., 1999; Klenner and Sullivan, 2003). *M. gapperi* seems to depend on mesic habitats in coniferous, deciduous, and mixed forests with an abundance of stumps, rotting logs, and exposed roots that help to provide a moist microclimate. Development of understory shrubs and young conifers may also help to ameliorate microclimatic conditions for this species (Moses and Boutin, 2001). Sullivan et al. (2005) reviewed the mean and maximum levels of abundance of *M. gapperi* in uncut mature/old-growth forest in several ecological zones across BC. The relatively dry interior forests such as those in the Interior Douglas-fir (IDF) ecological zone, do not appear to support high populations of *M. gapperi*. However, no one has investigated the responses of forest floor small mammal communities to several of the harvesting options in dry Douglas-fir forests.

Thus, this study was designed to test the hypotheses that abundance, reproduction, and survival of (i) *M. gapperi*, a species associated with closed-canopy forests, will decline with decreasing levels of tree retention; (ii) *P. maniculatus*, a habitat generalist species, will be similar across the levels of tree retention and (iii) *M. pennsylvanicus* and *T. amoenus*, species associated with early successional habitats, will increase with decreasing levels of tree retention.

2. Materials and methods

2.1. Study area

This study was conducted as part of the Opax Mountain Silvicultural Systems project in the southern interior of BC, Canada (50°48′N; 120°27′W) (Fig. 1). This project was established to investigate the influence of alternative harvesting systems on a

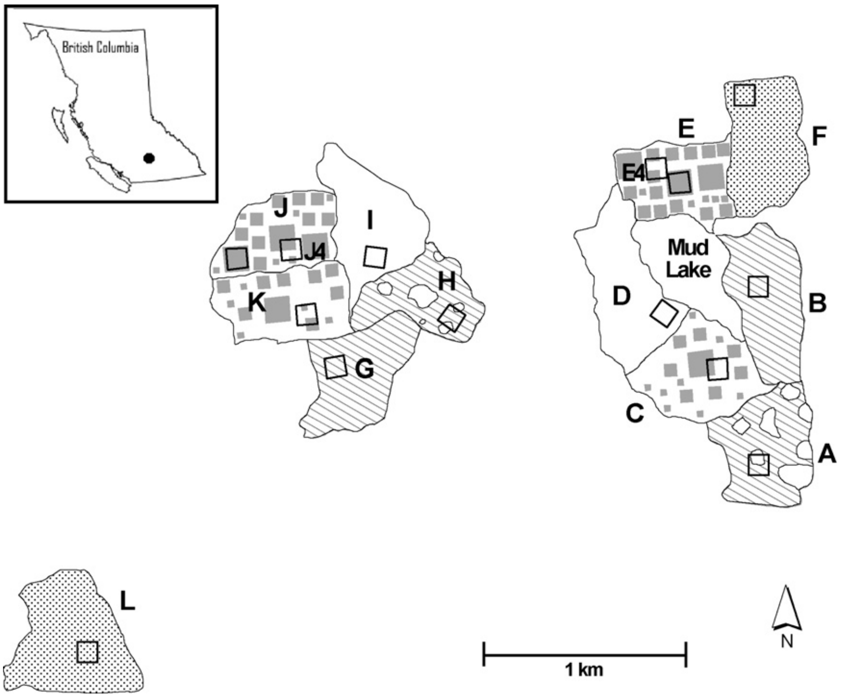


Fig. 1. Location (inset) of the Opax Mountain Silvicultural Systems Project (●) within British Columbia, Canada. Location of small mammal trapping grids indicated by open squares. Harvesting treatments were: (1) uncut controls (units D, I); (2) 20% volume removal using uniform individual-tree selection (units F, L); (3) patch cuts of 0.1 ha, 0.4 ha, and 1.6 ha on 20% of the treatment unit (grey squares, units C, K); (4) 35% volume removal, consisting of 75% of the treatment unit area harvested as 50% volume removal using uniform individual-tree selection, and 25% of the treatment unit area retained as uncut reserves (units A, H); (5) 50% volume removal using uniform individual-tree selection (units B, G); (6) patch cuts of 0.1, 0.4, and 1.6 ha on 50% of the treatment unit (grey squares, units E, J); and (7) one of the 1.6 ha openings (trapping grid identified as CC) in units E and J was used to sample response to clearcut harvesting.

wide range of biotic and abiotic factors in a dry Douglas-fir–lodgepole pine forest 20 km northwest of Kamloops, BC, in two IDF biogeoclimatic subzones: the dry cool (IDF_{dk}) and very dry hot (IDF_{xh}) (Lloyd et al., 1990).

Most stands in the southern interior have been logged at least once and records show that some stands have been logged three times in the last 90 years (Vyse et al., 1991). Douglas-fir is still the dominant species and, as in the past (judged by old photographs), size distributions are still irregular with varying numbers of regeneration, poles, and canopy stems. The largest trees rarely exceed 30 m in height and 70 cm in diameter. Stand volumes range widely, but reach 250–300 m^3/ha in relatively undisturbed stands. Stand conditions vary widely at the local level, but the same pattern is repeated throughout the region.

Parts of the study area had been partially harvested with a limited-diameter partial-cut in 1956–1957; other areas were unharvested. The area had rolling topography, and an open forest canopy of Douglas-fir with some lodgepole pine. Trembling aspen (*Populus tremuloides*) and Sitka alder (*Alnus sitchensis*) were present in moister areas. The forest was generally multi-storied with some pockets of shrubs such as birch-leaved spirea (*Spiraea betulifolia*), rose (*Rosa* spp.), soopolallie (*Shepherdia canadensis*), and twinflower (*Linnaea borealis*). Herbaceous vegetation was relatively sparse, composed primarily of racemose pussytoes (*Antennaria racemosa*) and pinegrass (*Calamagrostis rubescens*).

2.2. Harvesting treatments and experimental design

Our study was conducted in twelve 20–25-ha harvest treatment units; six at a low-elevation (950–1100 m above sea level, asl) block, and six at a higher-elevation block (Mud Lake) (1200–1370 m asl) (Fig. 1). The following six harvest treatments were randomly assigned to each of the two blocks: (1) control (no harvest), (2) 20% volume removal by individual-tree selection, (3) 20% patch cut: volume removal using patch cuts of 0.1, 0.4, and 1.6 ha on 20% of treatment area, (4) 35% volume removal, consisting of 75% of the treatment area harvested as 50% merchantable volume removal using individual-tree selection, and 25% of the treatment unit area retained as uncut reserves, (5) 50% volume removal by individual-tree selection, and (6) 50% patch cut: volume removal using patch cuts of 0.1, 0.4, and 1.6 ha on 50% of treatment area. One of the 1.6-ha patch cuts was a seventh treatment in each block used to sample the response to a small clearcut.

