Influence of Variable Retention Harvests on Forest Ecosystems. II. Diversity and Population Dynamics of Small Mammals

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Summary

1. Variable retention harvests in temperate coniferous forests provide various intensities and sizes of disturbance across a gradient, from clear-cutting to single-tree harvesting. These 'green-tree retention systems' leave large live trees after harvest (i.e. residual trees) to increase structural diversity of the regenerating stand. It is unclear what effect these harvesting patterns will have on wildlife in general, and small mammals in particular.

2. This study was designed to test the hypotheses that: (i) the abundance and diversity of forest-floor small mammals will decline with lower levels of tree retention; (ii) the abundance, reproduction and survival of *Microtus* spp. and southern red-backed vole *Clethrionomys gapperi* populations will decline and increase, respectively, with the basal area and density of residual trees after harvest; and (iii) habitat heterogeneity generated by variable retention harvesting will limit population size of *Microtus*, thereby reducing feeding damage to tree seedlings planted on harvested areas.

3. Small mammals were intensively live-trapped from 1996 to 1999 in replicated clear-cut, single seed-tree, group seed-tree, patch-cut and uncut forest sites in mixed natural forests of Douglas fir *Pseudotsuga menziesii*–lodgepole pine *Pinus contorta* in southern British Columbia, Canada. The seed-tree harvesting system leaves a few wind-firm seed trees standing singly, or in groups, to provide seed to regenerate an area naturally. The patch-cut system harvests timber from small (< 1-ha) units dispersed over a given area of forest.

4. Contrary to hypothesis (i), the mean total abundance of small mammals was similar among sites, and mean species richness and diversity of small mammals was lowest in the uncut forest but similar across the other four treatments.

5. The overall mean abundance (ha^{-1}) of *Microtus* spp. was higher on clear-cut (11·3) sites than single seed-tree (6·0), group seed-tree (3·9), patch-cut (1·8) or uncut forest (0·1) sites. Overall mean abundance (ha^{-1}) of *C. gapperi* was similar in uncut forest (16·2) and group seed-tree (10·0) sites, which were both higher than patch-cut (6·4), clear-cut (4·2) or single seed-tree (2·7) sites.

6. The recruitment of new *Microtus* spp. differed significantly among sites, declining from clear-cut to uncut forest. The recruitment of *C. gapperi* exhibited the opposite trend. The mean number of successful pregnancies was similar among treatments for *Microtus* spp. but for *C. gapperi* was highest in uncut forest, group seed-tree and patch-cut sites. The survival of each vole species was similar across treatment sites.

7. Hypothesis (ii) was supported. The mean abundance of *Microtus* spp. was inversely, and that of *C. gapperi* positively, related to mean basal area and density of residual trees after harvest. The mean abundance of *Microtus* spp. was also inversely related to percentage cover and crown volume index of residual trees, and positively related to number of lodgepole pine cones (seeds) in logging debris.

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8. In terms of hypothesis (iii), vole feeding damage to planted lodgepole pine seedlings appeared highest in the patch-cut sites during the 1997–98 and 1998–99 overwinter periods, and appeared to have been caused mainly by *C. gapperi* rather than *Microtus* spp.

9. The group seed-tree and patch-cut systems achieved both aims of *C. gapperi* persistence and prevention of *Microtus* outbreaks. These harvesting methods are as good for overall small mammal abundance, species richness and diversity as any other.

Key-words: *Clethrionomys gapperi*, coniferous forests, feeding damage, habitat heterogeneity, *Microtus* spp., silvicultural systems, voles.

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Introduction

The disturbance of forest land by tree harvesting has profound implications for subsequent vegetative succession and wildlife habitat. The intensity and degree of disturbance decrease in a gradient from clear-cutting to single tree selection (Smith 1986; Emmingham, Holthausen & Vomocil 1992). Variable retention harvests or 'green-tree retention systems' in temperate coniferous forests are an example of this gradient of changes in forest ecosystem conditions (Franklin *et al.* 1997). Green-tree retention leaves large live trees after harvest (i.e. residual trees) to provide mature forest habitat and increase structural diversity of the regenerating stand. The seed-tree harvesting system leaves a few wind-firm seed trees standing singly, or in groups, to provide seed to regenerate an area naturally. The patch-cut system harvests timber from small (< 1-ha) units dispersed over a given area of forest. There is now considerable interest in expanding these silvicultural systems to many new situations. However, it is unclear what effect these harvesting patterns will have on wildlife in general, and herbivorous small mammals in particular.

