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Small mammal response to group selection silvicultural systems in Engelmann spruce–subalpine fir forests

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Abstract

We measured small mammal response to several different group selection silvicultural systems that varied by opening size (0.03, 0.13, and 1.0 ha) but maintained a consistent 30% area removal. The southern red-backed vole (*Clethrionomys gapperi*), followed by the common shrew (*Sorex cinereus*) and dusky shrew (*S. monticolus*), were the most abundant species pre- and post-harvest. There was no evidence that the minimum number alive estimates for red-backed voles differed significantly ($\alpha = 0.05$) among treatments pre-harvest ($p = 0.67$) or post-harvest (1993, $p = 0.98$; 1994, $p = 0.84$). However, red-backed voles used harvested openings less than the surrounding forest within each treatment. Common shrews showed some preference for the unlogged controls and the treatment units containing 1.0-ha openings. Dusky shrews showed no treatment preference. Overall, we conclude that the group selection silvicultural systems did not substantially change the relatively rich, abundant small mammal community present before harvesting.

KEYWORDS: *small mammals, southern red-backed vole (*Clethrionomys gapperi*), common shrew (*Sorex cinereus*), dusky shrew (*Sorex monticolus*), group selection silvicultural systems, Engelmann Spruce–Subalpine Fir zone*

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Introduction

The Engelmann Spruce–Subalpine Fir (ESSF) biogeoclimatic zone covers approximately 13.3 million ha of British Columbia. The increase in forest management activities in these high-elevation forests has led to concern about the potential impacts on wildlife populations, habitats, and associated ecosystems. The choice of silvicultural system will affect habitat composition and structure, in turn affecting wildlife populations and communities. Of specific concern is the effect of forest management practices on mountain caribou (*Rangifer tarandus caribou*) which have been designated nationally as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). This concern was acknowledged in the Cariboo-Chilcotin Land Use Plan (Province of British Columbia 1995) that specified the maintenance of habitat values for mountain caribou populations as an overriding objective.

To meet this objective within the managed forest, group selection silvicultural systems were developed for application to over 53 000 ha of high-elevation ESSF forest in the Cariboo-Chilcotin Land Use Plan (CCLUP) area. These group selection systems may also be applied to tens of thousands of hectares in other areas of the province where mountain caribou occur in the ESSF zone. The implications to other wildlife species based on wide application of these systems are largely unknown. However, group selection systems may provide more opportunities to maintain biodiversity and reduce the time required for ecological recovery compared with clearcutting (Carey and Johnson 1995). Considering this potential, it is essential to understand the impacts of these silvicultural systems on various faunal and floral communities, including small mammals.

Small mammals are an important component of subalpine forest ecosystems. They provide a prey base for numerous predator species (Banfield 1974), and can impact forest development as they feed on various invertebrates (Getz 1961; Radvanyi 1973; Van Horne 1982; McCay and Storm 1997), fungal sporocarps, fruticose lichens, and conifer seeds (Martell 1981; Ure and Maser 1982). Forest management can affect several key habitat attributes necessary to maintain small mammal communities: water (Getz 1968), fungal sporocarps (Ure and Maser 1982), lichens (Ure and Maser 1982), mature or old stand structure (Raphael 1988; Nordyke and Buskirk 1991; Hayward and Hayward 1995), coarse woody debris (Tevis 1956; Nordyke and Buskirk 1988; Carey and Johnson 1995), and understory cover (Nordyke and Buskirk 1991; Carey and Johnson 1995).

Although many studies have investigated the effects of forest harvesting on small mammal populations, most of these studies focused on clearcut harvesting (Tevis 1956; Gashwiler 1970; Hooven and Black 1976; Ramirez and Hornocker 1981; Walters 1991; Sekgororoane and Dilworth 1995; Sullivan *et al*. 1999). A few studies have documented the effects of small patch clearcuts (<4 ha) on small mammals (Scott *et al.* 1982; Hayward *et al.* 1999; Menzel *et al.* 1999). Also, several older, small studies from the United States and Canada document the effects of partial cutting (West *et al.* 1980; Martell 1983; Medin and Booth 1989). More recently published studies from British Columbia have documented the effects of silvicultural systems, other than clearcutting, on small mammal populations in low-elevation forests (Steventon *et al.* 1998; Von Trebra *et al.* 1998; Sullivan *et al.* 2000; Sullivan and Sullivan 2001). Except for Klenner (1997) and Klenner and Sullivan (2003), the response of small mammals to selection silvicultural systems in high-elevation ESSF forests in British Columbia has not been documented.

Our silvicultural systems trial, although primarily designed to study caribou habitat, also allowed us to test the response of the small mammal community to group selection silvicultural systems. These systems are all based on 30% area removal but vary by harvested opening size (0.03 ha, 0.13 ha, and 1.0 ha).

Our study describes the small mammal community pre- and post-harvest, and attempts to answer the following questions:

1. Does the abundance of red-backed voles, common shrews, and dusky shrews change in response to group selection silvicultural systems?
2. Do red-backed voles use the harvested and forested portions of the group selection treatment units equally when both portions are available?
3. Does the size of the harvested opening affect the intensity of use by red-backed voles?
4. Does the use of the forest around harvested openings change with opening size for red-backed voles?

Study Sites

The study was conducted on three sites located 12–28 km east of Likely, British Columbia, in the Southern Interior Forest Region. Two of the sites, Upper and Lower Grain Creeks, (52°41'29"N, 121°12'02"W and 52°40'45"N, 121°10'52"W, respectively) are located within the Grain Creek watershed. The third site is located in the Blackbear Creek watershed (52°36'37"N, 121°24'30"W). All study sites are submesic to mesic within the Engelmann Spruce–Subalpine Fir wet, cold biogeoclimatic subzone variant (ESSFwc3). The elevation of the sites extends from 1440 to 1690 m. Above this elevation, the forest becomes subalpine parkland, then gives way to alpine. Slopes are similar at all sites, ranging from 24 to 32%, while aspect is northeast at Blackbear Creek, northwest at Lower Grain Creek, and west at Upper Grain Creek.

The forest is dominated by subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). The oldest trees are spruce aged from 280 to 300 years on the Blackbear Creek site and from 440 to 460 years on the Grain Creek sites. Spruce is more prevalent at the Blackbear Creek site while subalpine fir is more common on the Grain Creek sites. Stands are multi-aged as the fire return intervals are very long; forest replacement typically occurs as individual or small groups of mature and old trees succumb to insects, disease, and/or windthrow. Several small (<0.1 ha), wet subalpine meadows are scattered throughout the Lower and Upper Grain Creek study sites.

Based on pre-harvest cruise data, gross timber volumes ranged from 300 to 387 m³/ha (>17.5 cm diameter at breast height [dbh]), stem densities from 283 to 474 stems/ha (>12.5 cm dbh), and snag density from 68 to 262 stems/ha (>12.5 cm dbh). On the three sites, pre-harvest woody debris was measured using 700–1300 m of transect line per site. Volumes ranged from 186 to 321 m³/ha (>10 cm diameter). Woody debris was measured again in 2001 in the uncut control units and the openings within the treatment units using 200 m of transect per treatment unit (>7.4 cm diameter). Across the sites, the woody debris volumes were 184–248 m³/ha; however, volumes differed among treatments (Table 1). The most woody debris occurred in the controls and the least in the large openings.

