Partial and clear-cut harvesting of high-elevation spruce–fir forests: implications for small mammal communities

Walt Klenner and Thomas P. Sullivan

Abstract: Subalpine spruce (*Picea*) – fir (*Abies*) forests occur throughout the Cordillera of western North America. A variety of alternative silvicultural systems to clear-cutting are being investigated in these high-elevation forests in terms of their impacts on ecosystem components. We tested the hypotheses that abundance, reproduction, and survival of populations of (*i*) southern red-backed voles (*Clethrionomys gapperi* Vigors) will decline, (*ii*) long-tailed voles (*Microtus longicaudus* Merriam) and northwestern chipmunks (*Tamias amoenus* J.A. Allen) will increase, and (*iii*) deer mice (*Peromyscus maniculatus* Wagner) will be similar, with respect to decreasing levels of tree retention. Small mammal populations were live-trapped from 1994 to 1998 in replicated sites of uncut forest, single tree selection, 0.1-ha patch cuts, 1.0-ha patch cuts, a 10.0-ha clearcut, and edges in an Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) – subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forest near Sicamous, British Columbia, Canada. *Clethrionomys gapperi* dominated the small mammal community, reaching a peak abundance of 80 animals/ha with mean values ranging from 31 to 50 animals/ha. Over the 4 postharvest years, abundance, reproduction, and survival of *C. gapperi* populations were consistently similar among uncut forest, single tree selection, and patch cut treatments compared with clear-cut sites where this species declined to extirpation. *Microtus longicaudus* and *T. amoenus* occurred predominantly in clearcut sites, whereas *P. maniculatus* was present in low numbers on all sites. With respect to small mammals, partial harvesting systems appear to provide a means for combining timber extraction with maintenance of mature forest habitat in these subalpine ecosystems.

Résumé : Des forêts subalpines d'épinette (*Picea*) et de sapin (*Abies*) croissent un peu partout dans la Cordillère de l'ouest de l'Amérique du Nord. Les impacts écosystémiques de plusieurs systèmes sylvicoles sont actuellement étudiés comme solution de rechange à la coupe à blanc dans ces forêts de haute altitude. Nous avons testé les hypothèses voulant que l'abondance, la reproduction et la survie de populations vont, en relation avec une diminution du niveau de rétention d'arbres : (*i*) diminuer chez le campagnol à dos roux de Gapper (*Clethrionomys gapperi* Vigors); (*ii*) augmenter chez le campagnol à longue queue (*Microtus longicaudus* Merriam) et le tamia du Nord-Ouest (*Tamias amoenus* J.A. Allen); et (*iii*) rester stables chez la souris sylvestre (*Peromyscus maniculatus* Wagner). Les populations de petits mammifères ont fait l'objet de piégeage non mortel de 1994 à 1998 dans des sites répétés de forêt intacte, de jardinage par pied d'arbre, de coupes par trouées de 0,1 ha, de coupes par trouées de 1,0 ha, de coupes à blanc de 10,0 ha et de bordures, dans une forêt d'épinettes d'Engelmann (*Picea engelmannii* Parry ex Engelm.) et de sapins subalpins (*Abies lasiocarpa* (Hook.) Nutt.) près de Sicamous, en Colombie-Britannique, au Canada. *Clethrionomys gapperi* dominait la communauté de petits mammifères, avec une abondance maximale atteignant 80 individus/ha et des valeurs moyennes de 31 à 50 individus/ha. Durant les 4 années après coupe, l'abondance, la reproduction et la survie des populations de *C. gapperi* étaient de façon soutenue semblables dans la forêt intacte, le jardinage par pied d'arbre et les coupes par trouées en comparaison avec les coupes à blanc où l'espèce a diminué jusqu'à l'extirpation. *Microtus Longicaudus* et *T. amoenus* occupaient surtout les coupes à blanc tandis que *P. maniculatus* était présent partout mais peu abondant. Les systèmes de coupe partielle semblent donc, quant aux petits mammifères, un moyen de combiner la récolte ligneuse et le maintien d'habitats de forêt mature dans ces écosystèmes subalpins.

[Traduit par la Rédaction]

Introduction

Green-tree retention systems have become more common across a range of forested ecosystems in North America where clear-cutting has been the dominant method of forest harvesting. Variable retention harvesting systems can maintain or increase structural diversity of the regenerating stand and provide some mature forest habitat (McComb et al. 1993; Franklin et al. 1997). Retention of structural characteristics includes not only "green trees" but also snags, logs,

---

Received 18 November 2002. Accepted 2 June 2003. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 19 November 2003.

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

[1] Corresponding author (e-mail: Sullivan@telus.net).

system structure and function and enhance connectivity across the forested landscape.

The sustainability of clear-cutting has been questioned (Franklin 1995; Wagner et al. 1998) and the practice is particularly under scrutiny with respect to subalpine forests in the southern interior of British Columbia (Vyse 1999). These high-elevation forests are projected to be a major source of timber over the next several decades. In addition, clear-cut harvesting near the highest elevations, close to the tree line, has prompted concerns about forest regeneration (Vyse 1999). These forests may be at the "physiological edge" where low temperatures, high winds, and deep snowfalls combine to reduce biological activity above and below ground and hence tree regeneration (Vyse 1997). Although much work on regeneration at high elevations has been done in North America (see review by Alexander 1986), there is little information on the responses of other ecosystem components to forest harvesting and stand regeneration.

A major component of the fauna in these high-elevation Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) – subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forests is the small mammal community. Forest floor small mammals provide a measure of ecosystem function and may be indicators of sustainability of forests in the Pacific Northwest and elsewhere (Carey and Harrington 2001; Sullivan and Sullivan 2001). Ecosystem functions include serving as prey for a wide variety of reptiles, carnivores, hawks, and owls (Verts and Carraway 1998), consumption of invertebrates (Buckner 1966; Gunther et al. 1983) and various plant products (Sullivan et al. 1990; Carey et al. 1999), and dispersal of fungal spores (Maser et al. 1978). Thus, the abundance and dynamics of small mammal populations may serve as a measure of the impact of alternative harvesting treatments on ecosystem function in subalpine forests.

The southern red-backed vole (*Clethrionomys gapperi* Vigors) is a common inhabitant of late successional coniferous and deciduous forests across temperate North America (Merritt 1981) and may be an important indicator species of "old-forest conditions". This vole occurs in substrates with abundant organic debris composed of stumps, logs, and exposed roots (Martell and Radvanyi 1977; Yahner 1986) that maintain hypogeous ectomycorrhizal fungi as a major food supply (Maser et al. 1978). Other prominent forest floor species include the deer mouse (*Peromyscus maniculatus* Wagner), long-tailed vole (*Microtus longicaudus* Merriam), meadow vole (*Microtus pennsylvanicus* Ord), and northwestern chipmunk (*Tamias amoenus* J.A. Allen). The deer mouse is a habitat generalist occupying a wide variety (type and age) of forested habitats (Baker 1968; Martell 1983; Sullivan et al. 1999). *Tamias amoenus* is also a habitat generalist found primarily in early successional harvested sites (Sutton 1992; Sullivan and Sullivan 2001). The preference of *M. longicaudus* and *M. pennsylvanicus* for early successional habitats after natural or forest harvesting disturbances may be related to the abundance of herbs and grasses that provide food and cover (Reich 1981; Getz 1985).

Clethrionomys gapperi is often the most abundant species in montane and old-growth subalpine spruce–fir forests (Medin and Booth 1989; Steventon et al. 1998; Von Trebr al. 1998; Sullivan and Sullivan 2001). In subalpine spru fir forests, patch cutting appeared to have little effect on abundance of *C. gapperi* (Hayward et al. 1999). Howeve comprehensive evaluation of the responses of *C. gapp* and other small mammal species to a range of partial cutt treatments in subalpine spruce–fir forests has not been do

We tested the hypotheses that abundance, reproducti and survival of (*i*) *C. gapperi*, a species associated w closed canopy forests, will decline with decreasing levels tree retention, (*ii*) *M. longicaudus* and *T. amoenus*, spec associated with early successional habitats, will incre with decreasing levels of tree retention, and (*iii*) *P. ma culatus*, a habitat generalist species, will be similar acr the levels of tree retention.