Forest-floor small mammal communities provide a measure of ecosystem function within temperate coniferous forests (Maser, Trappe & Nussbaum 1978; Aubry, Crites & West 1991; Carey & Johnson 1995; Pearson 1999). Small mammals fulfil a number of ecological roles, such as consumption of invertebrates (Buckner 1966), distribution of beneficial mycorrhizal fungi (Ure & Maser 1982), consumption of plants and plant products (Sullivan, Harestad & Wikeem 1990; Carey *et al.* 1999), and serving as prey for a wide variety of avian, reptilian and mammalian predators (Martin 1994; Carey & Johnson 1995). Thus, abundance and diversity of forest-floor small mammals, as a group, may serve as indicators of change in forest structure.

Several species of voles (genera *Microtus* and *Clethrionomys*) have been identified as mammals that inflict feeding damage to coniferous seedlings in young plantations in temperate and boreal forests (Sartz 1970; Hansson 1985; Bergeron & Jodoin 1989; Sullivan & Martin 1991; Sullivan *et al.* 1991). These herbivorous rodents feed on the bark, vascular tissues and sometimes roots of trees, particularly during winter months when alternative foods are limited. Vole damage may result in direct mortality from girdling and clipping of tree stems, or reduced growth from sublethal injuries. This feeding damage may limit regeneration of appropriate tree species in certain forest ecosystems.

Feeding damage appears to be associated with high populations of *Microtus* spp. in early successional habitats that develop after harvesting. Such habitats are composed of herb (particularly grasses) and shrub species that provide food and cover for voles (Bergeron & Jodoin 1989; Hansson 1989; Sullivan & Martin 1991). Some *Microtus* populations tend to have cyclic fluctuations in northern latitudes with a peak every 3–5 years, although these periods may be interspersed with annual fluctuations in abundance (Taitt & Krebs 1985; Krebs 1996). *Clethrionomys* populations occupy a variety of habitats, from early successional forest to tundra for *Clethrionomys rufocanus* Sundevall in Europe and Asia (Shu 1985; Hambäck, Schneider & Oksanen 1998), to mature and old-growth forest for the southern red-backed vole *Clethrionomys gapperi* Vigors in North America (Merritt 1981; Nordyke & Buskirk 1991). *Clethrionomys gapperi* appears not to have cyclic fluctuations in abundance compared with other species of *Clethrionomys* (Fuller 1985; Hansson & Henttonen 1985).

Because of these habitat preferences, *Microtus* spp. occur frequently on forested areas harvested by clear-cutting, up to almost 10 years after logging (Sullivan & Krebs 1981; Van Horne 1982; Sullivan & Martin 1991). Conversely, *C. gapperi* appears to decline in abundance within 1 or 2 years after clear-cut logging in western North America (Gashwiler 1970; Ramirez & Hornocker 1981; Halvorson 1982; Sullivan, Lautenschlager & Wagner 1999). A literature review by Kirkland (1990) concluded that the species principally responsible for the greater abundance of microtine rodents on recent clear-cuts was *C. gapperi*, which increased in abundance in 15 of 21 studies. However, *C. gapperi* may persist on clear-cuts up to 5 years after harvesting and then decline in subsequent years. There has been much research on the theoretical importance of habitat heterogeneity in population dynamics of small mammals (Hansson 1977; Myllymäki 1977; Stenseth 1980; Bondrup-Nielsen 1987; Sherratt *et al.*

2000). Clear-cutting of forests yields relatively homogeneous early successional habitats. Alternative harvesting practices, such as group seed-tree and patch-cutting systems, produce heterogeneous habitat patterns compared with clear-cutting. Thus, how might populations of *Microtus* spp. and *C. gapperi* respond to the heterogeneous habitats generated by variable retention harvests?