The treatments used did not represent operational prescriptions, but instead were focused on creating or removing specific stand structures (e.g., number of large-diameter trees >35 cm) and creating a range of canopy gaps (e.g., 0.01–0.05 ha in the partial-cutting units, and 1–4 tree heights wide (0.1, 0.4, and 1.6 ha)) in the patch-cut units. The treatments were applied by harvesting 20-ha blocks in two different ways (small patch cuts versus uniform selection) at two levels of cutting intensity (20% and 50% of stand volume).

The study had a randomized-block design with two replicate sites of each treatment. Within each block, there were six sites: uncut forest (UF); 20% individual-tree selection (20% ITS); 20% patch cut (20% PC); 35% individual-tree selection (35% ITS); 50% individual-tree selection (50% ITS); and 50% patch cut (50% PC). A small (1.6 ha) clearcut (CC) was added as a seventh treatment site at each block.

The study area was harvested during the winter of 1993–1994. Operational site-preparation (spot screefing with an excavator) in spring 1994 was followed by planting of conifer seedlings in openings. Clearcut areas were heavily vegetated by 2 years post-harvest. Clearcuts were dominated by shrubs such as rose, birch-leaved spirea, and common snowberry (*Symphoricarpos albus*), pinegrass, and herbs such as showy aster (*Aster conspicuus*), wild strawberry (*Fragaria virginiana*) and racemose pussytoes.

2.3. Coniferous stand structure

Basal area (m^2/ha), density (stems/ha), dbh (diameter at breast height, 1.3 m above the soil surface) and tree height of the overstory coniferous trees (primarily Douglas-fir) were measured in 25, 5.65-m radius plots (0.01 ha) uniformly distributed across each small mammal trapping grid and centered on alternating trapping stations. Canopy closure was measured at each of these plots using a vertical percent cover estimate (“moosehorn” technique; Garrison, 1949). Five readings (at plot center and 5.65 m from center to the N, S, E and W) were taken at each plot for a total of 125 readings that were averaged for an overall estimate of canopy cover.

2.4. Small mammal populations

Forest floor small mammal populations were sampled at 2–4-week intervals from May to October in 1994, 1995, and 1996, and from April to May 1997. One trapping grid (1 ha) was located on each site. On the 20% removal patch-cut treatment, the trapping grid was designed to represent the habitat types following harvest: approximately 80% of the trapping grid was in forested habitat, while 20% was in the patch cut. On the 50% patch-cut treatment, one sampling grid was placed within the largest harvest opening (1.6 ha), and another straddled a 0.4-ha opening and leave strips between the harvest openings (Fig. 1). Trapping on one replicate of the 20% patch cut and both replicates of the 50% patch-cut treatments did not begin until 1995. Each grid had 49 (7 × 7) trap stations at 14.3-m intervals with one Longworth live-trap at each station. Additional traps were added when capture success exceeded 80%. Traps were supplied with whole oats, sunflower seed, with a slice of apple, and cotton as bedding. Traps were set on the afternoon of day 1, checked on the morning and afternoon of day 2 and morning of day 3, and then locked open between trapping periods.

The major species of forest floor small mammals sampled by this procedure included *M. gapperi*, *P. maniculatus*, *M. pennsylvanicus*, and *T. amoenus*. Other less common species included the long-tailed vole, heather vole (*Phenacomys intermedius*), jumping mouse (*Zapus* spp.), shrews (*Sorex* spp.), and short-tailed weasel (*Mustela erminea*). All small mammals (except *Sorex* spp. and *M. erminea*) captured were ear-tagged and immediately released at the point of capture (Krebs et al., 1969).

2.5. Demographic analysis

Trappability (susceptibility to capture) and population density per ha were measured to determine the effects of the harvest treatments on abundance of the four major species. Jolly trappability was calculated as per the estimate reported by Krebs and Boonstra (1984). Abundance estimates of *C. gapperi*, *P. maniculatus*, *M. pennsylvanicus*, and *T. amoenus* were derived from the Jolly–Seber (J–S) stochastic model (Seber, 1982). The minimum number of animals known to be alive (MNA) (Krebs, 1966) was used as the population estimate for the first and last sampling weeks of the study when the J–S estimate cannot be calculated. Abundance of small mammals was calculated using the estimated abundance of each species for a given sampling period, and also averaged over the number of sampling periods for each year.

We evaluated reproduction, recruitment and survival of *M. gapperi* and *P. maniculatus*. Reproductive performance was based on the number of successful pregnancies calculated for each population in 1994 through 1997. A pregnancy was considered successful if a female was lactating during the period following the estimated time of birth of a litter. Each record of a lactating female was considered an independent litter based on a 3-week nursing period within our 3-week trapping intervals. Early juvenile survival is an index relating recruitment of young into the trappable population to the number of lactating females (Krebs, 1966). A modified version of this index is number of juvenile animals at week *t* divided by the number of lactating females caught in week *t*–3. Mean J–S 28-day survival rates were calculated for each population during summer (June to September) and winter (October to May) periods each year.

We used age at sexual maturity to determine age classes of animals. Body weight was used as an index of age. Animals were classified as juvenile (includes juvenile and subadult classes pooled) or adult by body weight: *M. gapperi*, juvenile = 1–18 g, adult ≥19 g; *P. maniculatus*, juvenile = 1–15 g, adult ≥16 g. Juveniles were considered to be young animals recruited during the study. Recruits were defined as new animals that entered the population through reproduction and immigration.

2.6. Statistical analyses

A repeated-measures analysis of variance (RM-ANOVA) (SPSS 16.0 SPSS Institute Inc., 2007) was used to determine the effect of harvest treatments on mean abundance, mean number of successful pregnancies, mean number of recruits, mean index of juvenile survival, and mean J–S summer and winter survival for each of the major species during the post-harvest period (1994–1997). In some cases, there were insufficient data to permit RM-ANOVA calculations. A randomized-block one-way ANOVA (Model III) was used to compare levels of BA and percentage canopy closure for the seven treatment stands. Data not conforming to properties of normality and equal variance were subjected to various transformations (Zar, 1999). Sphericity (independence of data among repeated measures) was not detected in any of the datasets, which were subjected to Mauchly's *W*-test statistic (Littel, 1989; Kuehl, 1994). A simple linear regression analysis was conducted to determine the relationship between mean abundance of red-backed voles and basal area and canopy closure of the treatment stands.

Proportional data were arcsine-transformed prior to analysis (Zar, 1999). Duncan's multiple range test (DMRT) was used to compare mean values based on ANOVA results. If there was a significant treatment effect and significant treatment x time interaction, a one-way ANOVA (and DMRT) was conducted for each post-treatment year. If there was a significant treatment effect but not a significant treatment × time interaction, DMRT was conducted on the overall set of post-treatment years. In all cases, the level of significance was at least $P = 0.05$.