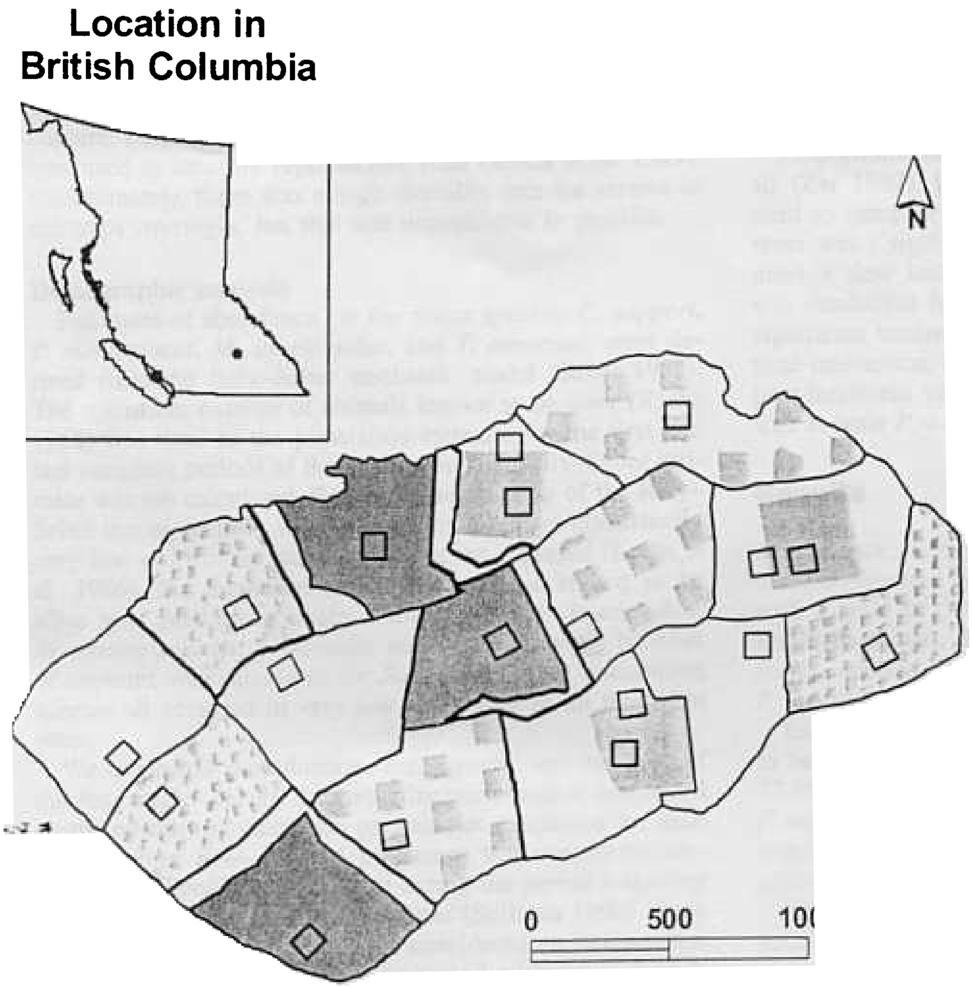
Materials and methods

Study area

As part of the Sicamous Creek Silvicultural Systems P ject, this study was located in the Salmon Arm Forest D trict, south of the north fork of Sicamous Creek and north Mount Mara, near Sicamous, British Columbia, Can (50°50′N, 119°50′W). The forest corresponds to the Eng mann Spruce Subalpine Fir (ESSF) biogeoclimatic z (Meidinger and Pojar 1991) and is representative of ESSF wet cold subzone (ESSFwc2) described by Lloyd al. (1990). This subzone is the largest of the seven ES subzones in the Kamloops Forest Region and is very simi to the cold, wet ESSF subzones in the neighbouring Nel and Cariboo forest regions. The site elevation ranges fr 1530 to 1830 m and the tree line is found between 1850 1900 m immediately to the south. The forest is a mat stand of subalpine fir and Engelmann spruce that origina approximately 300 years ago and has experienced individ tree or group mortality since the mid-1800s (Parish et 1999). The standing volume of live timber on the area estimated to be 264 m^3/ha, of which approximately 35% spruce and 65% was subalpine fir. Thirty percent of standing trees were snags. The understory vegetation primarily white rhododendron (*Rhododendron albiflor* Hook.), black huckleberry (*Vaccinium membranac* Dougl.), and oval-leaved blueberry (*Vaccinium ovalifoli* Smith). The project area forms part of the Sicamous Cr Community Watershed (Vyse 1999).

The project area was divided into three blocks based elevation (mean values 1615 m for block A, 1690 m block B, and 1750 m for block C), and five harvesting tre ments representative of a range of tree retention patte were applied to each block (Fig. 1). All treatments were h vested in the winter of 1994–1995. The largest opening of 10 ha (320 m × 320 m) was planned with a 100-m-w buffer strip of mature forest, and other buffer strips were as needed to separate the treatment units. Each unit was proximately 30 ha. After harvesting, most treatment u were site prepared in 1995 using excavators to create sn mounds (<1 m^2 and raised 30 cm) and then planted in 1 with Engelmann spruce seedlings. Some small portions

. Location of the Sicamous Creek site in south-central British Columbia and the arrangement of treatment units at the site. d areas indicate harvested units and dark grey areas are the single tree selection units.



atment areas were neither site prepared nor planted 1999).

five treatments were as follows. (*i*) Control: no re- of trees; (*ii*) single tree cut: 33% volume removal by on over 30 ha by cutting every fifth tree using fallers' (no tree marking), with marked skid trails, but with empt to "improve the stand"; (*iii*) 0.1-ha patch cut: moval of volume over a 30-ha area by cutting approx- sixty 0.1-ha square openings with 60 m between and skid trails linking all groups, (*iv*) 1.0-ha patch % removal of volume over a 30-ha area by cutting roups of 1 ha each with 200 m between centres and nking skid trails; (*v*) 10-ha clearcut: 33% removal of over a 30-ha area by cutting one 10-ha opening ap- iately 330 m square.

mental design

study had a randomized-block design with three repli- es of each treatment. Within each block, there were s: uncut forest (UF), single tree selection (STS), patch cut (0.1 PC), 1.0-ha patch cut (1.0 PC), 10.0-ha (10.0 CC), and an edge habitat. On the patch cut nts, the trapping grids were positioned to represent itat types following harvest. For example, on the 0.1-ha sites, the trapping grids extended across several openings, with about 60% of the sampling area in uncut forest. The edge sites were located on the forest–opening interface of the 10.0-ha clearcut. These sites were established to determine the responses of small mammals to the edges and leave strips created during harvesting.

Small mammal populations

Populations of forest floor small mammals were live-trapped at 3-week intervals from July to September 1994, 1995, and 1996, from June to September 1997, and from June to August 1998. One trapping grid (1 ha), with 49 (7 × 7) trap stations at 15.0-m intervals and one or two Longworth-type live-traps at each station, was located on each site (Ritchie and Sullivan 1989). The 1.0-ha patch cut and edge sites were not trapped in 1994. Traps were baited with a mixture of whole oats, sunflower seeds, and a slice of apple. The nest chamber of each trap was filled with coarse brown cotton for insulation. During each trapping session, traps were set for two consecutive nights and were locked open during the day. Between trapping sessions, traps were locked open to allow animals to enter and maintain familiarity with the traps. When capture success exceeded 80% of the 49 traps on a sampling grid on both days of the trapping

Forest floor small mammal species sampled by this protocol included *C. gapperi*, *M. longicaudus*, *P. maniculatus*, *T. amoenus*, heather vole (*Phenacomys intermedius* Merriam), northern bog lemming (*Synaptomys borealis* Richardson), water vole (*Microtus richardsoni* DeKay), jumping mouse (*Zapus* sp.), and shrews (*Sorex* spp.). Captured animals were marked with unique numeric ear tags, and the species, mass (Pesola® spring balance), sex, and reproductive condition recorded before release at the point of capture. Palpation of male testes and mammaries of females was used to measure reproductive state (Krebs et al. 1969). Unfortunately, there was a high mortality rate for shrews in the traps overnight, but this was unavoidable in practice.

Demographic analysis

Estimates of abundance for the major species, *C. gapperi*, *P. maniculatus*, *M. longicaudus*, and *T. amoenus*, were derived from the Jolly–Seber stochastic model (Seber 1982). The minimum number of animals known to be alive (Krebs 1966) was used as the population estimate for the first and last sampling periods of the study when the Jolly–Seber estimate was not calculated. Because the reliability of the Jolly–Seber model declines when population sizes are consistently very low and (or) no marked animals are captured (Krebs et al. 1986), the minimum number of animals known to be alive was used to estimate abundance of *P. intermedius*, *M. pennsylvanicus*, *S. borealis*, and *M. richardsoni*. Number of captures was calculated for *Sorex* spp. These uncommon species all occurred in very low abundance in all treatment sites.

We evaluated reproduction, recruitment, and survival of the four major species. Reproductive performance was based on the number of successful pregnancies calculated for each population in 1994–1998. A pregnancy was considered successful if a female was lactating during the period following the estimated time of birth of a litter (Sullivan 1990). 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 the number of juvenile animals at week t divided by the number of lactating females caught in week $t - 3$. Mean Jolly–Seber 28-day survival rates were calculated for each population during the summer (June–September) and winter (October–May) periods each year.