This is the second component of a forest ecosystems study investigating variable retention harvests of clear-cut, single seed-tree, group seed-tree, patch-cut and uncut forest. Responses of diversity of stand structure attributes to a range of green-tree retention are reported in Sullivan, Sullivan & Lindgren (2001).

This study was designed to test the hypotheses that: (i) the abundance and diversity of forest-floor small mammals will decline with lower levels of tree retention; (ii) the abundance, reproduction and survival of *Microtus* spp. and *C. gapperi* will decline and increase, respectively, with the basal area and density of residual trees after harvest; and (iii) habitat heterogeneity generated by variable retention harvesting will limit population size of *Microtus*, thereby reducing feeding damage to tree seedlings planted on harvested areas.

Materials and methods

STUDY AREA AND EXPERIMENTAL DESIGN

A description of the study area and experimental design is given in Sullivan, Sullivan & Lindgren (2001).

SMALL MAMMAL POPULATIONS

Populations of forest-floor small mammals were live-trapped at 4-week intervals from September to October 1996 and May to October 1997, 1998 and 1999. One trapping grid (1 ha), with 49 (7 × 7) trap stations at 14·3-m intervals, and one Longworth live-trap at each station were located on each site (Ritchie & Sullivan 1989). Traps were supplied with whole oats and carrot, and cotton as bedding. Traps were set on the afternoon of day 1, checked on the morning and afternoon of day 2 and morning of day 3, and then locked open between trapping periods.

Forest-floor small mammal species sampled by this procedure included the deer mouse *Peromyscus maniculatus* Wagner, north-western chipmunk *Tamias amoenus* J.A. Allen, meadow vole *Microtus pennsylvanicus* Ord, long-tailed vole *Microtus longicaudus* Merriam, southern red-backed vole *C. gapperi*, heather vole *Phenacomys intermedius* Merriam, western jumping mouse *Zapus princeps* J.A. Allen, montane shrew *Sorex monticolus* Merriam, common shrew *Sorex cinereus* Kerr, and short-tailed weasel *Mustela erminea* L.

All small mammals (except shrews and weasels) captured were ear-tagged with individually numbered tags, sexed, reproductive condition noted, weighed on Pesola spring balances, and released at point of capture. Palpation of male testes and mammaries of females was used to measure reproductive state (Krebs, Keller & Tamarin 1969). Unfortunately, there was a high mortality rate for shrews in the traps overnight, but this was unavoidable in practice. Shrews that died in traps were collected and identified according to Nagorsen (1996).

DEMOGRAPHIC ANALYSIS

Abundance estimates of *Peromyscus maniculatus*, *T. amoenus*, *C. gapperi*, *M. longicaudus*, *M. pennsylvanicus* and *Phenacomys intermedius* were derived from the Jolly–Seber (J–S) stochastic model (Seber 1982). The minimum number of animals known to be alive (MNA; Krebs 1966) was used as the population estimate for the first and last sampling periods of the study when the J–S estimate was not calculated. The reliability of the J–S model declines when population sizes are very low and no marked animals are captured (Krebs *et al.* 1986). In these cases, the total number of individuals captured was used to estimate populations of *Z. princeps*, *S. monticolus*, *S. cinereus* and *Mustela erminea*. The species diversity (Shannon–Wiener index; Sullivan, Sullivan & Lindgren 2001) of small mammals was calculated using the estimated abundance of each species for a given sampling period and averaged over the number of sampling periods for each year.

We evaluated reproduction, recruitment and survival as additional demographic parameters of these vole populations. Reproductive performance was based on the number of successful pregnancies calculated for each vole population in 1997, 1998 and 1999. 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 4-week trapping intervals. Voles captured for the first time on a site were called recruits. Mean J–S 28-day survival rates were calculated for each vole population during summer (May–September) and winter (October–April) periods each year.

HABITAT VARIABLES

Measurement of habitat variables included basal area, density, percentage cover and crown volume index of residual trees after harvesting. Volume of fallen wood (i.e. dead wood or woody debris) and crown volume index of herbs in 1996–99, herbs in 1998 only, shrubs, mosses and lichens were also investigated, as reported in Sullivan, Sullivan & Lindgren (2001). An additional parameter was the abundance of lodgepole pine *Pinus contorta* Dougl. var. *latifolia* Engelm. cones, which occurred in the logging debris after harvesting. These cones tend to be serotinous and will open to release their seeds when high ambient temperatures from wildfire break resin seals on cone scales (Lotan 1975).