3. Results

3.1. Coniferous stand structure

Mean BA/ha of coniferous trees was significantly ($F_{6,6} = 10.73$; $P < 0.01$) different among sites, with all sites having a higher (DMRT; $P = 0.05$) amount of BA than the clearcuts (Table 1). The UF and 20% ITS also had greater (DMRT; $P = 0.05$) amounts of BA than the 50% PC. Mean percentage canopy closure was also significantly ($F_{6,6} = 29.87$; $P < 0.01$) different among sites, with all sites having higher (DMRT; $P = 0.05$) canopy closure than the clearcuts (Table 1). Similarly, there were significant differences in mean canopy closure from uncut forests to 50% patch-cut sites as the amount of overhead forest cover declined (Table 1).

3.2. Abundance of small mammals

A total of 26 trapping periods were conducted in this 4-year study. *M. gapperi* was the most abundant species with a total of 2954 individuals captured (65.9% of total small mammals). Total numbers of individuals of the other major species were 902 for *P. maniculatus*, 267 for *M. pennsylvanicus*, and 260 for *T. amoenus*. Estimates of trappability (susceptibility to capture) tended to be variable among species, with overall mean values ranging from 77.5% for *M. gapperi*, 57.8% for *M. pennsylvanicus*, 57.2% for *P. maniculatus*, to 69.0% for *T. amoenus*. Thus, J–S population estimates were used for this study, for the reasons given in Jolly and Dickson (1983).

The abundance of *M. gapperi* was significantly ($F_{5,5} = 11.17$; $P = 0.01$) different among sites, with higher (DMRT; $P = 0.05$) mean numbers occurring in all stands than the small clearcuts in 1996 and 1997 (Table 2 and Fig. 2). Mean numbers per ha of *M. gapperi* ranged from 33 to 51 in 1994 and 13 to 38 in 1995 when there were no differences among treatment stands in these first two post-harvest years (Table 2). Abundance of *M. gapperi* was very high in October 1994, reaching peak populations of 74–98 animals/ha (Fig. 2). Numbers were lowest in the clearcut sites dropping to <1 animal/ha during the third and fourth post-harvest years. Overall, *M. gapperi* populations generally declined with time ($F_{3,15} = 83.15$; $P < 0.01$).

Mean abundance of *P. maniculatus* was similar ($F_{5,5} = 2.06$; $P = 0.22$) among stands, with higher ($F_{3,15} = 12.43$; $P < 0.01$) mean numbers in 1994 than in subsequent years (Table 2 and Fig. 3). Overall, mean abundance levels were ≤21 animals/ha. The clearcut sites seemed to be favored by *P. maniculatus* in the post-harvest years 1995 and 1996 (Fig. 3).

Abundance of *M. pennsylvanicus* was significantly ($F_{5,5} = 5.64$; $P = 0.04$) different among sites with highest (DMRT; $P = 0.05$) relative numbers in the clearcut sites followed by similar numbers of voles in the 50% PC and 50% ITS (Table 2). Clearcut sites tended to

Table 1
Mean ($n = 2$ replicate stands) ± S.E. basal area (m^2/ha) and percentage canopy closure for the seven treatment stands, and results of ANOVA. Treatment columns with different letters are significantly different by Duncan's multiple range test.

Treatment[1]							ANOVA	
UF	20% ITS	20% PC	35% ITS	50% ITS	50% PC	CC	Treatment	
							$F_{6,6}$	P
Total basal area/ha								
$25.50^{a} \pm 4.80$	$25.65^{a} \pm 3.35$	$22.67^{ab} \pm 2.22$	$17.74^{ab} \pm 4.28$	$14.53^{b} \pm 2.22$	$16.33^{ab} \pm 0.88$	$0.00^{c} \pm 0.00$	10.73	<0.01
Canopy closure								
$58.83^{a} \pm 3.12$	$49.07^{ab} \pm 3.31$	$46.54^{bc} \pm 4.15$	$45.34^{bcd} \pm 3.13$	$37.17^{cde} \pm 8.82$	$32.66^{e} \pm 5.56$	$0.00^{f} \pm 0.00$	29.87	<0.01

$^{a-f}P = 0.05$.

[1] Uncut forest (UF); 20% individual-tree selection (20% ITS); 20% patch cut (20% PC); 35% individual-tree selection (35% ITS); 50% individual-tree selection (50% ITS); 50% patch cut (50% PC); and small clearcut (CC).

Table 2
Mean ($n = 2$ replicate stands) ± S.E. abundance by treatment, species, and year. Results of RM-ANOVA are also provided. No correlation of data among measures (years) was observed for these data. Treatment columns with different capital letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts, and reveal the location of overall treatment effects as indicated by RM-ANOVA (due to missing data during 1994, these overall post hoc tests were performed for data from 1995 to 1997 only). When a significant time × treatment interaction occurred, one-way ANOVA's were used to test for treatment effects among each year and significant differences are indicated with lowercase letters.

Year	Treatment[1]							RM-ANOVA					
	UF	20% ITS	20% PC	35% ITS	50% ITS	50% PC	CC	Treatment		Time		Time × treatment	
								$F_{5,5}$	P	$F_{3,15}$	P	$F_{15,15}$	P
Myodes gapperi													
								11.17	0.01	83.15	<0.01	5.13	<0.01
1994	$43.76^a \pm 6.17$	$36.64^a \pm 10.10$	51.00	$33.27^a \pm 12.23$	$42.25^a \pm 10.14$	–	$33.65^a \pm 5.39$						
1995	$38.39^a \pm 3.95$	$33.11^a \pm 10.98$	$27.21^a \pm 7.25$	$34.71^a \pm 7.61$	$36.99^a \pm 8.60$	$31.23^a \pm 1.58$	$13.26^a \pm 4.9$						
1996	$17.20^a \pm 4.52$	$17.05^a \pm 0.06$	$13.49^a \pm 7.61$	$10.47^a \pm 3.51$	$16.77^a \pm 8.06$	$10.83^a \pm 2.78$	$0.69^b \pm 0.56$						
1997	$9.25^a \pm 2.25$	$10.50^a \pm 1.50$	$7.03^a \pm 2.03$	$6.68^a \pm 1.33$	$6.25^a \pm 1.25$	$9.50^a \pm 1.50$	$0.25^b \pm 0.25$						
Peromyscus maniculatus													
								2.06	0.22	12.43	<0.01	1.26	0.33
1994	8.24 ± 3.10	8.61 ± 0.98	11.77	14.85 ± 2.15	12.23 ± 1.43	–	12.32 ± 1.53						
1995	2.90 ± 1.90	3.34 ± 2.34	4.68 ± 2.51	2.23 ± 1.45	3.22 ± 0.89	7.60 ± 0.15	15.25 ± 1.59						
1996	2.94 ± 2.06	1.51 ± 0.63	9.05 ± 1.61	9.46 ± 1.68	7.12 ± 0.42	9.47 ± 1.79	21.07 ± 7.94						
1997	0.25 ± 0.25	0.50 ± 0.50	3.50 ± 1.00	4.75 ± 0.25	3.00 ± 2.50	1.50 ± 0.50	6.35 ± 6.35						
Microtus pennsylvanicus													
	C	BC	BC	C	BC	AB	A	5.64	0.04	0.70	0.57	1.18	0.37
1994	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	–	3.02 ± 1.12						
1995	0.00 ± 0.00	0.00 ± 0.00	0.88 ± 0.88	0.00 ± 0.00	0.72 ± 0.72	2.57 ± 0.43	3.06 ± 1.73						
1996	0.00 ± 0.00	0.00 ± 0.00	0.13 ± 0.13	0.00 ± 0.00	1.44 ± 1.44	4.09 ± 1.46	13.92 ± 1.94						
1997	0.00 ± 0.00	0.00 ± 0.00	0.25 ± 0.25	0.00 ± 0.00	1.50 ± 1.50	0.75 ± 0.25	11.25 ± 9.75						
Tamias amoenus													
								3.24	0.11	8.91	<0.01	0.69	0.76
1994	1.13 ± 1.13	1.29 ± 1.29	2.11	2.50 ± 1.21	1.00 ± 0.43	–	3.31 ± 0.40						
1995	0.78 ± 0.78	0.34 ± 0.34	2.73 ± 0.16	4.31 ± 0.55	2.89 ± 1.56	4.43 ± 1.22	4.02 ± 1.02						
1996	0.44 ± 0.44	0.88 ± 0.88	3.36 ± 0.38	6.31 ± 1.21	3.41 ± 0.53	7.46 ± 1.27	6.21 ± 4.73						
1997	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00	1.00 ± 1.00	0.25 ± 0.25	2.25 ± 0.25	0.25 ± 0.25						