We used age at sexual maturity to determine age-classes of voles. Body mass was used as an index of age. Animals were classified as juvenile (juvenile and subadult classes pooled) or adult by body mass: *C. gapperi*, juvenile 1–18 g, adult ≥19 g; *M. longicaudus*, juvenile 1–26 g, adult ≥27 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.

Statistical analyses

A repeated-measures analysis of variance (RM-ANOVA) was used to determine the effect of harvest treatments on the major species, and mean index of juvenile survival and mean Jolly–Seber summer and winter survival for *C. gapperi* only, during the post-treatment period (1995–1998). A one-way ANOVA was conducted on these same variables during the pretreatment year (1994). 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 data sets, which were subjected to Mauchly's W test statistic (Littel 1989; Kuehl 1994).

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 × 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 $P = 0.05$.

Results

Abundance

Clethrionomys gapperi was the most abundant species with a total of 3998 individuals captured (66.9% of total small mammals). Total numbers of individuals of the other major species were 713 for *M. longicaudus*, 646 for *P. maniculatus*, and 278 for *T. amoenus*.

Estimates of trappability (susceptibility to capture) tended to be variable among species, with overall mean values of 77.5% for *C. gapperi*, 57.8% for *M. longicaudus*, 57.2% for *P. maniculatus*, to 69.0% for *T. amoenus*. Thus, Jolly–Seber population estimates were used for this study, for the reasons given in Jolly and Dickson (1983).

The abundance of *C. gapperi* was significantly ($F_{[5,10]} = 132.94$, $P < 0.01$) different among sites, with the highest mean numbers occurring in the uncut, single tree selection, and patch cut sites in 1995, ranging from 31.1 to 49.7 voles/ha (Table 1; Fig. 2). Numbers of *C. gapperi* were lowest in the clear-cut sites during all postharvest years. Overall, *C. gapperi* populations generally declined with time ($F_{[3,36]} = 26.24$, $P < 0.01$). By 4 years postharvest, abundance of *C. gapperi* was highest in the uncut forest and single tree selection, with no differences among any of the partial harvesting methods and edge habitats (Table 1). This microtine had all but disappeared from the clear-cut sites by the third year postharvest.

Abundance of *M. longicaudus* was significantly ($F_{[5,10]} = 4.30$, $P = 0.02$) different among sites and over time ($F_{[3,36]} = 10.43$, $P < 0.01$) with the highest relative numbers in 1994 and 1998 (Table 1; Fig. 3). Clear-cut sites tended to have the highest mean abundance at 16.2 voles/ha in 1998. *Microtus longicaudus* disappeared from the uncut forest after 1995 (Table 1).

Numbers of *P. maniculatus* were also similar ($F_{[5,10]} = 0.11$, $P = 0.99$) among sites but with relatively high numbers in 1994 and 1998 as indicated by the significant ($F_{[3,36]} = 6.90$, $P < 0.01$) difference among years (Table 1).

Table 1. Mean [illegible] (*n* = 3 replicate sites) abundance per hectare for *Clethrionomys gapperi*, *Microtus longicaudus*, *Peromyscus maniculatus*, and *Tamias amoenus* for the treatments during 1 pretreatment year (1994) with results of a one-way ANOVA and 4 post-treatment years (1995–1998) with results of RM-ANOVA.

Species and year	Uncut forest	Single tree selection	0.1-ha patch	1.0-ha patch	10.0-ha clearcut	Edge	Treatment	Time	Treatment × time
Clethrionomys gapperi									
1994	32.5±1.8	43.5±8.1	32.4±2.4	—	34.3±3.7	—	$F_{[3,8]} = 1.27$, $P = 0.35$		
1995	31.1±3.6ab	44.0±8.3a	49.7±3.0a	38.1±6.0ab	10.8±0.4c	24.7±5.1b	$F_{[5,10]} = 132.94$, $P < 0.01$	$F_{[3,36]} = 26.24$, $P < 0.01$	$F_{[15,36]} = 6.81$, $P <$
1996	26.9±1.2a	24.2±1.7a	21.1±7.7a	20.7±3.4a	2.7±0.3b	18.9±3.9a			
1997	33.2±6.0a	20.8±2.2a	27.8±4.3a	20.0±2.1a	0.2±0.2b	19.5±4.8a			
1998	30.0±2.2a	22.8±0.7ab	18.7±3.8b	18.0±0.8b	0.1±0.1c	19.0±3.8b			
Microtus longicaudus									
1994	7.7±1.8	3.6±2.5	6.8±4.3	—	7.1±3.4	—	$F_{[3,8]} = 0.35$, $P = 0.79$		
	B	B	B	B	A	B			
1995	8.5±2.9	1.2±0.2	2.6±0.6	1.4±0.7	6.4±2.3	3.5±1.8	$F_{[5,10]} = 4.30$, $P = 0.02$	$F_{[3,36]} = 10.43$, $P < 0.01$	$F_{[15,36]} = 1.73$, $P =$
1996	0.0	0.0	0.4±0.3	0.2±0.2	2.6±0.6	0.4±0.3			
1997	0.0	1.3±0.6	1.9±0.9	1.5±1.1	9.6±2.3	2.5±1.3			
1998	0.0	3.4±1.5	4.5±1.9	2.6±1.6	16.2±3.5	3.9±2.0			
Peromyscus maniculatus									
1994	11.0±2.1	7.3±3.8	8.6±1.0	—	4.4±1.0	—	$F_{[3,8]} = 1.45$, $P = 0.30$		
1995	3.1±2.2	0.4±0.2	0.4±0.2	2.0±1.9	0.8±0.2	2.2±1.4	$F_{[5,10]} = 0.11$, $P = 0.99$	$F_{[3,36]} = 6.90$, $P < 0.01$	$F_{[15,36]} = 0.69$, $P =$
1996	1.2±0.7	0.4±0.3	1.3±1.3	3.3±2.1	2.0±1.5	0.8±0.7			
1997	1.5±1.3	4.0±3.4	1.9±1.7	4.5±7.2	0.8±0.4	0.2±0.2			
1998	3.8±1.0	3.8±1.7	5.1±1.4	3.2±1.9	5.0±2.0	4.4±1.9			
Tamias amoenus									
1994	0.1±0.1	0.2±0.2	1.0±0.4	—	0.3±0.2	—	$F_{[3,8]} = 3.21$, $P = 0.08$		
	C	BC	A	AB	A	BC			
1995	0.2±0.1	1.1±0.5	3.4±0.3	2.2±0.8	1.9±1.0	0.5±0.4	$F_{[5,10]} = 6.46$, $P < 0.01$	$F_{[3,36]} = 1.47$, $P = 0.24$	$F_{[15,36]} = 0.90$, $P =$
1996	0.8±0.8	0.8±0.4	3.4±0.7	2.4±1.1	4.8±0.4	0.7±0.4			
1997	0.2±0.0	1.1±0.6	3.3±0.3	2.4±1.0	6.0±0.3	1.1±0.9			
1998	0.6±0.6	1.4±0.2	2.9±0.4	2.4±0.9	3.7±0.7	1.6±0.9			

Note: Within a year (lowercase) or overall (uppercase), mean values followed by different letters are significantly different by Duncan's multiple range test