Before harvest, the thick shrub layer was dominated by white-flowered rhododendron (*Rhododendron albiflorum*) (45%) and a lesser component of black huckleberry (*Vaccinium membranaceum*) (7%). The fairly abundant herb layer consisted mostly of Sitka valerian (*Valeriana sitchensis*) (10%), oak fern (*Gymnocarpium dryopteris*) (7%), mountain arnica (*Arnica latifolia*) (5%), rosy twistedstalk (*Streptopus roseus*) (4%), and foamflower (*Tiarella trifoliata*) (3%). The bryophyte layer was fairly continuous at 40%. Within 2 years of harvesting, the shrub and bryophyte layers in the openings had declined by more than half while the herb layer had increased by 10–20% cover (Table 2). White-flowered rhododendron, black huckleberry, Sitka valerian, and oak fern remained the most abundant species in the harvested openings.

Methods

Experimental Design and Harvesting

The design is a randomized complete block with three sites representing the blocking factor. Each study site was approximately 40 ha and was divided into four 10-ha treatment units. One treatment unit was an uncut control and the three group selection treatments differed by opening size: 0.03 (small), 0.13 (medium), and 1.0 (large) ha. The four treatments were randomly assigned within each site. In each partially cut treatment unit, about 30% of the forested area (including skid trails) was removed using feller-bunchers and grapple skidders from December 1992 to January 1993. On average, the treatment units contained three 1.0-ha openings, seventeen 0.13-ha openings, and sixty 0.01-ha openings. Harvesting was done on a snowpack of 0.5–1.5 m to minimize forest floor disturbance. Permission was obtained from the Workers' Compensation Board of British Columbia to retain safe snags in the adjacent forest that would normally be felled during conventional ground-based harvesting.

TABLE 1. Total woody debris volume by treatment (openings) within sites in 2001

	Total woody debris volume (m³/ha) (>7.5 cm)			
	Treatment			
Site	Control	0.03 ha	0.13 ha	1.0 ha
Blackbear Creek	317	147	156	117
Lower Grain Creek	354	205	191	107
Upper Grain Creek	352	275	252	112
Mean	341	209	200	112
Standard deviation	21	64	49	5

TABLE 2. Mean and standard deviation (SD) of percentage cover by layer and treatment in 1992 (n = 24; 400 m² plots per treatment) and 1994 (n = 9; 400 m² plots per treatment in openings)

		Percentage cover by layer							
		Moss		Herb		Shrub		Tree	
Year	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
	1.0	35.6	21.4	32.6	15.5	57.4	24.3	17.9	7.5
1992	0.13	47.1	17.9	40.2	18.0	56.9	16.0	22.9	8.1
	0.03	47.7	15.2	40.4	19.0	54.2	21.5	20.6	8.0
	1.0	16.0	9.4	45.6	18.3	21.3	8.9	0.0	0.0
1994	0.13	25.9	12.2	51.4	20.4	18.0	9.4	0.0	0.0
	0.03	30.9	15.5	60.6	21.7	22.4	16.3	0.0	0.0

Trapping Method

Pre-harvest (1992), a grid of 24 Longworth live-traps was placed in the centre of each control and treatment unit. The trapping grids were a 6 × 8 configuration (6 lines, each with 8 stations), with the lines and stations at 14.4-m intervals to enable density estimations for an area of 1 ha (Ritchie and Sullivan 1989). Traps were located at every second station, alternating stations on each line.

Post-harvest (1993), the traps were moved so that approximately 33% of the grid fell in the harvested portions of each treatment unit. This permitted us to test for differences in use between treatment openings and forested areas. Also, the number of traps per treatment unit was increased to 48 to fully use the 6 × 8 trapping grid configuration. Three trapping sessions (commencing mid-July) were conducted at 4-week intervals during 1992 and 1993. In 1994, only two trapping sessions were conducted due to late spring snow melt followed by early autumn snow cover.

The grids and traps were laid out and pre-baited in June (2–3 weeks before trapping began), with trap doors locked open to allow the small mammals time to become familiar with the traps. The traps were lined with raw cotton for bedding, baited with whole oats and carrots, and set during the afternoon of day 1 of a given trapping session. On day 2, the traps were checked for small mammal captures, re-baited, and reset. All small mammals were ear-tagged and recorded by tag number, species, trap location, sex, weight, and reproductive state (Krebs *et al.* 1969), and status (alive or dead). On day 3 of each trapping session, previously untagged mammals were tagged and the above information was recorded for new and recaptured mammals. The trap doors were then locked open until the next trapping session.

Statistical Analyses

Two approaches were taken based on the type of data. The population of red-backed voles was sufficient to calculate the minimum known number alive (MNA) (Krebs 1966), which is continuous data. MNA estimates were tested using analysis of variance based on the randomized block design. All other data were based on the number of captures (counts) per treatment so were suited to contingency table and log-linear analyses. A significance level (α) of 0.05 was used for all statistical analyses.

For each year, the MNA data were analyzed using a repeated measures multivariate analysis (MANOVA). The analyses were based on successive differences between trapping sessions. A MANOVA statement within PROC GLM (SAS Institute Inc. 1990) was used to test for multivariate and univariate treatment effects. Wilks' Lambda is the only multivariate test statistic presented because the other statistics indicated similar results. Changes in population due to trapping session, and interactions between trapping session and site, and trapping session and treatment were analyzed using the REPEATED statement within PROC GLM (SAS Institute Inc. 1990). Power analysis was used to determine the study's ability to detect a false null hypothesis based on the MNA estimates for red-backed voles for the last trapping session in 1993 and 1994. These data were chosen because they showed the minimum and maximum values of sigma (variance) needed to calculate the size effect.

We were unable to calculate MNA for common and dusky shrews due to high mortality in the traps. Instead, for each year (captures from each session summed), we used contingency tables in the PROC FREQ procedure (SAS Institute Inc. 1990) to test for differences in shrew abundance among the treatments and to test for interactions between sites and treatments. Capture effort between the treatments was equal (equal number of traps), samples were independent, and the probability of capture was mainly attributed to treatment and site.

The number of captures (count data) of red-backed voles was also used to compare: (1) use of the openings and forest within each treatment, (2) use of the three opening sizes, and (3) use of the forested areas adjacent to the different-sized openings. Count data were based on the number of captures (not the number of individuals) per habitat (openings/forest) per treatment per year. For red-backed voles this involved a few repeat captures of individuals from session to session within each year. Animals were drawn from a large population in each trapping session; therefore, the requirement of independence of observations for chi-square was not violated.