[1] Uncut forest (UF); 20% individual-tree selection (20% ITS); 20% patch cut (20% PC); 35% individual-tree selection (35% ITS); 50% individual-tree selection (50% ITS); 50% patch cut (50% PC); and small clearcut (CC).

have the highest mean abundance at 13.9 voles/ha in 1996. Few *M. pennsylvanicus* were captured in other than the clearcut, 50% PC, and 50% ITS sites during these post-harvest years (Table 2).

Abundance of *T. amoenus* was similar ($F_{5,5} = 3.24$; $P = 0.11$) among sites, with higher ($F_{3,15} = 8.91$; $P < 0.01$) mean numbers in 1996 than in previous years (Table 2). Overall, mean abundance levels ranged from 0 to 7.5 chipmunks/ha. The uncut forest and 20% ITS stands seemed to be least favored by *T. amoenus* in the post-harvest years 1995 and 1996 (Table 2).

3.3. Reproduction and recruitment

Reproductive performance of males, as measured by the number of scotal animals, was similar among stands for *M. gapperi*

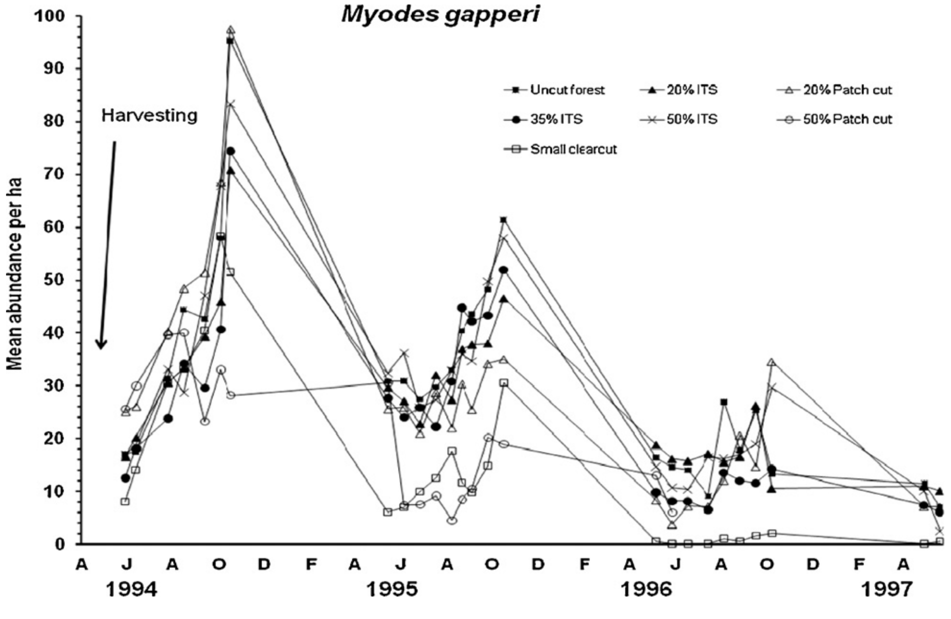


Fig. 2. Mean ($n = 2$) abundance per ha of *Myodes gapperi* during 1994–1997 at each of the seven treatments.

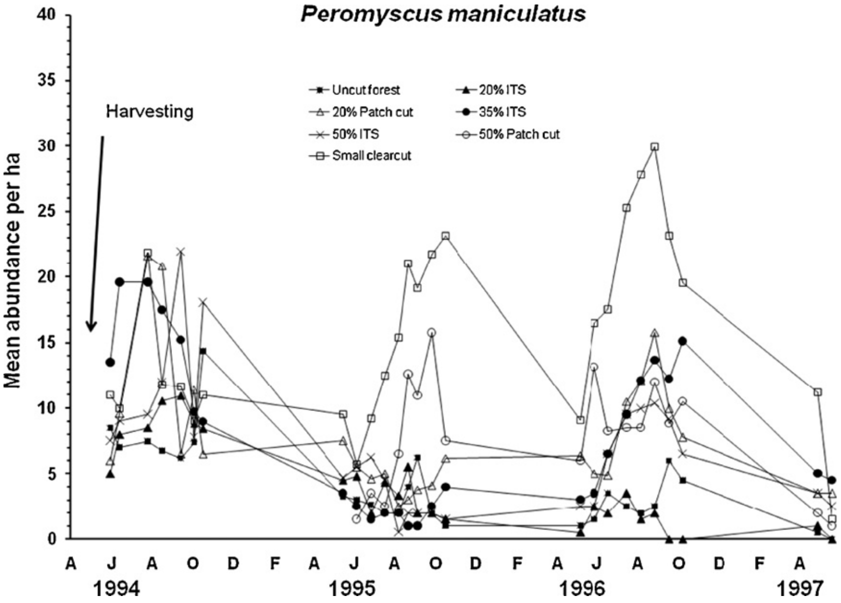


Fig. 3. Mean ($n = 2$) abundance per ha of *Peromyscus maniculatus* during 1994–1997 at each of the seven treatments.