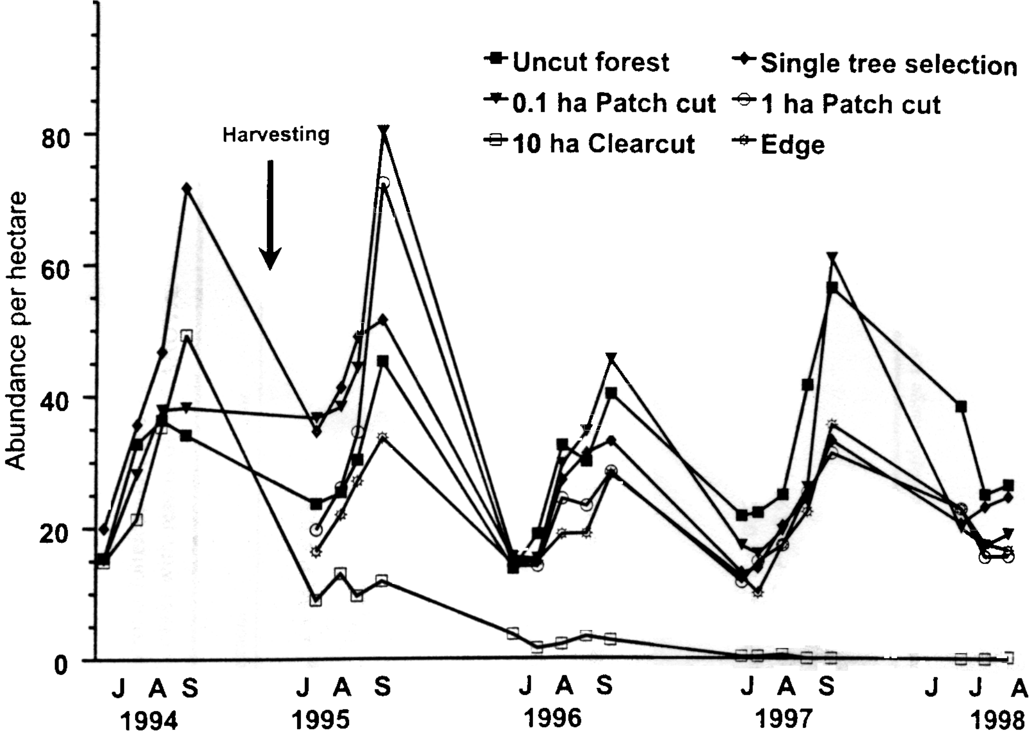
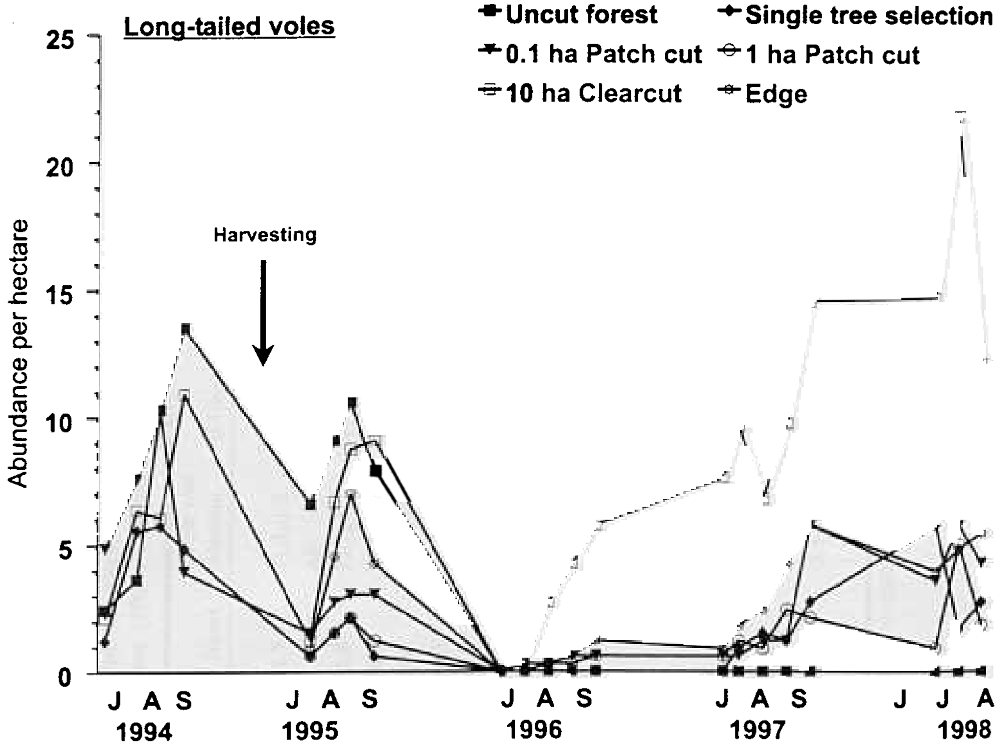


Fig. 3. Mean ($n = 3$ replicate sites) population density of long-tailed voles (Jolly–Seber) for the six treatments, 1994–1998.



Abundance of *T. amoenus* was significantly ($F_{[5,10]} = 6.46$; $P < 0.01$) different among sites, with the highest numbers recorded in the clearcut and 0.1-ha patch cuts during 1995–1997 (Table 1); mean abundance ranged from 0.1 to 6.0/ha.

Reproduction and recruitment

Reproductive performance, as measured by the number of successful pregnancies, was significantly ($F_{[5,10]} = 65.52$, $P <$ 0.01) different among sites for *C. gapperi*. After no differences among stands in the pretreatment year, clear-cut sites consistently had the lowest number of successful pregnancies, with few differences among the other sites in 1995–1998 (Table 2). This measure of reproductive performance appeared to generally decline with time ($F_{[3,36]} = 4.64$, $P < 0.01$).

Table 2. Mean ± SE (n = 3 replicate sites) number of successful pregnancies for *Clethrionomys gapperi*, *Microtus longicaudus*, and *Peromyscus maniculatus* for the six trea ments during 1 pretreatment year (1994) with results of one-way ANOVA and 4 post-treatment years (1995–1998) with results of RM-ANOVA.

Species and year	Uncut forest	Single tree selection	0.1-ha patch	1.0-ha patch	10.0-ha clearcut	Edge	Treatment	Time	Treatment × time
Clethrionomys gapperi									
1994	18.3±1.3	11.3±1.7	18.0±4.0	—	15.3±3.3	—	$F_{[3,8]}$ = 1.34, P = 0.33		
	A	AB	AB	B	C	B			
1995	16.7±5.8	22.7±4.7	19.0±2.1	14.0±2.5	4.7±1.5	14.0±3.2	$F_{[5,10]}$ = 65.52, P < 0.01	$F_{[3,36]}$ = 4.64, P < 0.01	$F_{[15,36]}$ = 1.86, P =
1996	18.7±0.3	13.0±2.3	13.0±3.5	10.0±2.5	2.3±0.7	9.7±4.3			
1997	23.0±4.0	13.3±0.9	13.7±3.4	12.7±2.3	0.0	8.7±1.7			
1998	15.7±0.3	12.0±0.6	8.3±2.0	10.7±0.3	0.0	11.3±2.8			
Microtus longicaudus									
1994	4.0±1.0	2.7±1.5	3.7±3.7	—	6.7±3.3	—	$F_{[3,8]}$ = 0.43, P = 0.74		
	B	B	B	B	A	B			
1995	5.0±3.6	0.7±0.3	1.7±0.9	0.3±0.3	4.3±1.2	3.7±1.9	$F_{[5,10]}$ = 4.18, P = 0.03	$F_{[3,36]}$ = 4.11, P = 0.01	$F_{[15,36]}$ = 0.68, P =
1996	0.0	0.0	0.0	0.0	2.7±1.2	0.0			
1997	0.0	2.3±1.5	1.0±0.6	0.7±0.7	7.3±1.5	2.3±1.5			
1998	0.0	2.0±1.5	2.3±1.9	1.0±1.0	12.7±2.0	3.7±1.9			
Peromyscus maniculatus									
1994	0.7±0.3	1.0±1.0	1.3±0.3	—	0.0	—	$F_{[3,8]}$ = 1.06, P = 0.42		
1995	0.7±0.7	0.3±0.3	0.3±0.3	0.7±0.7	0.0	0.7±0.3	$F_{[5,10]}$ = 0.23, P = 0.94	$F_{[3,36]}$ = 8.14, P < 0.01	$F_{[15,36]}$ = 1.07, P =
1996	0.0	0.0	0.0	0.7±0.7	0.7±0.7	0.0			
1997	0.3±0.3	0.3±0.3	0.3±0.3	1.3±1.3	0.3±0.3	0.0			
1998	1.3±0.9	1.7±0.9	1.0±0.6	1.0±1.0	3.7±1.7	0.7±0.3			

Note: Within a year (lowercase) and overall (uppercase), mean values followed by different letters are significantly different by Duncan's multiple range test.

caudus also differed ($F_{[5,10]} = 4.18$, $P = 0.03$) among sites. At 2 years postharvest, *M. longicaudus* on clear-cut sites had the most successful pregnancies, and this trend continued in 1997 and 1998 as well, with the edge sites in both years and the single tree selection sites in 1997 having numbers comparable with the clear-cut sites (Table 2).

This measure of reproductive effort was similar ($F_{[5,10]} = 0.23$, $P = 0.94$) among sites for *P. maniculatus* and was considerably lower than that for *C. gapperi* or *M. longicaudus* throughout the study (Table 2).

Recruitment of new *C. gapperi* was significantly ($F_{[5,10]} = 40.80$, $P < 0.01$) different among sites, with lower numbers of first captures in the clearcut than in the other sites (except edge sites in 1995) in all postharvest years (Table 3). Mean number of recruits ranged from 66.0 to 82.0 among sites in the preharvest year of 1994. Thereafter, mean numbers of recruits were similar among the uncut and partially harvested sites.

Recruitment of *M. longicaudus* was also significantly ($F_{[5,10]} = 9.74$, $P < 0.01$) different among sites, with the clear-cut sites at high numbers of first captures in 1996–1998 (Table 3). Edge sites in 1997–1998 and the 0.1-ha patch cut site in 1998 had numbers of vole recruits similar to those of the clear-cut sites.