Cones in logging slash (i.e. tree debris from harvesting) may be exposed to high surface temperatures during the summer periods after harvesting, which will also cause seeds to be released. *Microtus pennsylvanicus*, *M. longicaudus*, and *C. gapperi* were reported to feed on lodgepole pine seed (Radvanyi 1971; Sullivan & Sullivan 1982).

Lodgepole pine cones were counted in 20 0·44-m^2 circular plots located randomly within the 36 units of the 7 × 7 checkerboard live-trapping grid at each site. Only 'open' cones that had released their seeds were included in the sample, which was conducted in September 1999. The vast majority of cones in the logging debris had shed their seed over the 4-year period since harvesting in 1996. Cones were not sampled in the uncut forest because their age and time of seed release were unknown.

The number of cones per ha was calculated for each site and then multiplied by 16 seeds per cone, which is the average value for the number of viable seeds per cone in natural stands of lodgepole pine in southern British Columbia (Ying & Illingworth 1986). This measurement provided an estimate of available lodgepole pine seed for voles and other seed-eating small mammals during the study.

FEEDING DAMAGE TO TREE SEEDLINGS

Overwinter feeding damage by voles to planted lodgepole pine seedlings on the 12 harvested sites was evaluated in May 1998 and May 1999. One-year-old nursery-raised containerized seedlings were planted on the harvested sites in the spring of 1997 at an average density of 1111 trees ha^{-1} (range 915–1246). Seedling species composition was, on average, 86% lodgepole pine and 14% Douglas fir *Pseudotsuga menziesii* Mirbel (Franco) or interior spruce *Picea glauca* Moench (Voss) × *Picea engelmannii* Parry. Because voles feed preferentially on lodgepole pine (Sullivan, Harestad & Wikeem 1990), this tree species was sampled for evidence of feeding damage during the two winters. One-hundred sample seedlings were chosen randomly on each site in the autumn of 1997 prior to the onset of the first winter of feeding damage. Clipping of terminal and lateral shoots was recorded for each sample seedling. Removal of the terminal shoot was considered mortality unless another vigorous lateral shoot was available to replace it.

STATISTICAL ANALYSES

A repeated-measures analysis of variance (RM-ANOVA) was used to determine the effect of harvest treatments on mean abundance of each species, total abundance, mean species richness, and mean species diversity of the small mammal communities. It was also used to evaluate mean number of successful pregnancies, mean number of recruits, and mean summer and winter survival among treatments. Before performing any analyses, data not conforming to properties of normality and equal variance were subjected to various transformations to best approximate the assumptions required by any ANOVA (Zar 1984). Mauchly's *W*-test statistic was used to test for sphericity (independence of data among repeated measures; Littel 1989; Kuehl 1994). For data found to be correlated among years, the Huynh–Feldt (H–F) correction (Huynh & Feldt 1976) was used to adjust the degrees of freedom of the within-subjects *F*-ratio.

A one-way ANOVA was conducted to compare the proportion of planted seedlings eaten by voles and the number of lodgepole pine cones among the harvested sites. A simple linear regression analysis was used to determine the relationship between mean abundance of *C. gapperi* and *Microtus* spp. and the habitat variables of basal area, density, percentage cover and crown volume index of residual trees, volume of fallen wood, crown volume index of herbs, shrubs, mosses and lichens, and available lodgepole pine seed.

Proportional data were arcsine-transformed prior to analysis (Zar 1984). Duncan's multiple range test (DMRT) was used to compare mean values based on ANOVA results. In all analyses, the level of significance was at least $P = 0{\cdot}05$.

Results

SMALL MAMMAL ABUNDANCE AND DIVERSITY

Mean total abundance of small mammals per ha was similar among sites, with the highest numbers of each species occurring in 1998 in all treatments (Table 1 and Fig. 1). Mean species richness was significantly ($F_{4,10} = 4{\cdot}77$; $P = 0{\cdot}02$) different among sites, with the uncut forest having the lowest richness in 1997 and 1998 (DMRT; $P = 0{\cdot}05$). Mean species diversity also followed this pattern ($F_{4,10} = 3{\cdot}44$; $P = 0{\cdot}05$). Mean total abundance and mean species richness and species diversity were at their highest levels in 1998 in all treatments (Table 1).