($F_{5,5} = 0.95$; $P = 0.52$) and for *P. maniculatus* ($F_{5,5} = 0.64$; $P = 0.68$). The number of successful pregnancies measured female reproductive activity and was also similar ($F_{4,2} = 0.82$; $P = 0.61$) among stands for *M. gapperi* (Table 3). However, a significant ($F_{12,6} = 4.37$; $P = 0.04$) time × treatment interaction did indicate that more successful pregnancies for *M. gapperi* occurred in the 20% ITS and 20% PC than the 50% levels of these treatments (Table 3).

Recruitment of new *M. gapperi* was significantly ($F_{5,5} = 14.02$; $P < 0.01$) different among sites, with lower numbers of first captures in the clearcut than other sites in 1996 and 1997 (Table 4). Mean numbers of *M. gapperi* recruits ranged from 48 to 117 in the first two post-harvest years. These mean values ranged from 30 to 57 in 1996 and from 5 to 14 in 1997 in the non-clearcut treatments (Table 4). As with mean abundance, recruitment declined significantly ($F_{3,15} = 2.77$; $P = 0.04$) with time. Mean numbers of *P. maniculatus* recruits were similar ($F_{5,5} = 2.83$; $P = 0.14$) among sites, but did change significantly ($F_{3,15} = 41.30$; $P < 0.01$) with time, being high in 1994 and again in 1996 (Table 4).

3.4. Survival

Mean estimates of J–S summer survival for *M. gapperi* were similar ($F_{5,5} = 1.17$; $P = 0.44$) among sites. In winter, mean J–S survival of red-backed voles was significantly ($F_{5,5} = 13.62$; $P < 0.01$) different among sites, being lowest (DMRT; $P = 0.05$) in the 20% patch cut and clearcut sites over the 1994–1995 winter. Mean survival for *P. maniculatus* was similar among sites for both summer and winter seasons. An index of early juvenile survival appeared similar among sites for *M. gapperi*, particularly during the first two post-harvest years, ranging from 1.53 to 3.10. These estimates increased to a range of 2.37–5.31 in 1996, with no juvenile survival data for the clearcut site.

3.5. Red-backed voles and habitat

There was a positive relationship between mean abundance of *M. gapperi* and mean BA ($r = 0.67$; $P < 0.01$) and mean canopy closure ($r = 0.65$; $P = 0.01$) in 1995 (Fig. 4), when numbers of animals were still reasonably high after the peak year in abundance in 1994 (Fig. 2). This pattern was repeated in 1996 at lower overall numbers of *M. gapperi*, again showing positive relationships with BA ($r = 0.69$; $P < 0.01$) and canopy closure ($r = 0.62$; $P = 0.02$).

4. Discussion

4.1. Response to harvesting treatments

Our study is the first detailed evaluation of the responses of forest floor small mammals to a range of harvesting strategies in

Table 3

Mean ($n = 2$ replicate stands) ± S.E. number of successful pregnancies by treatment and year for *M. gapperi*. Results of RM-ANOVA are also provided. No correlation of data among measures (years) was observed for these data. When a significant time × treatment interaction occurred, one-way ANOVA's were used to test for treatment effects within each year. Within a given year, treatment means with different lowercase letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts.

Year	Treatment[1]							RM-ANOVA					
	UF	20% ITS	20% PC	35% ITS	50% ITS	50% PC	CC	Treatment		Time		Time × treatment	
								$F_{4,2}$	P	$F_{3,6}$	P	$F_{12,6}$	P
Myodes gapperi								0.82	0.61	97.04	<0.01	4.37	0.04
1994	$29.00^a \pm 5.00$	$22.50^a \pm 9.50$	52.00	$27.50^a \pm 18.50$	$24.00^a \pm 7.00$	–	$40.50^a \pm 0.50$						
1995	$28.50^a \pm 3.50$	$32.50^a \pm 8.50$	$21.00^a \pm 7.00$	$31.00^a \pm 11.00$	$29.50^a \pm 16.50$	$25.50^a \pm 1.50$	$10.50^a \pm 2.50$						
1996	$6.50^a \pm 2.50$	$11.50^a \pm 1.50$	$5.50^a \pm 3.50$	4.00	$15.50^a \pm 6.50$	$5.00^a \pm 1.00$	0.00 ± 0.00						
1997	1.00	3.00^a	$2.00^a \pm 1.00$	2.00	$0.00^b \pm 0.00$	$0.00^b \pm 0.00$	–						

[1] Uncut forest (UF); 20% individual-tree selection (20% ITS); 20% patch cut (20% PC); 35% individual-tree selection (35% ITS); 50% individual-tree selection (50% ITS); 50% patch cut (50% PC); and small clearcut (CC).

Table 4
Mean ($n = 2$ replicate stands) ± S.E. total recruitment by treatment and year for the two major species. Results of RM-ANOVA are also provided. *F*-values identified by an asterisk were calculated using the H–F correction factor, which decreased the stated degrees of freedom because of correlation of data among measures (years). When a significant time × treatment interaction occurred, one-way ANOVA's were used to test for treatment effects among each year and significant differences are indicated with lowercase letters. Within a given year, treatment means with different lowercase letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts.

Year	Treatment[1]							RM-ANOVA					
	UF	20% ITS	20% PC	35% ITS	50% ITS	50% PC	CC	[Treatment		Time		Time × treatment	
								$F_{5,5}$	P	$F_{3,15}$	P	$F_{15,15}$	P
Myodes gapperi													
								14.02	<0.01	86.55*	<0.01	2.77*	0.04
1994	$110.50^a \pm 6.50$	$93.00^a \pm 15.00$	117.00	$86.50^a \pm 27.50$	$104.00^a \pm 11.00$	–	$103.50^a \pm 16.50$						
1995	$98.00^a \pm 10.00$	$92.00^a \pm 24.00$	$78.50^a \pm 16.50$	$82.50^a \pm 16.50$	$100.00^a \pm 25.00$	$92.00^a \pm 12.00$	$47.50^a \pm 6.50$						
1996	$50.50^a \pm 9.50$	$46.50^a \pm 2.50$	$34.50^a \pm 6.50$	$30.00^a \pm 9.00$	$56.50^a \pm 22.50$	$36.50^a \pm 6.50$	$4.50^b \pm 3.50$						
1997	$9.50^{ab} \pm 0.50$	$14.00^a \pm 4.00$	$8.00^{ab} \pm 2.00$	$4.50^b \pm 0.50$	$9.00^{ab} \pm 4.00$	$12.00^{ab} \pm 0.00$	$0.50^c \pm 0.50$						
Peromyscus maniculatus													
								2.84	0.14	41.30	<0.01	1.35	0.28
1994	19.50 ± 5.50	22.50 ± 0.50	27.00	33.50 ± 3.50	25.00 ± 1.00	–	28.00 ± 3.00						
1995	5.50 ± 1.50	6.00 ± 2.00	15.50 ± 5.50	7.50 ± 5.50	8.00 ± 3.00	20.00 ± 0.00	44.50 ± 5.50						
1996	11.50 ± 4.50	8.50 ± 4.50	31.00 ± 8.00	26.50 ± 2.50	22.00 ± 1.00	30.50 ± 5.50	56.00 ± 12.00						
1997	0.00 ± 0.00	1.00 ± 1.00	4.00 ± 1.00	3.00 ± 0.00	4.00 ± 3.00	1.00 ± 1.00	2.50 ± 2.50						