Numbers of *P. maniculatus* recruits were similar ($F_{[5,10]} = 0.17$, $P = 0.97$) among sites (Table 3). However, recruitment did appear to change significantly ($F_{[3,36]} = 5.07$, $P < 0.01$) with time, being high in 1994 and again in 1998. Recruitment of *T. amoenus* was also variable but was significantly ($F_{[5,10]} = 5.68$, $P < 0.01$) different among sites (Table 3). The harvested sites and edges tended to have somewhat similar levels of chipmunk recruitment in the postharvest years.

Survival

Mean estimates of Jolly–Seber survival for *C. gapperi* were similar among sites during the summer and winter periods but declined dramatically on clear-cut sites (Table 4). Mean survival for *M. longicaudus* and *P. maniculatus* was variable across seasons and sites. An index of early juvenile survival was similar among sites for *C. gapperi* but again was negligible on clear-cut sites in 1997 and 1998 (Table 5). Early juvenile survival was variable across sites for both *M. longicaudus* and *P. maniculatus*.

Discussion

Small mammal communities

This investigation is the first evaluation of the population dynamics of small mammals over a range of harvesting treatments in high-elevation spruce–fir forests. Although 10 small mammal species were sampled during the study, the majority captured were *C. gapperi*. Abundance of this microtine peaked at 80 animals/ha with mean values of 31–50 voles/ha, indicating that these old-growth Engelmann spruce – subalpine fir forests provided prime habitat for *C. gapperi*. This finding was similar to reports elsewhere for *C. gapperi* in montane and old-growth forests dominated by spruce or true firs in western North America (Raphael 1988; Nordyke and Buskirk 1991; Hayward and Hayward 1995; Sullivan et al. 1999). Subalpine and boreal spruce–fir forests (Merritt 1981; Tanner 1986), hypogeous fungi, which are major determinants of optimum habitat for *C. gapperi* (Getz 1968; Maser et al. 1978). In addition, woody debris in these forests may provide protection during critical periods of freezing and thawing (Merritt and Merritt 1978; Merritt 1985).

Clethrionomys gapperi is considered an indicator of old-growth forest conditions (Nordyke and Buskirk 1988). This definition is partly attributable to the above habitat requirements and also because this microtine is an important prey species for several carnivores (Hayward and Verner 1994; Ruggiero et al. 1995). Therefore, maintenance of *C. gapperi* in forest harvesting treatments should also be potentially favourable to predators (Garton et al. 1989).

Response to harvesting treatments

Because *C. gapperi* are closely associated with closed-canopy forests, we expected them to respond negatively in terms of abundance, reproduction, and survival to decreasing levels of tree retention, as per the prediction of hypothesis (*i*). However, these demographic attributes were consistently similar among the uncut forest, single tree selection, and patch cut treatments compared with clear-cut sites where *C. gapperi* declined markedly. In most years, population dynamics in the edge habitats were also similar to the partial harvesting treatments. Thus, our hypothesis is only partially supported, at least with respect to total removal of tree cover on clearcuts and the partial harvesting treatments (see Fig. 4).

Medin (1986) similarly reported that *C. gapperi* disappeared from plots when the basal area was reduced from 20.7 to 5.1 m^2/ha, but no difference in numbers of this microtine was recorded after one third of the stand volume was removed (Medin and Booth 1989). In contrast, Monthey and Soutiere (1985) reported greater abundance of *C. gapperi* in partially cut stands (50% basal area reduction) and regenerating clearcuts than in uncut stands. West et al. (1980) reported similar numbers of northern red-backed voles (*Clethrionomys rutilus*) in shelterwood and uncut forest 1 year after harvest. Von Trebra et al. (1998) and Steventon et al. (1998) reported higher abundance of *C. gapperi* in light removal and shelterwood stands than in uncut forest in the first 1 or 2 years postharvest in west-central British Columbia. Retention of 10% basal area and woody debris seemed to maintain *C. gapperi* in aspen mixedwood forests (Moses and Boutin 2001).

Although not statistically significant, we also observed slightly higher numbers of *C. gapperi* in the single tree selection and 0.1-ha patch cut than in the uncut forest in the first year after harvesting (Table 1; Fig. 2). As discussed by Von Trebra et al. (1998), some partial cutting treatments or "light disturbance" of the forest may temporarily enhance local forage and cover by increasing availability of insects and seeds that were dislodged from the canopy or exposed in the duff layer of the forest floor. Tree removal may expose hypogeous fungi and some cover requirements may improve because of additional coarse woody debris on the site after logging (Tallmon and Mills 1994).

Similar to the results reported by Hayward et al. (1999) and Sullivan and Sullivan (2001), *C. gapperi* populations

Table 3. Mean ± SE (n = 3 replicate sites) number of first captures (recruits) for *Clethrionomys gapperi*, *Microtus longicaudus*, *Peromyscus maniculatus*, and *Tamias* for the six treatments during 1 pretreatment year (1994) with results of a one-way ANOVA and 4 post-treatment years (1995–1998) with results of RM-ANOVA.

Species and year	Uncut forest	Single tree selection	0.1-ha patch	1.0-ha patch	10.0-ha clearcut	Edge	Treatment	Time	Treatment ×
Clethrionomys gapperi									
1994	66.0±3.1	77.0±12.3	77.7±2.9	—	82.0±12.0	—	$F_{[3,8]} = 0.59$, $P = 0.64$		
1995	62.0±4.0ab	79.7±20.4ab	88.0±6.1a	66.3±10.4ab	28.0±1.2c	46.0±9.6bc	$F_{[5,10]} = 40.80$, $P < 0.01$	$F_{[3,36]} = 44.50$, $P < 0.01$	$F_{[15,36]}$ = 5.
1996	70.7±2.4a	62.7±2.8a	64.0±4.6a	48.7±4.1a	6.0±2.1b	43.3±2.4a			
1997	72.3±12.9a	50.3±3.7a	44.7±6.3a	38.7±7.4a	1.0±1.0b	34.3±4.9a			
1998	35.0±2.5a	29.3±1.5a	23.0±5.1ab	22.3±0.3ab	0.3±0.3c	13.3±4.3b			
Microtus longicaudus									
1994	14.0±3.1	10.7±3.7	17.7±8.7	—	18.7±8.7	—	$F_{[3,8]} = 0.31$, $P = 0.82$		
1995	16.0±4.6a	3.3±0.3ab	7.3±2.4ab	3.7±2.0b	20.0±7.5a	10.0±2.5ab	$F_{[5,10]} = 9.74$, $P < 0.01$	$F_{[3,36]} = 22.56$, $P < 0.01$	$F_{[15,36]}$ = 3.
1996	0.0c	0.0c	1.3±0.9bc	1.0±0.6bc	9.0±1.0a	2.0±0.6b			
1997	0.0c	4.7±1.8b	7.0±2.5b	4.3±2.0b	22.3±2.6a	10.3±1.8ab			
1998	0.0c	6.3±3.8b	9.0±3.1ab	4.7±2.0b	26.3±4.3a	9.3±2.8ab			
Peromyscus maniculatus									
1994	22.3±5.3	21.3±7.2	26.0±3.0	—	11.7±0.9	—	$F_{[3,8]} = 1.66$, $P = 0.25$		
1995	5.0±1.5	1.7±0.7	1.0±0.6	4.7±4.2	2.3±1.2	4.3±2.4	$F_{[5,10]} = 0.17$, $P = 0.97$	$F_{[3,36]} = 5.07$, $P < 0.01$	$F_{[15,36]}$ = 0.5
1996	2.3±1.2	1.0±0.6	2.3±2.3	8.3±5.6	8.0±5.1	3.3±2.4			
1997	4.3±3.4	6.3±4.4	5.3±3.9	8.7±6.7	3.3±0.7	1.0±0.6			
1998	8.0±1.5	7.7±2.4	13.0±2.5	6.3±3.5	13.7±4.7	12.0±4.9			
Tamias amoenus									
1994	0.7±0.3	0.7±0.7	2.3±0.9	—	3.3±1.3	—	$F_{[3,8]} = 2.23$, $P = 0.16$		
	D	CD	AB	ABC	A	BCD			
1995	0.7±0.3	3.0±0.6	4.7±1.7	4.7±0.9	3.7±0.3	2.0±1.0	$F_{[5,10]} = 5.68$, $P < 0.01$	$F_{[3,36]} = 0.30$, $P = 0.82$	$F_{[15,36]}$ = 0.7
1996	0.7±0.7	1.7±0.9	5.0±1.5	3.3±1.2	9.7±1.5	3.0±1.0			
1997	1.0±0.0	2.3±1.5	7.3±0.3	2.7±1.8	9.3±0.7	3.0±0.6			
1998	1.3±1.3	1.7±0.3	5.0±0.6	2.7±0.9	5.0±1.5	2.3±0.9			