To compare the use of openings to forest within each group selection treatment, a two-step approach was used. First, the interaction between site and treatment (openings/forest) was tested using a two-way contingency table. To do this, the count data were standardized because of unequal sampling effort. Of the 48 traps, one-third were in openings (about 16) and two-thirds in the forest (about 32) so the count data were standardized to captures per 24 traps (the number of captures were divided by the actual number of traps and multiplied by 24). In the second step, if an interaction was non-significant or explainable, a one-way contingency table was used to test for the treatment effect using the pooled original (non-standardized) data for the three sites. The expected values were calculated based on the actual number of traps per opening and forest.

Similarly, to compare use of the three opening sizes, data were standardized to counts per 16 traps to test for interactions between site and treatment. If interactions were non-significant, then the original (non-standardized) data were pooled over the three sites and tested with a one-way contingency table. Expected values were generated based on the actual number of traps. A similar method was used to compare the use of forests around each of the opening sizes except data were standardized to 32 traps. It was difficult in the field to lay out the grid to have exactly the same amount of trapping effort. The number of traps was within one or two of either 16 or 32.

All contingency tables were generated using the PROC FREQ procedure (SAS Institute Inc. 1990). For the contingency table results, the chi-square statistic is reported where there were more than 5 counts in 80% of the cells. Where there were fewer counts, the G-statistic (Likelihood Ratio Chi-square) is reported. Simultaneous Bonferroni confidence intervals (Byers and Steinhorst 1984) were calculated when chi-square analysis indicated a significant ($p \leq 0.05$) difference occurred for a main effect.

Results

Community Richness and Abundance

Six herbivores (southern red-backed vole [*Clethrionomys gapperi*], long-tailed vole [*Microtus longicaudus*], heather vole [*Phenacomys intermedius*], meadow vole [*Microtus pennsylvanicus*], deer mouse [*Peromyscus maniculatus*], and western jumping mouse [*Zapus princeps*]), two insectivores (common shrew [*Sorex cinereus*] and dusky shrew [*Sorex monticolus*]), and one mustelid (ermine [*Mustela erminea*]) species were captured pre-harvest and post-harvest. The number of captures (Table 3) remained stable between 1992 and 1993, but doubled in 1994 with all species of shrews and voles increasing on all sites and most treatments. The deer mouse and western jumping mouse did not follow this pattern and accounted for 0–6.5% of the total captures. Based on Table 3, the total number of captures of individuals visually appears similar among treatments within each sample year.

The red-backed vole was the most abundant species in all 3 years of the study. As a proportion of total captures, they represented 76%, 79%, and 57% in 1992, 1993, and 1994, respectively. In 1994, the number of individual red-backed voles captured increased by 30%, but declined in proportion to the total number of individuals for all species captured. This was caused by an increase in the number of shrews (*Sorex* spp.) captured. In 1993, common and dusky shrews represented 8% and 5%, but increased to 15% and 14%, respectively, of the total number of individuals captured in 1994. The three other vole species (long-tailed vole, and heather vole/meadow vole) decreased from 3–4% of the population in 1992 to 1% in 1993 but returned to the pre-harvest level in 1994.

Red-backed Voles

Use of Group Selection Treatments

The repeated measures multivariate analyses (Table 4) showed no significant interaction between trapping sessions and treatments for red-backed vole MNA estimates for any year of the study. There were no significant differences in the use of the group selection treatments in 1992, 1993, and 1994. Red-backed vole populations increased between trapping sessions in each year of the study ($p \leq 0.01$). Figure 1 illustrates the upward population trends that

TABLE 3. Number of individual small mammals captured by species, and treatment within sites

Year	Species	Study site and treatment units												Total
		Blackbear Creek				Lower Grain Creek				Upper Grain Creek				
		c [a]	0.03 ha	0.13 ha	1.0 ha	c	0.03 ha	0.13 ha	1.0 ha	c	0.03 ha	0.13 ha	1.0 ha	
1992	*Clethrionomys gapperi*	46	52	45	45	38	48	47	55	49	46	56	52	579
	Microtinae spp. [b]	6	0	3	0	3	0	2	2	4	2	1	2	25
	Microtus longicaudus	0	0	0	0	1	8	1	5	6	4	1	6	32
	Mustela erminea	0	0	0	1	0	0	0	0	0	0	0	0	1
	Peromyscus maniculatus	0	4	1	8	0	2	4	7	6	9	5	4	50
	Sorex cinereus	7	2	4	3	3	2	3	0	10	9	4	4	51
	Sorex monticolus	0	1	1	6	2	4	3	1	1	1	1	3	24
	Zapus princeps	0	0	0	0	0	1	0	0	0	0	1	0	2
	Total	59	59	54	63	47	65	60	70	76	71	69	71	764
1993	*Clethrionomys gapperi*	52	55	71	65	46	48	44	40	42	40	42	48	593
	Microtinae spp.	1	2	1	3	1	1	0	0	0	0	1	0	10
	Microtus longicaudus	0	0	2	0	0	1	0	0	0	1	0	0	4
	Mustela erminea	0	0	0	0	0	0	0	1	0	0	0	0	1
	Peromyscus maniculatus	2	0	3	0	0	2	5	10	4	1	0	2	29
	Sorex cinereus	4	3	7	12	1	3	3	7	10	3	2	1	56
	Sorex monticolus	4	0	7	4	1	0	2	4	6	2	2	2	34
	Zapus princeps	0	0	0	0	0	5	0	0	2	8	0	6	21
	Total	63	60	91	84	49	60	54	62	64	55	47	59	748
1994	*Clethrionomys gapperi*	76	102	91	59	67	49	47	55	70	47	46	59	768
	Microtinae spp.	9	17	7	12	0	1	5	0	1	6	2	7	67
	Microtus longicaudus	9	2	6	16	2	2	2	1	0	5	3	5	53
	Peromyscus maniculatus	15	4	9	7	0	0	1	1	6	1	5	8	57
	Sorex cinereus	23	5	14	20	21	21	16	25	17	11	7	17	197
	Sorex monticolus	28	4	20	16	19	22	15	22	11	15	8	11	191
	Zapus princeps	0	0	0	0	0	1	0	0	1	2	1	0	5
	Total	160	134	147	130	109	96	86	104	106	87	72	107	1338

[a] Treatment units. c = control (no harvesting); 0.03, 0.13, and 1.0 ha represent harvested opening sizes for a given treatment unit.

[b] Total number of individual *Phenacomys intermedius* and *Microtus pennsylvanicus* captured (not keyed out due to difficulty in identification in the field).

occurred within the controls and treatments between trap sessions for each study year. Also, the MNA estimates of red-backed vole density were similar between the pre-treatment and first post-treatment year, and rose substantially in all treatments in the second post-treatment year.