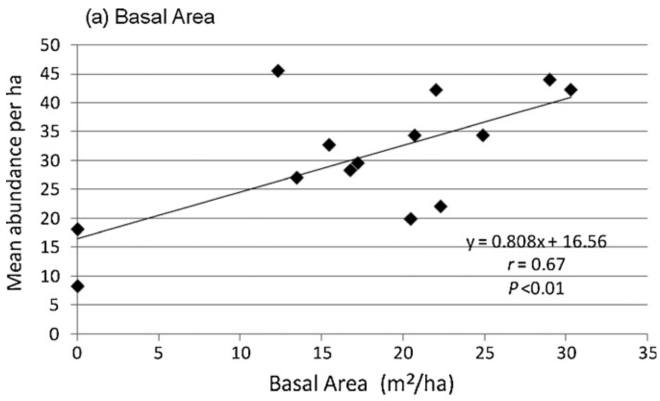
[1] Uncut forest (UF); 20% individual-tree selection (20% ITS); 20% patch cut (20% PC); 35% individual-tree selection (35% ITS); 50% individual-tree selection (50% ITS); 50% patch cut (50% PC); and small clearcut (CC).

dry Douglas-fir forests of the interior PNW. *M. gapperi* was the dominant species reaching peak populations of 74–98 animals/ha in 1994. Because of this abundance pattern, there were no differences among treatment sites in the first two post-harvest years, even on the clearcut sites. However, in the subsequent post-harvest years, *M. gapperi* all but disappeared from the clearcuts. Thus, our hypothesis (i) that *M. gapperi* would decline with decreasing levels of tree retention seemed to be supported.

This delayed response (1–2 years) of *M. gapperi* to clearcutting has been recorded elsewhere (Sullivan and Sullivan, 2001). Also, advanced coniferous regeneration in the boreal forest (Potvin et al., 1999), woody debris in aspen mixed wood forest (Moses and Boutin, 2001), and a variety of dispersed-aggregated retention in Douglas-fir-western hemlock forests (Gitzen et al., 2007) has helped to maintain *M. gapperi* longer on harvested sites. These aspects of habitat structure represented by relatively large amounts of understory vegetation and/or woody debris may be protection during critical periods of freezing and thawing (Merritt, 1981). Alternatively, other studies from western North America reported dramatic declines of *M. gapperi* on clearcuts (Martell and Radvanyi, 1977; Sullivan et al., 1999; Moses and Boutin, 2001; Klenner and Sullivan, 2003). This conclusion was countered by Kirkland's (1990) review suggesting that *M. gapperi* was the principal species contributing to the greater abundance of microtines on clearcuts in 15/21 studies, at least in eastern North America.

Basal area and density of residual trees appear to be critical components for maintaining *M. gapperi* on harvested sites. Our relationships of mean abundance of *M. gapperi* with BA and canopy closure of residual trees suggested that the critical threshold for this microtine lies between 0 and 15 m^2/ha BA or 0% and 25% canopy cover. Above these levels, populations of *M. gapperi* appeared little affected, and hence these habitat attributes would be poor predictors of abundance. Sullivan and Sullivan (2001) recommended patch-cut harvesting systems that leave 60–70% BA of uncut forest and group seed-tree or other aggregated reserves that leave at least 15 m^2/ha or 30% of uncut forest in patches may allow for persistence of *M. gapperi*. To date, short-term (up to 3 years post-harvest) results seem to support this pattern (Steventon et al., 1998; Von Trebra et al., 1998; Hayward et al., 1999; Moses and Boutin, 2001; Klenner and Sullivan, 2003). However, longer-term results found that up to 8 years post-harvest, *M. gapperi* did not persist on group seed-tree sites in montane spruce forest (Sullivan et al., 2008). At 14 years post-harvest in spruce-subalpine fir (*Picea engelmannii–Abies lasiocarpa*) forest, *M. gapperi* did persist at comparable abundance in 1-ha group selection harvests and uncut forest (Ransome et al., submitted for publication).

The demographic parameters of reproduction and survival followed the pattern of abundance of *M. gapperi* with similar responses to treatment conditions across the various retention systems, thereby also supporting hypothesis (i). This result was comparable to other studies where population dynamics have been measured in addition to abundance (Sullivan and Sullivan, 2001; Klenner and Sullivan, 2003).


(a) Basal Area

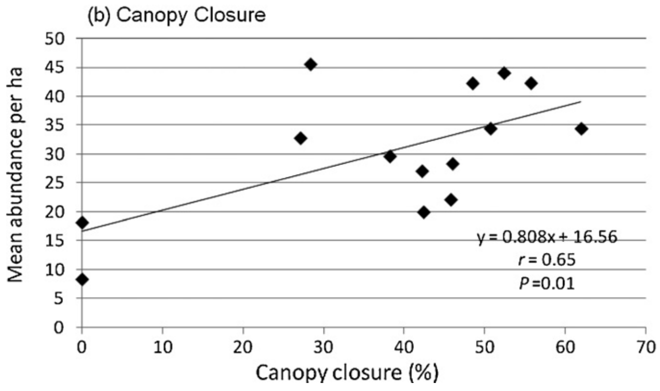

(b) Canopy Closure

Fig. 4. Linear regression analysis of the relationship between mean abundance per ha of *Myodes gapperi* in 1995 and (a) mean basal area (m^2/ha) and (b) mean canopy closure (%).

Contrary to hypothesis (ii) that the generalist *P. maniculatus* would be similar in population dynamics across the levels of tree retention, abundance of deer mice tended to be highest in the clearcut, although not formally significant, and less so in the uncut forest and 20% ITS. This general pattern for *P. maniculatus*, and *T. amoenus*, fits the prediction of Lehmkuhl et al. (1999) that habitat generalists will increase or have no change in abundance with decreasing levels of tree retention.

M. pennsylvanicus and *T. amoenus* responded positively to the clearcut sites, in terms of overall mean abundance, reproduction, and survival, as per hypothesis (iii). However, *T. amoenus* also appeared at comparable mean numbers in the 35% ITS and 50% PC sites and may be more appropriately classified as a habitat "generalist" than "specialist". Sullivan et al. (2008) reported the preference of this species for seed-tree sites was related to their "openness" combined with a high species diversity of shrubs and potential associated mycorrhizal fungal networks maintained by aggregates of residual trees.