Note: Within a year (lowercase) and overall (uppercase), mean values followed by different letters are significantly different by Duncan's multiple range test

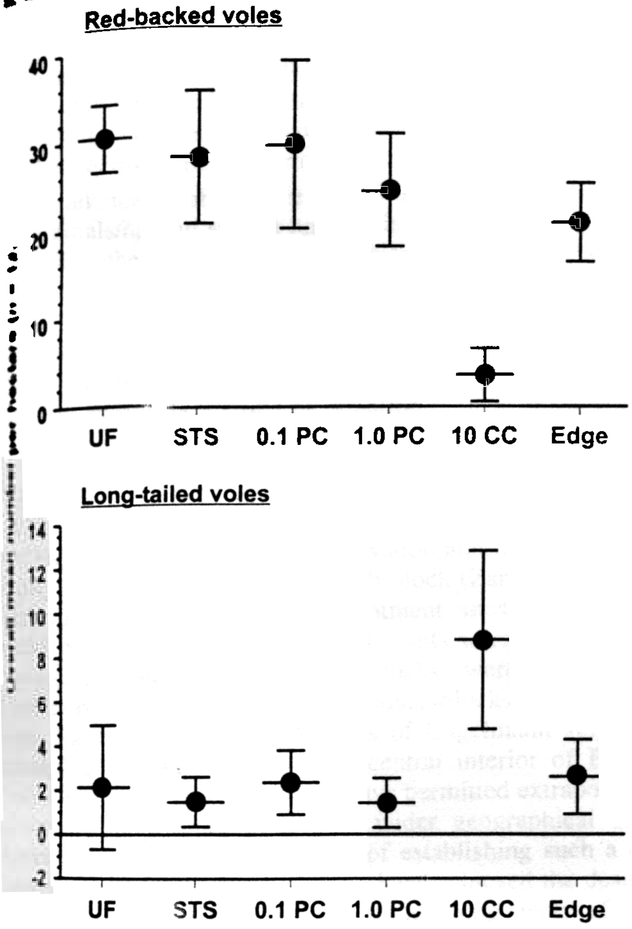
Table 4. Mean ± SE (*n* = 3 replicate sites) estimates of Jolly–Seber 28-day survival for *Clethrionomys gapperi* for the six treatments during 1994 (summer pretreatment) wit results of a one-way ANOVA and 1995–1998 (summer and winter post-treatment) with results of RM-ANOVA.

Year	Uncut forest	Single tree selection	0.1-ha patch	1.0-ha patch	10.0-ha clearcut	Edge	Treatment	Time	Treatment × time
Summer									
1994	0.70±0.17	0.80±0.07	0.62±0.11	—	0.67±0.03	—	$F_{[3,8]} = 0.53$, $P = 0.68$		
1995	0.60±0.11	0.63±0.09	0.52±0.07	0.54±0.04	0.39±0.11	0.66±0.03	$F_{[5,8]} = 0.94$, $P = 0.50$	$F_{[2,20]} = 11.96$, $P < 0.01$	$F_{[10,20]} = 5.90$, $P <$ 0.
1996	0.68±0.02	0.61±0.04	0.70±0.04	0.64±0.07	0.66±0.17	0.58±0.03			
1997	0.81±0.03	0.70±0.04	0.81±0.04	0.80±0.07	0.30	0.64±0.03			
Winter									
1995–1996	0.76±0.01	0.78±0.04	0.80±0.02	0.78±0.02	0.73±0.04	0.76±0.07	$F_{[4,8]} = 0.32$, $P = 0.85$	$F_{[2,20]} = 5.07$, $P = 0.02$	$F_{[8,20]} = 0.52$, $P =$ 0.
1996–1997	0.80±0.01	0.73±0.05	0.83±0.01	0.82±0.03	0.24±0.24	0.81±0.03			
1997–1998	0.84±0.03	0.86±0.01	0.83±0.02	0.84±0.02		0.85±0.02			

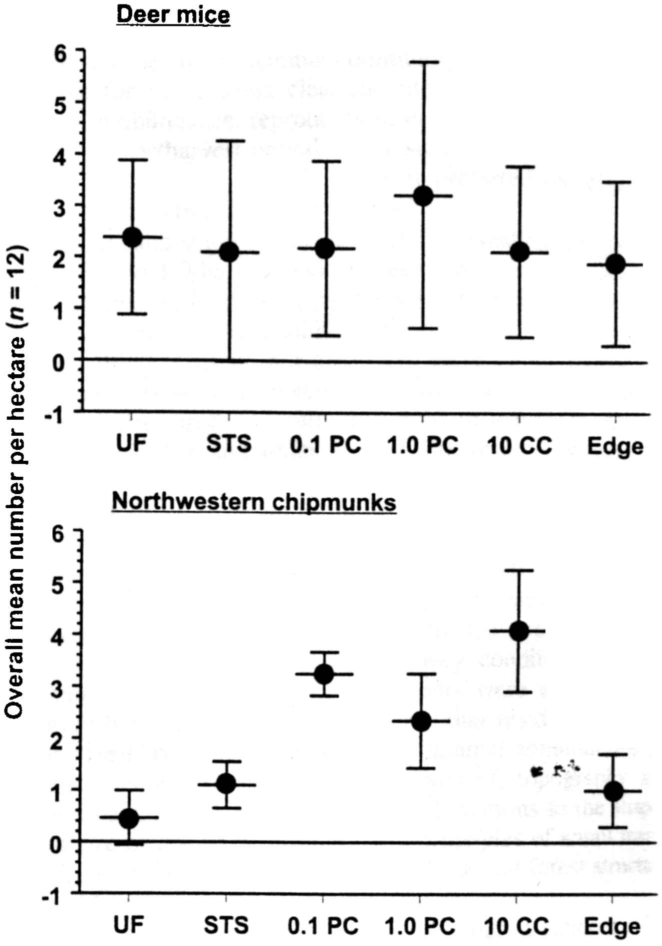
Table 5. Mean ± SE (*n* = 3 replicate sites) index of early juvenile survival (numbers of juvenile recruits per successful pregnancy) for *Clethrionomys gapperi* for the six trea ments during 1 pretreatment year (1994) with results of a one-way ANOVA and 4 post-treatment years (1995–1998) with results of RM-ANOVA.

Year	Uncut forest	Single tree selection	0.1-ha patch	1.0-ha patch	10.0-ha clearcut	Edge	Treatment	Time	Treatment × time
		2.23±0.23			1.47±0.21		$F_{[3,8]} = 4.59$, $P = 0.04$		
		1.89±0.09			4.55±1.99	2.02±0.44	$F_{[4,8]} = 0.73$, $P = 0.60$	$F_{[3,30]} = 19.41$, $P < 0.01$	$F_{12,30} = 0.35$, $P =$ 0.
		3.18±0.36			1.56±0.87	4.27±1.44			
		1.44±0.12			—	2.20±0.66			
		0.61±0.26				0.27±0.09			

fidence intervals for red-backed voles and long-tailed six treatments in the 4 postharvest years, 1995–1998.



confidence intervals for deer mice and northwestern chipmunks the six treatments in the 4 postharvest years, 1995–1998.



were maintained over the range of patch cuts up to, and including, 1.0 ha in area. Hayward et al. (1999) also reported [illegible] *C. gapperi* used edge habitats in a manner similar to their use of forest interior habitats. Although overall mean abundance of *C. gapperi* was lower in the edge than in the [illegible] forest, numbers of this microtine were similar in edge [illegible] partially harvested sites (Fig. 4). Conversely, Mills (1995) found that California red-backed voles (*Clethrionomys californicus*) avoided edges in a highly fragmented [illegible] landscape.

Other studies from western North America also reported [illegible] abundance of *C. gapperi* declined on clearcuts (Gashwiler 1970; Martell and Radvanyi 1977; Sullivan et al. [illegible]; Moses and Boutin 2001; Sullivan and Sullivan 2001). However, Kirkland's (1990) review of 21 published studies concluded that the species principally responsible for the greater abundance of microtine rodents on recent clearcuts [illegible] *C. gapperi*, which increased in abundance in 15 of 21 studies. This apparent contradiction may relate to differences [illegible] of *C. gapperi* in some parts of eastern North America [illegible] forest harvesting by clear-cutting has occurred for at [illegible] 300 years. It is possible that *C. gapperi* may have adapted to conditions in human-managed forests whereby behavioural and physiological changes allow substitution of [illegible] and lichens in their diet by other items such as seeds, leaves, and berries (Schloyer 1977; Gliwicz and Glowacki 2000).