Power analysis was used to explore our level of confidence in accepting the null hypothesis of no treatment effects based on MNA estimates (minimum and maximum mean from the four treatments) from the final trapping sessions in 1993 and 1994. The probability of rejecting a false null hypothesis was low (<0.2) in

TABLE 4. Repeated measures multivariate analysis (Wilks' Lambda statistic) of red-backed vole MNA estimates collected from three partially cut treatments and controls within three study sites

Test	1992				1993				1994			
	Value	F	Df (num, den)	P	Value	F	Df (num, den)	P	Value	F	Df (num, den)	P
Interactions between trapping session and treatments	0.31	1.30	6,10	0.34	0.71	0.32	6,10	0.91	0.76	0.61	3,6	0.63
Overall differences in treatment effects	0.28	0.74	9,10	0.67	0.66	0.21	9,10	0.98	0.63	0.44	6,10	0.84
Changes in populations between trapping sessions for each year	0.15	14.60	2,5	**<0.01**	0.09	26.89	2,5	**<0.01**	0.19	25.20	1,6	**<0.01**

each year. Based on our study design and calculations of variance, and a fixed 30% difference between means, 4–8 replicates of each treatment would be required to increase the maximum power of the study to 0.8.

Use of Openings and Forest within Group Selection Treatments

In each post-harvest study year, the number of red-backed voles captured in openings and forested areas of each group selection treatment were compared (Table 5). In 1993, there were no significant interactions between sites and habitat (forest/openings) within the large (1.0 ha) or small (0.03 ha) opening treatments. However, we found an interaction in the medium (0.13 ha) treatment where the forest was used at slightly higher intensity than the openings on Blackbear and Lower Grain, while a much higher use of the forest than the openings was observed on the Upper Grain site. When data were pooled from the three sites to test for treatment effects, red-backed voles used the forested areas more than expected and openings less than expected within all group selection treatments. In 1994, there were no significant interactions between site and habitat for any of the treatments. In each treatment, the greater use of the forest than the

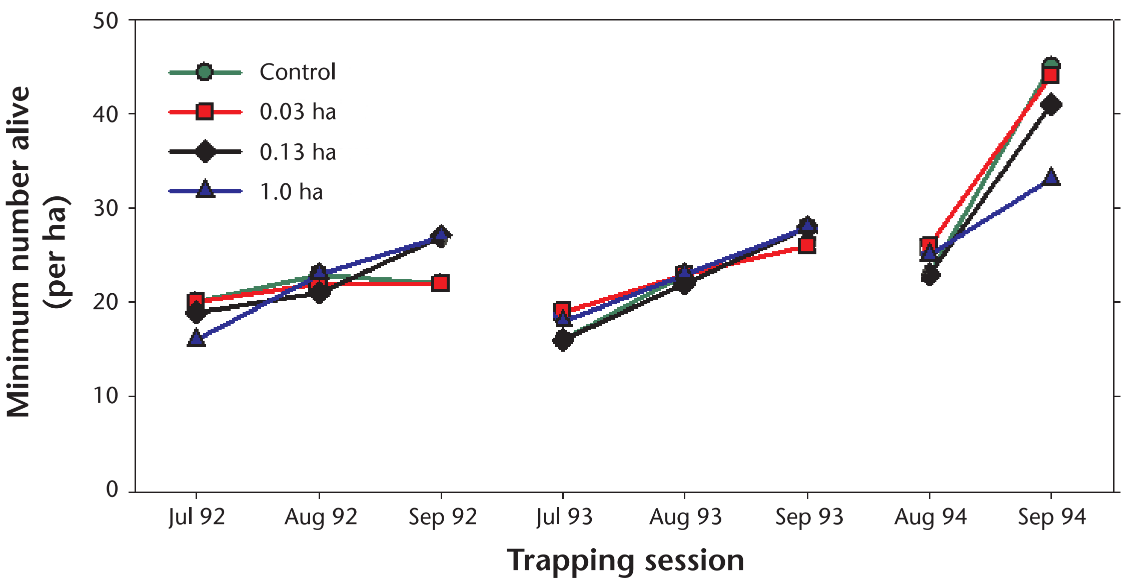

FIGURE 1. Mean red-backed vole MNA estimates by treatment and trapping session from 1992 to 1994.

TABLE 5. Summary of site by treatment interactions and pooled treatment effects for comparison of red-backed vole use of openings versus forest, three opening sizes, and forest around openings of three sizes

Habitat selection	Year	Opening size	Test of	Df	Chi	p
Openings versus forest	1993	0.03	interaction	2	1.00	0.61
			treatment	1	10.53	**0.01**
		0.13	interaction	2	9.45	**0.01**
			treatment	1	11.04	**0.01**
		1.0	interaction	2	0.10	0.95
			treatment	1	13.67	**0.01**
	1994	0.03	interaction	2	1.49	0.48
			treatment	1	8.45	**0.01**
		0.13	interaction	2	4.91	0.09
			treatment	1	40.63	**0.01**
		1.0	interaction	2	5.52	0.06
			treatment	1	23.26	**0.01**
Opening size (0.03, 0.13, or 1.0 ha)	1993		interaction	4	2.98	0.56
			treatment	2	1.17	0.56
	1994		interaction	4	12.46	**0.01**
			treatment	2	16.16	**0.01**
Forest around openings (0.03, 0.13, or 1.0 ha)	1993		interaction	4	3.41	0.49
			treatment	2	0.20	0.90
	1994		interaction	4	5.37	0.25
			treatment	2	2.48	0.29

openings was significant and more pronounced in 1994 than 1993 (Figure 2).

The same data were used to test whether the size of the openings affected use (Table 5). In 1993, there was no interaction between site and opening size or difference in use due to opening size. In 1994, the larger population year, a significant interaction between site and opening size was observed. At the Blackbear and Upper Grain Creek sites, there was much greater use of the small openings than the medium or large ones. However, at Lower Grain Creek the use of the large openings equalled that of the small openings while the medium openings were used the least. When data were pooled from the three sites, the treatment effect was significant but this was mostly due to the use patterns in Blackbear and Upper Grain Creek sites. Bonferroni confidence intervals (Table 6) confirm that the 0.03-ha openings were used more than either the 0.13- or 1.0-ha openings (Figure 2).

The forested areas surrounding the openings of different sizes were also compared. Both post-treatment years showed no significant site interactions or differences in use of the forest around the openings (Table 5).

Common and Dusky Shrews

For common shrews, there was no significant pre-treatment (1992) interaction between site and group selection treatment, and no significant treatment effect (Table 7). However, in 1993 there were significantly different patterns of use of the treatments between sites (Table 7). The greatest number of captures occurred in the large opening treatments on the Blackbear and Lower Grain Creek sites while the most captures on Upper Grain Creek occurred in the unlogged control. The treatment effect was non-significant. In 1994, the larger population year, the interaction between site and treatment was non-significant. When the data were pooled over the three sites, there were significantly more captures in the control (61 captures) and large (62 captures) treatments than the small (37 captures) or medium (37 captures) treatments.

For dusky shrews, in 1992 and 1993, there were no significant interactions between site and treatment, and no significant treatment effects. In 1994, there was a significant site by treatment interaction resulting from very low captures in the Blackbear Creek small treatment. When data were pooled, no treatment effects were observed (Table 7).