4.2. *M. gapperi* in dry fir forests

The distribution of *M. gapperi* extends across Canada (south of the tundra) and northern regions of the United States with southern extensions into the Rocky and Appalachian mountain chains (Merritt, 1981). A synthesis of mean and maximum population levels of *M. gapperi* in uncut mature/old-growth forests, across a range of latitudes and ecological zones in the interior of BC, reinforced the numerical dominance and ecological importance of this microtine to late successional forests (Sullivan et al., 2005). Maximum abundance per ha of *M. gapperi* ranged from 23 to 85 and mean annual abundance ranged from a low of 2 to a high of 47 voles. However, the relatively dry interior forests such as those in the IDF and Montane Spruce ecological zones do not appear to support high populations of *M. gapperi*. This conclusion contrasts strongly with our results which indicate very high populations of *M. gapperi* in 1994 and a pattern of mean abundance in 1995 well within the range of densities summarized by Sullivan et al. (2005).

Despite these differences, species in the genus *Clethrionomys*/*Myodes* appear to have highly variable population dynamics ranging from regular 3–4-year cycles to irregular fluctuations in Europe and Asia, but relatively stable numbers in North America (Henttonen et al., 1985; Fuller, 1985; Gilbert and Krebs, 1991). Fluctuating populations of voles may be related to specialist predators in Fennoscandia, or due to variable tree seed crops in central Europe (Pucek et al., 1993). There is a dearth of relatively long-term population data for *M. gapperi* and other small mammals in temperate and boreal forests of North America, and hence patterns of population fluctuations are not clear. Cheveau et al. (2004) have suggested that winter irruptions of owls in the boreal forest of eastern North America are related to population fluctuations of small mammals, particularly *M. gapperi*. Our data, although limited to only 4 years, seem to support this possibility.

4.3. Experimental design

This study had a randomized-block design with blocks assigned on the basis of elevation and treatments randomly assigned to sites within each of two blocks (Zar, 1999). Thus, there were only two true replicates of treatment sites, and three or more replicates would have been ideal, but was not possible in this logistical and operational scenario. The individual blocks were separated by 1 km, thereby fulfilling the requirement of independent blocks. Inferences from our results can be extrapolated locally to dry fir forests in the immediate vicinity, but possibly not to a wider geographic area. Additional regional replicates would be needed, but the costs and logistics of establishing such a design were prohibitive, and may not have achieved the desired experimental rigor needed for some components of this multi-disciplinary study.

Treatment sites were the size of typical forestry operations in the southern interior of BC, and perhaps for dry interior forests in other parts of the PNW. Our design did not test operational prescriptions per se, but the treatments of varying levels and patterns of green-tree retention were done at a real-world scale. As such, the responses of forest floor small mammal communities and other forest ecosystem components to these treatments was of a similar scale to those reported by Sullivan et al. (2008), Klenner and Sullivan (2003), and Gitzen et al. (2007). Inferences from our study reflect responses in small mammal communities during summer and autumn periods only and for the first four post-harvest years only. Periodic repeated sampling over decades will provide a more realistic and ecological understanding of the impact of these treatments.

5. Management implications

A range of retention levels was tested and results suggest that partial harvesting of dry Douglas-fir forests, using both individual-tree selection and patch cutting, did not negatively affect small mammal populations. Mean BA (m^2/ha) ranged from 25 in uncut forest to 16 in the 50% patch cut to 0 in the small clearcuts; with a similar magnitude of change for canopy closure (%) of 59 in uncut forest to 33 in the 50% patch cut to 0 in the clearcuts. *M. gapperi* comprised 65.9% of the small mammal community in these forests and was not affected in terms of abundance, reproduction, or survival attributes, except for the clearcuts, where they disappeared in the third and fourth years after harvest. The generalist *P. maniculatus* occupied all sites, but like the early successional species *M. pennsylvanicus* and *T. amoenus* seemed to prefer the clearcut sites.

These harvesting systems seem to provide a potential method for combining timber extraction with maintenance of mature forest habitat, a condition desirable for conservation of biodiversity and other non-timber values in dry Douglas-fir forests (McComb et al., 1993; Franklin et al., 2002). *M. gapperi* is clearly a good bio-indicator of late successional forest conditions, at least with respect to our treatments and those of other green-tree retention systems in coniferous forest ecosystems of North America. In a more complex operational environment, topography and both understory and overstory stand conditions will necessitate modifications to the shapes and size of openings, but the basic principles of small mammal community response to opening size and forest structure should remain applicable. Long-term habitat suitability of the different treatments needs to be considered, as well as the habitat requirements and landscape context for other species of wildlife.

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References

Aubry, K.B., Amaranthus, M.P., Halpern, C.B., White, J.D., Woodard, B.L., Peterson, C.E., Lagoudakis, C.A., Horton, A.J., 1999. Evaluating the effects of varying levels and patterns of green-tree retention: experimental design of the DEMO study. Northwest Sci. 73, 12–26.

Buckner, C.H., 1966. The role of vertebrate predators in the biological control of forest insects. Annu. Rev. Entomol. 11, 449–470.

Carey, A.B., Harrington, C.A., 2001. Small mammals in young forests: implications for management and sustainability. For. Ecol. Manage. 154, 289–309.

Carey, A.B., Kershner, J., Biswell, B., DeToledo, L.D., 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. Wildl. Monog. no. 142. The Wildlife Soc., Bethesda, MD.

Cheveau, M., Drapeau, P., Imbeau, L., Bergeron, Y., 2004. Owl winter irruptions as an indicator of small mammal population cycles in the boreal forest of eastern North America. Oikos 107, 190–198.

Franklin, J.F., Berg, D.R., Thornburgh, D.A., Tappeiner, J.C., 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. In: Kohm, K.A., Franklin, J.F. (Eds.), Creating a Forestry for the 21st Century: The Science of Ecosystem Management. Island Press, Washington, DC, pp. 111–139.

Franklin, J.F., Spies, T.A., Pelt, R.V., et al., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. 399–423.

Fuller, W.A., 1985. Demography of *Clethrionomys gapperi*, parapatric *C. rutilus*, and sympatric *Peromyscus maniculatus*. Ann. Zool. Fenn. 22, 229–241.

Garrison, G.A., 1949. Uses and modifications for "moosehorn" crown closure estimation. J. For. 47, 733–735.

Getz, L.L., 1985. Habitats. In: Tamarin, R.H. (Ed.), Biology of New World *Microtus*. Spec. Publ. No. 8. Amer. Soc. Mammal., Boston, MA, pp. 286–309.