Microtus longicaudus occurred predominantly in the clear-cut sites (Fig. 4). This pattern was similar to that recorded for *Microtus* spp. in other studies comparing a range of harvesting treatments (Moses and Boutin 2001; Sullivan and Sullivan 2001). The persistence of *M. longicaudus* on a variety of sites in our study fits the range of habitats occupied by this vole (Van Horne 1982; Smolen and Keller 1987). Habitats with some open areas and shrub and sapling cover up to 10 years after clear-cutting were optimum for *M. longicaudus* in Alaska (Van Horne 1982). Lower densities of this microtine occur in later seral stages that have less understory vegetation and a greater degree of canopy closure. High numbers of *M. longicaudus* in 1998 on clear-cut sites was similar to the high populations of this species recorded in clear-cut and seed-tree sites in a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) – lodgepole pine (*Pinus contorta* Dougl.ex Loud.) forest in 1998 (Sullivan and Sullivan 2001), thereby supporting the presumed synchronous nature of some vole population fluctuations (Taitt and Krebs 1985; Krebs 1996).

Tamias amoenus also was associated with early successional habitat on our clear-cut sites, albeit at overall mean numbers of <5 animals/ha (Fig. 5). *Tamias amoenus* edge sites. Subalpine forests in the southern interior of British Columbia appear to provide less suitable habitat for *T. amoenus* than mixed Douglas-fir – lodgepole pine forests at lower elevations (Sullivan et al. 2000; Sullivan and Sullivan 2001). Thus, hypothesis (*ii*), that abundance and related demographic attributes of *M. longicaudus* and *T. amoenus* will increase with decreasing levels of tree retention, seems to be supported.

Overall mean abundance of *P. maniculatus* was low (<4 animals/ha) but similar among sites (Fig. 5). Our prediction, hypothesis (*iii*), that a habitat generalist such as *P. maniculatus* will have similar demographic responses across a gradient of tree retention, appears to be supported and 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.

Experimental design

Our study was a classical randomized block design with blocks assigned on the basis of elevation and treatments randomly assigned to sites within each block (Zar 1999). There were three true replicates of treatment sites; however, it could be argued that these replicate units were not spatially segregated because the three blocks were contiguous (Hurlbert 1984). Ideally the individual blocks should have been located in independent areas of Engelmann spruce – subalpine fir forest in the south-central interior of British Columbia. Such a design would have permitted extrapolation of results and conclusions to a wider geographical area. However, the logistics and costs of establishing such a design were prohibitive and may not have achieved the desired experimental rigour needed for some components of this multidisciplinary study.

Treatment sites were the size of typical forestry operations in southern British Columbia and perhaps for subalpine forests in cordilleran regions of western North America. The study design tested operational-scale treatments of varying levels and patterns of green-tree retention on various forest ecosystem components as per Franklin et al. (1997), Aubry et al. (1999), and Sullivan et al. (2001). Inferences from our study reflect responses in small mammal communities in the first 4 postharvest years only. Longer-term (>5 years) measurement of responses will require periodic repeated sampling over decades to provide a clear understanding of the impact of these treatments.

The pretreatment year provided an important benchmark for assessing responses of small mammals to harvesting treatments. Ideally, all treatments should have been represented, but there were no pretreatment data for the 1.0-ha patch cut and edge sites because the precise locations of the treatment boundaries were not established until 1995. Responses of the forest floor small mammal communities to treatments represented relatively short summer and early autumn seasons and may not have been the same during winter months. However, there were 4 years of postharvest data and changes in abundance from one year to the next, during the overwinter periods when data were not available, were not qualitatively different from those of other forest small mammal studies.

The results of our study suggest that partial harvesting high-elevation spruce–fir forests, at least up to and includ 1.0-ha patch cuts or openings, did not negatively affect sm mammal populations. *Clethrionomys gapperi* accounted 66.9% of the small mammal community in these forests a except for the 10.0-ha clear-cut site, were not affected terms of abundance, reproduction, or survival attributes o a 4-year postharvest period. Early successional species su as *M. longicaudus* and *T. amoenus* preferred the clear-sites but occurred at low numbers.

Our results suggest that the partial harvesting (single t selection to 1.0-ha patches) of these forests may be one tential method for combining timber extraction with main nance of mature forest habitat (McComb et al. 1993; Han et al. 1995). Clearly, not all forest harvesting activities the same, as is often misconstrued by researchers and en ronmentalists in their communications to managers. As e denced by this and other studies, harvesting systems quite different from each other and clearly have different fects on forest-dwelling wildlife species. Thus, it may possible to conduct harvesting activities in these subalp forests without disrupting the small mammal communitie

Our experimental harvesting treatments were designed create a range of postharvest conditions that would help cl ify the influence of residual overstory condition on sm mammal communities. The treatments were conceptual nature but serve to illustrate the role that residual trees a gap size play in influencing small mammal communities. a more complex operational environment, topography a stand conditions will necessitate modifications to the shap and size of openings, but the basic principles of small ma mal community response to opening size and forest structu should remain applicable.

It is clear from our results that no single treatment is ther beneficial or detrimental to all species of small ma mals monitored at the Sicamous Creek study area. addition to the stand-level habitat effects on small mamm described in this paper, the operational application of t harvesting treatments at large spatial scales should consid a broader set of implications to small mammals and t overall biotic community. For example, partial-cut harve ing systems can maintain important structural features in t postharvest stand but create a more extensive network roads that may have undesirable ecological consequen (Forman et al. 2003). Similarly, treatment effects are m gated over time through forest growth and succession. the long-term habitat suitability of different treatments nee to be considered. Balancing the habitat requirements small mammals and other species of wildlife will require careful assessment of the costs and benefits associated w treatments that are evaluated in a landscape context.

Acknowledgements

We are grateful for the generous funding support provid by Forest Renewal B.C., the Silviculture Practices Branc and the Kamloops Region Silviculture Section, Ministry Forests. Riverside Forest Products Ltd. and the Salmon Ar Forest District provided operational support to impleme the harvesting treatments. This study would not have be would like to thank J. Alden, C. Bianchi, L. Blanchard, Bourdages, D. O'Brien, V. Craig, C. Dyck, D. Gum- D. Haag, M. Joyce, S. Lavallee, S. Pendray, Stiles, and K. Svendson. Thanks to D. Sullivan and Lindgren for reviewing an earlier draft of the manuscript. publication is part of the Sicamous Creek Silvicultural Project. Sicamous Creek is an interdisciplinary, in-agency research project investigating many aspects of aging high-elevation forests in the southern interior of sh Columbia.

References

nder, R.R. 1986. Ecology, silviculture, and management of the Engelmann spruce – subalpine fir type in the Central and Southern Rocky Mountains. U.S. Dep. Agric. Agric. Handb. 659.

K.B., Amaranthus, M.P., Halpern, C.B., White, J.D., oodard, B.L., Peterson, C.E., Lagoudakis, C.A., and Horton, 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.

R.H. 1968. Habitats and distribution. *In* Biology of *romyscus* (Rodentia). *Edited by* J.A. King. American Society of Mammalogists. Boston, Mass. pp. 125–167. Spec. Publ. 2.

ner, C.H. 19 The role of vertebrate predations in the biological control of forest insects. Annu. Rev. Entomol. **11**: 449–470.

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

A.B., Kershner, J., Biswell, B., and DeToledo, L.D. 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. The Wildlife Society, Bethesda, Md. Wildl. Monogr. 142.

an, R.T.T., erling, D., Bissonette, J.A., Clevenger, A.P., shall, C.D., Dale, V.H., Fahrig, L., France, R., Goldman, R. Heanue, K., Jones, J.A., Swanson, F.J., Turrentine, T., and ter, T.C. 2003. Road ecology: science and solutions. Island Press, Washington, D.C.

lin, J.F. 1989. Toward a new forestry. Am. For. **95**: 37–44.

lin, J.F. 1995. Sustainability of managed temperate forest ecosystems. *In* Defining and measuring sustainability: the geophysical foundations. *Edited by* M. Munasinghe and W. earer. The World Bank, Washington, D.C. pp. 355–385.

lin, J.F., Be D.R., Thornburgh, D.A., and Tappeiner, J.C. 1997. Alternative silvicultural approaches to timber harvesting: able retention harvest systems. *In* Creating a forestry for the 21st century. The science of ecosystem management. *Edited by* A. Kohm and J.F. Franklin. Island Press, Washington, D.C. pp. 111–139

E.O., Hayward, P.H., and Hayward, G.D. 1989. Managing populations to benefit raptor populations. *In* Proceedings of Western Raptor Management Symposium and Workshop. onal Wildlife Federation, Washington, D.C. pp. 298–304.

ler, J.S. 19 . Plant and mammal changes on a clearcut in -central Oregon. Ecology, **51**: 1018–1026.