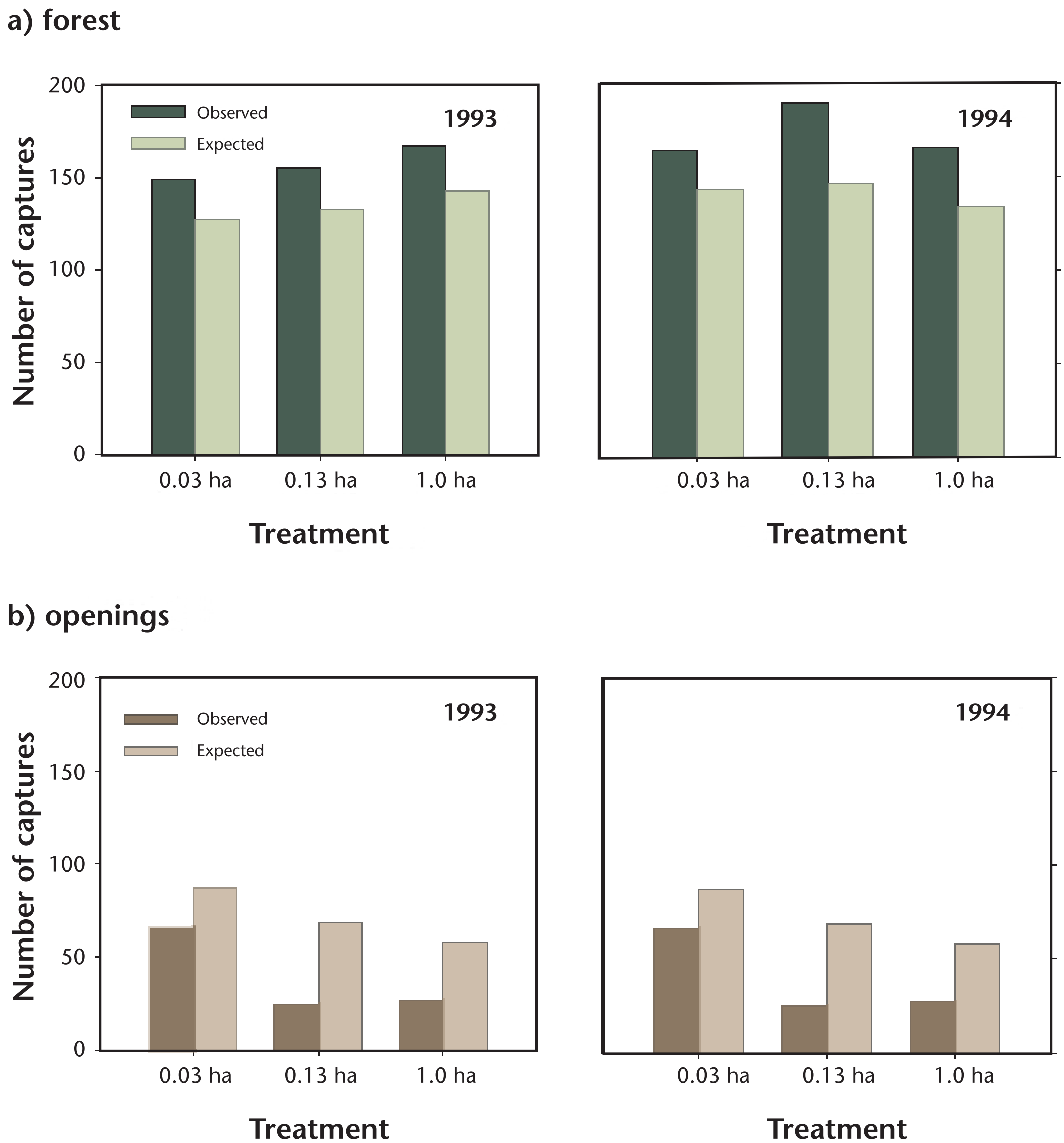

FIGURE 2. Observed and expected number of captures of red-backed voles within a) forested component of treatments and b) within treatment openings for 1993 and 1994 from three partially cut sites. Expected values were generated from the number of traps used in the forest and openings of each group selection treatment.

TABLE 6. Bonferroni confidence intervals for red-backed vole use within three opening sizes used in the group selection treatments in 1994. Expected use was generated from the number of traps set in the three opening sizes.

Treatment	No. traps	Observed voles	Expected voles	Observed proportion of use (Pi)	Expected proportion of use (Pi)	Bonferroni intervals for Pi
0.03 ha	55	66	44.8	0.56	0.38	$0.44 \leq P1 \leq 0.68$
0.13 ha	45	25	36.6	0.21	0.31	$0.11 \leq P2 \leq 0.31$
1.0 ha	44	27	36.6	0.23	0.31	$0.13 \leq P3 \leq 0.33$
Total	144	118	118	1	1	

TABLE 7. Common and dusky shrew use of the group selection treatments and unlogged controls in 1992, 1993, and 1994

Species	Year	Test of	Df	Chi	p
Common shrew	1992	interaction	6	5.99	0.42
		treatment	3	6.96	0.07
	1993	interaction	6	18.94	**0.01**
		treatment	3	4.71	0.19
	1994	interaction	6	8.84	0.18
		treatment	3	12.20	**0.01**
Dusky shrew	1992	interaction	6	10.03	0.12
		treatment	3	4.33	0.23
	1993	interaction	6	10.44	0.11
		treatment	3	6.71	0.08
	1994	interaction	6	18.96	**0.01**
		treatment	3	3.66	0.30

Discussion

Small Mammal Community

Despite the northerly latitude and high elevation, species richness and composition of the small mammal community in old Engelmann spruce–subalpine fir forest in central British Columbia is similar to that found in the same forest type further south. In our study, we found nine species and a community dominated by southern red-backed voles. The number of species (excluding woodrats and squirrels) reported by other studies in spruce–subalpine fir forests are as follows: 10 (Klenner and Sullivan 2003), 9 (Scott *et al.* 1982), 15 (Raphael 1988), and 9 (Hayward and Hayward 1995). In these studies plus Nordyke and Buskirk (1991), the red-backed vole is the most abundant species. In British Columbia's old, low-elevation forests, small mammal species richness ranges from 7 to 10 species in communities also dominated by red-backed voles (Steventon *et al.* 1998; Von Trebra *et al.* 1998; Sullivan *et al.* 1999; Sullivan *et al.* 2000; Sullivan and Sullivan 2001). In our study, common shrews, dusky shrews, and deer mice were the second most abundant species depending on the year. In the other British Columbia studies, except Steventon *et al.* (1998), deer mice and or yellow-pine chipmunks (*Tamias amoenus*) are often more abundant than shrews. The total abundance of small mammals found in our study was within the range of that reported for the studies in British Columbia.

In response to partial cutting, in our study, the number of species and the relative proportion of the common species in the community remained unchanged. In other British Columbia studies where overstory retention is at least 40% of the original, the composition of the community remains fairly stable (Klenner 1997; Steventon *et al.* 1998; Von Trebra *et al.* 1998; Klenner and Sullivan 2003). This is also reported in older partial cutting studies outside British Columbia (Scott *et al.* 1982; Martell 1983; Medin and Booth 1989).