Gilbert, B.S., Krebs, C.J., 1991. Population dynamics of *Clethrionomys* and *Peromyscus* in southwestern Yukon 1973–1989. Holarctic Ecol. 14, 250–259.

Gitzen, R.A., Stephen, D.W., Maguire, C.C., Manning, T., Halpern, C.B., 2007. Response of terrestrial small mammals to varying amounts and patterns of green-tree retention in Pacific Northwest forests. For. Ecol. Manage. 251, 142–155.

Hayward, G.D., Henry, S.H., Ruggiero, L.F., 1999. Response of red-backed voles to recent patch-cutting in subalpine forest. Conserv. Biol. 13, 168–176.

Henttonen, H., McGuire, A.D., Hansson, L., 1985. Comparison of amplitudes and frequencies of density variations in long-term data sets of *Clethrionomys* species. Ann. Zool. Fenn. 22, 221–227.

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

Kirkland Jr., G.L., 1990. Patterns of initial small mammal community change after clear-cutting of temperate North American forests. Oikos 59, 313–320.

Klenner, W., Sullivan, T.P., 2003. Partial and clear-cut harvesting of high-elevation spruce-fir forests: implications for small mammal communities. Can. J. For. Res. 33, 2282–2296.

Klenner, W., Vyse, A., 1998. The Opax Mountain Silvicultural Systems Project: Evaluating alternative approaches to managing dry Douglas-fir forests. In: Vyse, A., Hollstedt, C., Huggard, D. (Eds.), Managing the dry Douglas-fir forests of the southern interior: workshop proceedings, 29–30 April 1997, Kamloops, B.C. Research Branch, BC Min. For., Victoria, BC, Work. Pap. 34/1998, pp. 128–135.

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

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

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

Kuehl, R.C., 1994. Repeated measures designs (Chapter 15). In: Statistical Principles of Research Design and Analysis, Duxbury Press, Belmont, CA, pp. 499–528.

Lehmkuhl, J.F., West, S.D., Chambers, C.L., McComb, W.C., Manuwal, D.A., Aubry, K.B., Erickson, J.L., Gitzen, R.A., Leu, M., 1999. Assessing wildlife response to varying levels and patterns of green-tree retention in western Oregon and Washington. Northwest Sci. 73, 45–63.

Littel, R.C., 1989. Statistical analysis of experiments with repeated measures. Hortscience 24, 36–40.

Lloyd, D.A., Angove, K., Hope, G., Thompson, C., 1990. A guide to site identification and interpretation for the Kamloops Forest Region. Land Manage. Hdbk. No. 23. Victoria, BC Min. For.

Martell, A.M., 1983. Changes in small mammal communities after logging in north-central Ontario. Can. J. Zool. 61, 970–980.

Martell, A.M., Radvanyi, A., 1977. Changes in small mammal populations after clear-cutting of northern Ontario black spruce forest. Can. Field-Nat. 91, 41–46.

Martin, S.K., 1994. Feeding ecology of American martens and fishers. In: Buskirk, W.W., Harestad, A.S., Raphael, M.G., Powell, R.A. (Eds.), Martens, Sables, and Fishers. Biology and Conservation. Comstock Publ. Assoc., Cornell University Press, Ithaca, NY, pp. 297–315.

Maser, C., Trappe, J.M., Nussbaum, R.A., 1978. Fungal-small mammal inter-relationships with emphasis on Oregon coniferous forests. Ecology 59, 799–809.

McComb, W.C., Spies, T.A., Emmingham, W.H., 1993. Douglas-fir forests. Managing for timber and mature-forest habitat. J. For. 91, 31–42.

Merritt, J.F., 1981. *Clethrionomys gapperi.* Mammalian species. No. 146. Amer. Soc. Mammal., Provo, UT, USA.

Moses, R.A., Boutin, S., 2001. The influence of clear-cut logging and residual leave material on small mammal populations in aspen-dominated boreal mixed-woods. Can. J. For. Res. 31, 483–495.

Nordyke, K.A., Buskirk, S.W., 1991. Southern red-backed vole, *Clethrionomys gapperi,* populations in relation to stand succession and old-growth character in the central Rocky mountains. Can. Field-Nat. 105, 330–334.

Pearce, J., Venier, L., 2005. Small mammals as bioindicators of sustainable boreal forest management. For. Ecol. Manage. 208, 153–175.

Potvin, F., Courtois, R., Bélanger, L., 1999. Short-term response of wildlife to clear-cutting in Quebec boreal forest: multiscale effects and management implications. Can. J. For. Res. 29, 1120–1127.

Pucek, Z., Jedrzejewski, W., Jedrzejewski, B., Pucek, M., 1993. Rodent population dynamics in a primeval deciduous forest in relation to weather, seed crop, and predation. Acta Theriol. 38, 199–232.

Ransome, D.B., Lindgren, P.M.F., Waterhouse, M.J., Armleder, H.M., Sullivan, T.P., submitted for publication. Small mammal response to group-selection silvicultural systems in Engelmann spruce-subalpine fir forests: 14 years post-harvest. Can. J. For. Res.

Seber, G.A.F., 1982. The Estimation of Animal Abundance and Related Parameters., Second ed. Charles Griffin & Co. Ltd., London, England.

SPSS Institute Inc., 2007. Statistical Programs of the Social Sciences. Chicago, IL.

Steventon, J.D., MacKenzie, K.L., Mahon, T.E., 1998. Response of small mammals and birds to partial cutting and clearcutting in northwest British Columbia. For. Chron. 74, 703–713.

Sullivan, T.P., Lautenschlager, R.A., Wagner, R.G., 1999. Clear-cutting and burning of northern spruce-fir forests: implications for small mammal communities. J. Appl. Ecol. 36, 327–344.

Sullivan, T.P., Sullivan, D.S., 2001. Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. J. Appl. Ecol. 38, 1234–1252.

Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., 2008. Influence of variable retention harvests on forest ecosystems: plant and mammal responses up to 8 years post-harvest. For. Ecol. Manage. 254, 239–254.

Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., Ransome, D.B., 2005. Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest: II. Diversity and population dynamics of forest floor small mammals. For. Ecol. Manage. 205, 1–14.

Sutton, D.A., 1992. *Tamias amoenus*. In: Mammalian Species. Number 390, American Society of Mammalogists, Prova, UT, USA.

Von Trebra, C., Lavender, D.P., Sullivan, T.P., 1998. Relations of small mammal populations to even-aged shelterwood systems in sub-boreal spruce forest. J. Wildl. Manage. 62, 630–642.

Vyse, A., Smith, R.A., Bondar, B.G., 1991. Management of interior Douglas-fir stands in British Columbia: past, present and future. In: Baumgartner, D.M. (Ed.), Interior Douglas-fir: The Species and its Management. Symposium Proceedings, Washington State University, Dept. Natural Resource Sciences, Pullman, WA.

Zar, J.H., 1999. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ, pp. 663.