L.L. 1968. Influence of water balance and microclimate on local distribution of the redback vole and white-footed e. Ecology, **49**: 276–286.

L.L. 1985. Habitats. *In* Biology of New World *Microtus*. ed by R.H. Tamarin. American Society of Mammalogists, on, Mass. pp. 286–309. Spec. Publ. 8.

Clethrionomys species to forest disturbance in Europe and North America. Can. J. Zool. **78**: 1340–1348.

Gunther, P.M., Horn, B.S., and Babb, G.D. 1983. Small mammal populations and food selection in relation to timber harvest practices in the western Cascade Mountains. Northwest Sci. **57**: 32–44.

Hansen, A.J., Garman, S.L., Weigand, J.F., Urban, D.L., McComb, W.C., and Raphael, M.G. 1995. Alternative silvicultural regimes in the Pacific Northwest: simulations of ecological and economic effects. Ecol. Appl. **5**: 535–554.

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

Hayward, G.D., and Verner, J. 1994. Flammulated, Boreal, and Great Gray Owls in the United States: a technical conservation assessment. U.S. For. Serv. Gen. Tech. Rep. RM-253.

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

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

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

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

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

Krebs, C.J. 1996. Population cycles revisited. J. Mammal. **77**: 8–24.

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

Krebs, C.J., Gilbert, B.S., Boutin, S., Sinclair, A.R.E., and Smith, J.N.M. 1986. Population biology of snowshoe hares. I. Demography of food-supplemented populations in the southern Yukon. J. Anim. Ecol. **55**: 963–982.

Kuehl, R.C. 1994. Statistical principles of research design and analysis. Duxbury Press, Belmont, Calif.

Lehmkuhl, J.F., West, S.D., Chambers, C.L., McComb, W.C., Manuwal, D.A., Aubry, K.B., Erickson, J.L., Gitzen, R.A., and 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., and Thompson, C. 1990. A guide to site identification and interpretation for the Kamloops Forest Region. British Columbia Ministry of Forests, Victoria, B.C. Land Manage. Handb. 23.

Martell, A.M. 1983. Demography of southern red-backed voles (*Clethrionomys gapperi*) and deer mice (*Peromyscus maniculatus*) after logging in north-central Ontario. Can. J. Zool. **61**: 958–969.

Martell, A.M., and Radvanyi, A. 1977. Changes in small mammal populations following clearcutting of northern Ontario black spruce forest. Can. Field-Nat. **91**: 41–46.

Maser, C., Trappe, J.M., and Nussbaum, R.A. 1978. Fungal – small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology, **59**: 779–809.

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

ging in an Idaho Douglas-fir forest. U.S. For. Serv. Res. Note INT-362.

Medin, D.E., and Booth, G.D. 1989. Responses of birds and small mammals to single-tree selection logging in Idaho. U.S. For. Serv. Res. Note INT-408.

Meidinger, D., and Pojar, J. 1991. Ecosystems of British Columbia. B.C. Minist. For. Spec. Rep. Ser. 6.

Merritt, J.F. 1981. *Clethrionomys gapperi*. Mamm. Species, **146**: 1–9.

Merritt, J.F. 1985. Influence of snowcover on survival of *Clethrionomys gapperi* inhabiting the Appalachian and Rocky Mountains of North America. Acta Zool. Fenn. **173**: 73–74.

Merritt, J.F., and Merritt, J.M. 1978. Population ecology and energy relationships of *Clethrionomys gapperi* in a Colorado subalpine forest. J. Mammal. **59**: 576–598.

Mills, L.S. 1995. Edge effects and isolation: red-backed voles on forest remnants. Conserv. Biol. **9**: 395–403.

Monthey, R.W., and Soutiere, E.C. 1985. Responses of small mammals to forest harvesting in northern Maine. Can. Field-Nat. **99**: 13–18.

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

Nordyke, K.A., and Buskirk, S.W. 1988. Evaluation of small mammals as ecological indicators of old-growth conditions. *In* Management of amphibians, reptiles, and small mammals in North America. *Technical Editors*: R.C. Szaro, K.E. Severson, and D.R. Patton. U.S. For. Serv. Gen. Tech. Rep. RM-166. pp. 353–358.

Nordyke, K.A., and 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.

Parish, R., Antos, J.A., and Fortin, M.-J. 1999. Stand development in an old-growth subalpine forest in southern interior British Columbia. Can. J. For. Res. **29**: 1347–1356.

Raphael, M.G. 1988. Habitat associations of small mammals in a subalpine forest, southeastern Wyoming. *In* Management of amphibians, reptiles, and small mammals in North America. *Technical Editors*: R.C. Szaro, K.E. Severson, and D.R. Patton. U.S. For. Serv. Gen. Tech. Rep. RM-166. pp. 359–367.

Reich, L.M. 1981. *Microtus pennsylvanicus*. Mamm. Species, **159**: 1–8.

Ritchie, C., and Sullivan, T.P. 1989. Monitoring methodology for assessing the impact of forest herbicide use on small mammal populations in British Columbia. Canadian Forestry Service and British Columbia Ministry of Forests, Victoria, B.C. For. Resour. Dev. Agree. Rep. 081.

Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Lyon, L.J., and Zielinski, W.J. 1995. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. U.S. For. Serv. Gen. Tech. Rep. RM-254.

Schloyer, C.R. 1977. Food habits of *Clethrionomys gapperi* on clearcuts in West Virginia. J. Mammal. **58**: 677–678.

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

Smolen, M.J., and Keller, B.L. 1987. *Microtus longicaudus*. Mamm. Species, **271**: 1–7.

sponse of small mammals and birds to partial cutting a
cutting in northwest British Columbia. For. Chron. **74**: 7

Sullivan, T.P. 1990. Influence of forest herbicide on dee
and Oregon vole population dynamics. J. Wildl. Man
566–576.

Sullivan, T.P., and Sullivan, D.S. 2001. Influence of variab
tion harvests on forest ecosystems. II. Diversity and po
dynamics of small mammals. J. Appl. Ecol. **38**: 1234–

Sullivan, T.P., Harestad, A.S., and Wikeem, B.M. 1990. Co
mammal damage. *In* Regenerating British Columbia's
Edited by D.P. Lavender, R. Parish, C.M. Johnson, G. M
ery, A. Vyse, R.A. Willis, and D. Winston. University o
Columbia Press, Vancouver, B.C. pp. 302–318.

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

Sullivan, T.P., Sullivan, D.S., and Lindgren, P.M.F. 2000
mammals and stand structure in young pine, seed-tree, a
growth forest, southwest Canada. Ecol. Appl. **10**: 1367–

Sullivan, T.P., Sullivan, D.S., and Lindgren, P.M.F. 2001. In
of variable retention harvests on forest ecosystems. I. D
of stand structure. J. Appl. Ecol. **38**: 1221–1233.

Sutton, D.A. 1992. *Tamias amoenus*. Mamm. Species, **390**

Taitt, M.J., and Krebs, C.J. 1985. Population dynamics and
In Biology of New World *Microtus*. *Edited by* R.H. T
American Society of Mammalogists, Boston, Mass. p
620. Spec. Publ. 8.

Tallmon, D., and Mills, L.S. 1994. Use of logs within home
of California red-backed voles on a remnant of forest. J.
mal. **75**: 97–101.

Van Horne, B. 1982. Demography of the long-tail vole *M*
longicaudus in seral stages of coastal coniferous forest.
east Alaska. Can. J. Zool. **60**: 1690–1709.

Verts, B.J., and Carraway, L.N. 1998. Land mammals of
University of California Press, Berkeley, Calif.

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

Vyse, A. 1997. The Sicamous Creek Silvicultural Systems
how the project came to be and what it aims to accomp
Sicamous Creek Silvicultural Systems Project: W
Proceedings, 24–25 April 1996, Kamloops, B.C. *Edi*
C. Hollstedt and A. Vyse. B.C. Minist. For. Res. Prog
Pap. 24. pp. 4–14.

Vyse, A. 1999. Is everything all right up there? A long-ter
disciplinary silvicultural systems project in a high elevat
spruce forest at Sicamous Creek, B.C. For. Chron. **75**: 46

Wagner, R.G., Flynn, J., and Gregory, R. 1998. Public perc
of risk and acceptability of forest vegetation manageme
natives in Ontario. For. Chron. **74**: 720–727.

West, S.D., Ford, R.G., and Zasada, J.C. 1980. Population re
of the northern red-backed vole (*Clethrionomys rutilis*) to
entially-cut white spruce forest. U.S. For. Serv. Res. Note
362.

Yahner, R.H. 1986. Microhabitat use by small mammals i
aged forest stands. Am. Midl. Nat. **115**: 174–180.

Zar, J.H. 1999. Biostatistical analysis. Prentice Hall, Upper
River, N.J.