Often when the overstory has been removed (clearcut), the composition of the small mammal community shifts. Red-backed voles become less prominent while generalist or early seral species such as meadow voles, long-tailed voles, deer mice, and chipmunks are more prevalent (Ramirez and Hornocker 1981; Martell 1983; Steventon *et al.* 1998; Sullivan *et al.* 1999; Sullivan and Sullivan 2001; Klenner and Sullivan 2003). Clough (1987) and Parker (1989) both found less distinct differences in species composition between early successional and mature conifer stands. A literature review by Kirkland (1990) found an overall positive population response to clear-cutting in North America, due mostly to increases in red-backed voles. Given new studies, especially from conifer forests in western Northern America, the literature needs to be re-examined.

In our study, partial cutting did not change the total abundance of small mammals compared with the unlogged controls. When Sullivan and Sullivan (2001) compared various silvicultural systems, abundance was similar among treatments but they noted a rise in generalist species (meadow voles, deer mice, long-tailed voles, and dusky shrews) in seed tree and clearcut treatments (heavy canopy removals). Various studies attribute an increase in small mammal abundance to clearcutting (Parker 1989; Kirkland 1990; Sullivan *et al.* 1999).

Red-backed Voles

We found no short-term effects from the various group selection treatments on the population estimates of red-backed voles. Klenner and Sullivan (2003) found comparable results with a similar range of opening sizes (0.01–1.0 ha) and area removal (35%) in an old Engelmann spruce–subalpine fir forest in southern British Columbia. Scott *et al.* (1982) also reported that use of 1.2-ha patch cuts resulting in a 36% area removal did not affect the red-backed vole population in Engelmann spruce–subalpine fir forests in Colorado.

In other silvicultural systems trials in British Columbia, Steventon *et al.* (1998) found that within 2 years of light partial cutting (30% volume removal by single trees and groups) in the Interior Cedar–Hemlock biogeoclimatic zone, the red-backed vole population increased; on the other hand, clearcutting resulted in a decline. Von Trebra *et al.* (1998) likewise found that the red-backed vole population increased in Douglas-fir stands immediately after partial cutting compared with the heavily canopied uncut control areas. Sullivan and Sullivan (2001) also stated that red-backed vole populations decreased substantially in clearcut and single seed tree silvicultural systems, but remained relatively abundant in group seed tree, patch cut, and uncut Douglas-fir–lodgepole pine forests.

Although we found no overall treatment effects on the red-backed vole population, the patterns of habitat use within the treatment units changed. Counts of red-backed voles were lower in openings than in the forested matrix of all group selection treatments in both post-harvest years. Either more animals were in the uncut portions or the residents used the cut portions of their home ranges less intensively. In the higher population year (1994), red-backed voles used the 1.0-ha and 0.13-ha openings less than the 0.03-ha openings. Hayward *et al.* (1999) found statistically fewer red-backed voles in the interior of patch cuts compared with the surrounding forest in one of 2 years of study, although the patch cuts were used regularly. Menzel (1999) found low red-backed vole use in patch cuts where mowing greatly reduced cover and forage. In contrast, Scott *et al.* (1982) reported no difference in use between patch cuts and uncut areas based on data from only one harvested study block.

The group selection treatments retain important habitat attributes but the openings have shifted from a shrub- to a herb-dominated understory, characterized by reduced moisture conditions, reduced woody debris, lost arboreal lichen, probably lost fungi, and little mature/old stand structure. To some degree, red-backed voles must perceive this new habitat as less desirable than the uncut forest but more desirable than clearcuts. Many studies document a very strong negative response to clear-cutting, especially if followed by aggressive silvicultural treatments such as prescribed burning (Ramirez and Hornocker 1981; Halvorson 1982; Medin 1986; Sullivan *et al.* 1999). Sekgororoane and Dilworth (1995) indicated red-backed voles were not captured beyond 5 m from forest edges into three clearcuts (6–10 years old). Sullivan and Sullivan (2001), Steventon *et al.* (1998), Klenner and Sullivan (2003), and Craig *et al.* (1997) found reduced use of clearcuts (≥10 ha) compared with uncut controls within 2–4 years of harvesting. Other studies (Martell 1983; Walters 1991; Gagné *et al.* 1999) have found red-backed voles commonly inhabiting older clearcut areas not subject to aggressive site preparation and conifer release treatments.

Understory cover is identified as a key habitat component (Nordyke and Buskirk 1991; Carey and Johnson 1995). Gagné *et al.* (1999) reported that the numbers of red-backed voles were reduced for 1–2 years after conifer release treatments that greatly decreased deciduous tree species and raspberry shrub layers, while the herb and other shrub layers remained steady or increased. This finding is similar to our study where, within the openings, the shrub layer decreased from a pre-harvest level of 57% to 21% at two growing seasons post-harvest. White-flowered rhododendron, the main component of the shrub layer, was snapped under the snowpack by the feller-bunchers. The herb layer responded quickly to the improved light conditions, increasing from about 38% cover pre-treatment to 53% two growing seasons post-treatment. Retention of the shrub layer may be particularly important in the spring and late fall when herb cover is poor because it could increase moisture retention through shading, trap snow such that subnivian tunnels are more easily constructed, and provide strong visual cover from aerial predators.

Tree, shrub, herb, and woody debris layers reduce drying of the ground from sun and wind, thereby helping to maintain the moist conditions favoured by red-backed voles (Getz 1968) and shrews (Getz 1961). We could not directly measure moisture levels but accumulated growing degree days, based on air temperature (15 cm above ground), were lower in the uncut controls and 0.03-ha openings than the two larger size openings (Stathers *et al.* 2001).

Martell (1981), and Ure and Maser (1982) indicated, respectively, that epigeous and hypogeous (on and below ground surface) fungal sporocarps were an important component of red-backed vole diet and that the disappearance of voles from deforested areas may be a result of fungi no longer fruiting after forest removal. Arboreal lichens are also eaten and become more important with increased elevation (Ure and Maser 1982). These lichens are ubiquitous within our study sites and are likely an important component in the diet of red-backed voles in these communities. Although lichens are available as litterfall from the forested part of the treatment units, they become less available with distance into the openings.

Coarse woody debris has also been identified as an important habitat attribute (Tevis 1956; Nordyke and Buskirk 1988; Carey and Johnson 1995). In our study, a substantial amount of woody debris is in the partial cut openings (about 200 m^3/ha in the medium and small openings and 100 m^3/ha in the large openings) but this is less than in the unlogged controls (about 340 m^3/ha). Sullivan and Sullivan (2001) found no relationship between red-backed vole numbers and woody debris, which ranged from 110 to 210 m^3/ha across their treatments.

The lack of mature and old trees in the openings ultimately affects moisture, woody debris recruitment, shrub/herb development, arboreal lichen abundance, fungus abundance, and predator–prey relationships (Raphael 1988; Nordyke and Buskirk 1991; Hayward and Hayward 1995); however, these factors may be modified by opening size. It is possible that the close proximity to forest cover from within the 0.03-ha openings (maximum of 10 m to forest edge) provides a greater range of habitat attributes. For example, the smaller openings may also be moister as they are less exposed to desiccation from the sun and wind. Armleder *et al.* (2000) reported the least reduction in growth rates of arboreal lichen in the forested portion of the small opening treatments, indicating the least change to the ambient microclimate. Additionally, the small-sized openings may supply preferred food such as fungal sporocarps and arboreal lichen litterfall. Also, as openings are only about one tree length wide, snags may fall completely across openings, increasing the amount of woody debris. Opening size may also affect predator–prey relationships. Huggard (1999) found marten used smaller openings (0.10 ha) more than larger openings (1.0 ha) or clearcuts (10 ha) in old, ESSF forest in southern British Columbia. Raptors may find smaller openings more difficult habitat for hunting due to the proximity of forest cover. As the conifer forest, shrub layer, and other attributes develop over time, we expect that red-backed vole use will increase in all opening sizes.

Despite the reduced use of the harvested openings in the short term, the combination of openings and the adjacent forested areas within the treatment units provided habitat sufficient for maintaining red-backed vole populations. This result agrees with other reported studies. However, the results of the power analysis showed that the probability of rejecting a false null hypothesis was low (<0.2). Given the experimental design and a fixed 30% difference in treatment means, up to eight replicates would be required to strengthen the power of our study when variability in the MNA estimates is high. However, a multi-year study with even three replicates of four treatments like ours is costly. Therefore, results from several smaller studies should be published so the data are available for a larger synthesis.

Common and Dusky Shrews

The abundance of common shrews has been related to moist environmental conditions (Getz 1961) and the abundance of invertebrates found within moist forests (McCay and Storm 1997). Parker (1989) demonstrated a positive correlation between ground cover (slash and early succession herbaceous species) and insectivore abundance; the cover would be conducive to high insect densities.

In the high-population year of 1994, we found that common shrews used the unlogged control and large treatment units more than the small or medium treatments. This may indicate some preference for less fragmented and moister, undisturbed habitat. Martell (1983), Walters (1991), and Sekgororoane and Dilworth (1995) found shrews (predominantly common) to be equally abundant in clearcuts of various ages and uncut older forest. Steventon *et al.* (1998) found no difference within 2 years of harvesting in use of clearcuts, partial cuts, or uncut forests for shrews (dusky and common). Sullivan and Sullivan (2001) found no difference in abundance of common shrews in various silvicultural systems, though the populations were low. Clough (1987) found common shrews to be more abundant in early successional than mature conifer forests where ground cover of vegetation was greater. Similarly, Parker (1989) reports that common shrews were most abundant in a 2-year-old spruce plantation, followed by mature black spruce forests then older spruce plantations.

In our study, the population of dusky shrews increased dramatically from 1993 to 1994, as did that of the common shrew. Unlike the common shrew, the dusky shrew showed no response to the group selection treatments. Carey and Johnson (1995) could not correlate dusky shrew abundance to coarse woody debris, shrub, or herbaceous cover. Terry (1981) found abundance related to dead wood and debris rather than vegetative factors. Sullivan and Sullivan (2001) found more dusky shrews in clearcuts and seed-tree silvicultural systems than in treatments with heavier residual basal areas.

Our data confirm that dusky shrews may be generalists; therefore, partial cutting does not influence their habitat selection. On the other hand, common shrews exhibit some preference for treatments with more contiguous portions of intact forest within the first 2 years of harvest. This effect should be further investigated because it has not been previously reported.

Management Implications

To maintain mountain caribou habitat within the Cariboo-Chilcotin Land Use Plan area, over 53 000 ha of ESSF forest type may be harvested with selection silvicultural systems similar to those used in this study (Caribou Strategy Committee 2000). Stevenson *et al.* (2001) recommend similar partial cutting for all the managed forest range of mountain caribou in British Columbia. This could potentially increase the use of this approach tenfold. Additionally, to meet broader biodiversity objectives, group selection silvicultural systems could be applied to forests in the Engelmann Spruce–Subalpine Fir biogeoclimatic zone not dedicated to mountain caribou management.

Because a large amount of ESSF forest may be cut using selection silvicultural systems similar to those used in this study, small mammal communities may be affected. We found that within the first few years of partial cutting, the small mammal community maintained stable composition, richness, and abundance. Red-backed voles were less impacted by smaller openings and common shrews may favour the large opening treatment. A mix of opening sizes (0.03–1.0 ha) within a cutblock could best address the range of small mammal habitat requirements. In the longer term, the small mammal community should remain stable due to the long cutting cycles of 80 years and low area removal (33%) per entry. This prescription will retain trees up to 240 years old, a mosaic of forest structure, arboreal lichens, and fungi; and will ensure the recruitment of snags and coarse woody debris. To confirm the effects of this prescription, the small mammal community should be monitored over time.

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References

Armleder, H.M., J.A. Young, and J.A. Youds. 2000. A management strategy for mountain caribou—the Cariboo Region example. *In* Proceedings of a conference on the biology and management of species and habitats at risk conference. L. Darling (editor). February 19–21, 1999, Kamloops, B.C. B.C. Ministry of Environment, Lands and Parks, Victoria, B.C. and University College of the Cariboo, Kamloops, B.C., pp. 645–651.

Banfield, A.W.F. 1974. The mammals of Canada. University of Toronto Press, Toronto, Ontario.

Byers, C.R. and R.K. Steinhorst. 1984. Clarification of a technique for analysis of utilisation-availability data. Journal of Wildlife Management 48:1050–1053.

Carey, A.B. and M.L. Johnson. 1995. Small mammals in managed, naturally young, and old-growth forests. Ecological Applications 5:336–352.

Caribou Strategy Committee. 2000. Mountain caribou strategy. Cariboo Mid-Coast Interagency Management Committee, Williams Lake, B.C. Cariboo-Chilcotin Land Use Plan special report.

Clough, G.C. 1987. Relations of small mammals to forest management in northern Maine. Canadian Field-Naturalist 101:40–48.

Craig, V., W. Klenner, and T. Sullivan. 1997. Relationships between small mammals and downed wood at Sicamous Creek. *In* Sicamous Creek silvicultural systems project: workshop proceedings. C. Hollstedt and A. Vyse (editors). April 24–25, 1996, Kamloops, B.C. B.C. Ministry of Forests, Research Branch, Victoria, B.C., Working Paper No. 24, pp. 243–253.

Gagné, N., L. Bélanger, and J. Huot. 1999. Comparative responses to small mammals, vegetation, and food sources to natural regeneration and conifer release treatments in boreal balsam fir stands of Quebec. Canadian Journal of Forest Research 29:1128–1140.

Gashwiler, J.S. 1970. Plant and mammal changes on a clearcut in west-central Oregon. Ecology 51:1018–1026.

Getz, L.L. 1961. Factors influencing the local distribution of shrews. American Midland Naturalist 65:67–88.

________. 1968. Influence of water balance and micro-climate on the local distribution of the red-backed vole and white-footed mouse. Ecology 49:276–286.

Halvorson, C.H. 1982. Rodent occurrence, habitat disturbance, and seed fall in a larch-fir forest. Ecology 63:423–433.

Hayward, G.D. and P.H. Hayward. 1995. Relative abundance and habitat associations of small mammals in Chamberlain Basin, central Idaho. Northwest Science 69:114–125.

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

Hooven, E.F. and H.C. Black. 1976. Effects of some clear-cutting practices on small-mammal populations in western Oregon. Northwest Science 50:189–208.

Huggard, D.J. 1999. Marten use of different harvesting treatments in high-elevation forest at Sicamous Creek. B.C. Ministry of Forests, Victoria, B.C. Research Report No. 17.

Kirkland, G.L. 1990. Patterns of small mammal change after clearcutting. Oikos 59:313–320.

Klenner, W. 1997. Effects of harvest treatments on the abundance of small mammals at Sicamous Creek. *In* Sicamous Creek silvicultural systems project: workshop proceedings. C. Hollstedt and A. Vyse (editors). April 24–25, 1996, Kamloops, B.C. B.C. Ministry of Forests, Research Branch, Victoria, B.C., Working Paper No. 24, pp. 234–242.

Klenner, W. and T.P. Sullivan. 2003. Partial and clearcut harvesting of high elevation spruce-fir forests: implications for small mammal communities. Can. J. For. Res. 33:2283–2296.

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

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

Martell, A.M. 1981. Food habits of southern red-backed voles (*Clethrionomys gapperi*) in northern Ontario. Canadian Field-Naturalist 95:325–328.

________. 1983. Changes in small mammal communities after logging in north-central Ontario. Canadian Journal of Zoology 61:970–980.

McCay, T.S. and G.L. Storm. 1997. Masked shrew (*Sorex cinereus*) abundance, diet and prey selection in an irrigated forest. American Midland Naturalist 138:268–275.

Medin, D.E. 1986. Small mammal responses to diameter-cut logging in an Idaho Douglas-fir forest. U.S. Department of Agriculture Forest Service, Research Note INT-362.

Medin, D.E. and G.D. Booth. 1989. Responses of birds and small mammals to single-tree selection logging in Idaho. U.S. Department of Agriculture Forest Service, Research Note INT-408.

Menzel, M.A., W.M. Ford, J. Laerm, and D. Krishon. 1999. Forest to wildlife opening: habitat gradient analysis among small mammals in the southern Appalachians. Forest Ecology and Management 114:227–232.

Nordyke, K.A. and S.W. Buskirk. 1988. Evaluation of small mammals as ecological indicators of old-growth conditions. *In* Proceedings Management of amphibians, reptiles, and small mammals in North America. R.C. Szaro, K.E. Severson, and D.R. Patton (technical coordinators). July 19–21, 1988, Flagstaff, Arizona. U.S. Department of Agriculture Forest Service, General Technical Report RM-166, pp. 353–358.

________. 1991. Southern red-backed vole, *Clethrionomys gapperi*, populations in relation to stand succession and old-growth character in the central Rocky Mountains. Canadian Field-Naturalist 105:330–334.

Parker, G.R. 1989. Effects of reforestation upon small mammal communities in New Brunswick. Canadian Field-Naturalist 103:509–519.

Province of British Columbia. 1995. Cariboo-Chilcotin land use plan: ninety day implementation process and final report. Victoria, B.C.

Radvanyi, A. 1973. Seed losses to small mammals and birds. *In* Direct seeding symposium. J.H. Cayford (editor). Canadian Forest Service Publication 1339, pp. 67–75.

Ramirez, P., Jr. and M. Hornocker. 1981. Small mammal populations in different-aged clearcuts in north-western Montana. Journal of Mammalogy 62:400–403.

Raphael, M.G. 1988. Habitat associations of small mammals in a subalpine forest, southeastern Wyoming. *In* Proceedings Management of amphibians, reptiles, and small mammals in North America. R.C. Szaro, K.E. Severson, and D.R. Patton (technical coordinators). July 19–21, 1988, Flagstaff, Arizona. U.S. Department of Agriculture Forest Service, General Technical Report RM-166, pp. 359–367.

Ritchie, C. and T.P. Sullivan. 1989. Monitoring methodology for assessing the impact of forest herbicide use on small mammal populations in British Columbia. Forestry Canada and B.C. Ministry of Forests, Victoria, B.C. FRDA 081.

SAS Institute Inc. 1990. SAS procedures guide. Version 6. Third edition. Cary, N.C.

Scott, V.E., G.L. Crouch, and J.A. Whelan. 1982. Responses of birds and small mammals to clearcutting in a subalpine forest in central Colorado. U.S. Department of Agriculture Forest Service, Research Note RM-422.

Sekgororoane, G.B. and T.G. Dilworth. 1995. Relative abundance, richness, and diversity of small mammals at induced forest edges. Canadian Journal of Zoology 73:1432–1437.

Stathers, R.J., T. Newsome, M.J. Waterhouse, and C. Sutherland. 2001. Microclimate studies on a group selection silvicultural system in a high elevation ESSFwc3 forest in the Cariboo Forest Region. B.C. Ministry of Forests, Victoria, B.C. Working Paper No. 58.

Stevenson, S.K., H.M. Armleder, M.J. Jull, D.G. King, B.N. McLellan, and D.S. Coxson. 2001. Mountain caribou in managed forests: recommendations to managers. Second edition. B.C. Ministry of Environment, Lands and Parks, Victoria, B.C. Wildlife Report No. R-26.

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

Sullivan, T.P. and D.S. Sullivan. 2001. Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. Journal of Applied Ecology 38:1234–1252.

Sullivan, T.P., R.A. Lautenschlager, and R.G. Wagner. 1999. Clearcutting and burning of northern spruce-fir forests: implications for small mammal communities. Journal of Applied Ecology 36:327–344.

Sullivan, T.P., D.S. Sullivan, and P.M.F. Lindgren. 2000. Small mammals and stand structure in young pine, seed-tree, and old-growth forest, southwest Canada. Ecological Applications 10:1367–1383.

Terry, C.J. 1981. Habitat differentiation among three species of *Sorex* and *Neurotrichus gibbsi* in Washington. American Midland Naturalist 106:119–125.

Tevis, L., Jr. 1956. Responses of small mammal populations to logging of Douglas-fir. Journal of Mammalogy 37:189–196.

Ure, D.C. and C. Maser. 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian Journal of Zoology 60:3307–3315.

Van Horne, B. 1982. Niches of adult and juvenile deer mice (*Peromyscus maniculatus*) in seral stages of coniferous forest. Ecology 63:992–1003.

Von Trebra, C., D.P. Lavender, and T.P. Sullivan. 1998. Relations of small mammal populations to even-aged shelterwood systems in sub-boreal spruce forest. Journal of Wildlife Management 62:630–642.

Walters, B.B. 1991. Small mammals in a subalpine old-growth forest and clearcuts. Northwest Science 65:27–31.

West, S.D., R.G. Ford, and J.C. Zasada. 1980. Population response of the northern red-backed vole (*Clethrionomys rutilus*) to differentially cut white spruce forest. U.S. Department of Agriculture Forest Service, Research Note PNW-362.