Of the five major species, abundance of *Peromyscus maniculatus* was similar among sites, with the highest numbers in 1998 (Table 2). *Tamias amoenus* abundance was significantly ($F_{4,10} = 4{\cdot}70$; $P = 0{\cdot}02$) different among sites, particularly in 1998, with the highest numbers of this chipmunk in the seed-tree sites (DMRT; $P = 0{\cdot}05$; Fig. 2). Abundance of *Phenacomys intermedius* appeared higher in clear-cut and seed-tree sites than at other sites (Table 2). The insectivore *S. monticolus* occurred at highest numbers in the clear-cut and seed-tree sites, whereas *S. cinereus* was at comparable densities across all sites (Table 2).

VOLE POPULATION DYNAMICS

Population changes of *M. longicaudus* and *M. pennsylvanicus* indicated similar numbers among sites in all years (Table 2). Analysis of both species of *Microtus*

Table 1. Mean (n = 3 replicate sites) ± SE total abundance ha^{-1} and species richness and species diversity for the five treatments during 1996–99 and results of RM-ANOVA. Mean values followed by different letters are significantly different by DMRT. *F*-values identified by * were calculated using an H–F correction factor, which decreased the stated degrees of freedom due to correlation of data among repeated measures (years)

						Overall analysis					
						Treatment		Time		Treatment × time	
Parameter and year	Clear-cut	Single seed-tree	Group seed-tree	Patch-cut	Uncut forest	$F_{4,10}$	P	$F_{3,30}$	P	$F_{12,30}$	P
Total abundance						2·50	0·11	76·52	< 0·01	3·10	< 0·01
1996	26·0 ± 2·3	23·5 ± 1·8	22·4 ± 2·4	15·3 ± 2·0	29·7 ± 6·1						
1997	34·4 ± 4·7	33·9 ± 4·0	38·1 ± 3·3	26·0 ± 1·9	29·2 ± 6·5						
1998	61·6 ± 6·3	40·9 ± 6·1	50·1 ± 7·1	34·8 ± 2·6	32·7 ± 0·9						
1999	21·0 ± 0·8	20·2 ± 1·7	25·7 ± 3·3	18·5 ± 5·5	16·8 ± 1·1						
Species richness						4·77	0·02	17·47	< 0·01	1·06	0·42
1996	3·50 ± 0·50^{a}	4·17 ± 0·73^{a}	3·67 ± 0·60^{a}	3·67 ± 0·60^{a}	2·83 ± 0·17^{a}						
1997	5·11 ± 0·15^{a}	4·50 ± 0·10^{ab}	4·11 ± 0·31^{b}	4·39 ± 0·20^{b}	3·22 ± 0·11^{c}						
1998	5·61 ± 0·24^{a}	5·11 ± 0·39^{a}	5·61 ± 0·45^{a}	4·94 ± 0·53^{a}	3·28 ± 10·11^{b}						
1999	3·94 ± 0·34^{ab}	3·94 ± 0·36^{ab}	4·17 ± 0·60^{a}	3·61 ± 0·36^{ab}	2·83 ± 0·10^{b}						
Species diversity						3·44	0·05	8·29*	< 0·01	1·97*	0·07
1996	1·19 ± 0·23^{a}	1·64 ± 0·19^{a}	1·16 ± 0·34^{a}	1·62 ± 0·16^{a}	1·27 ± 0·11^{a}						
1997	1·78 ± 0·09^{a}	1·75 ± 0·06^{ab}	1·56 ± 0·04^{b}	1·72 ± 0·08^{ab}	1·06 ± 0·04^{c}						
1998	1·78 ± 0·13^{a}	1·77 ± 0·07^{a}	1·96 ± 0·11^{a}	1·84 ± 0·12^{a}	1·28 ± 0·06^{b}						
1999	1·43 ± 0·21^{a}	1·65 ± 0·11^{a}	1·52 ± 0·19^{a}	1·64 ± 0·15^{a}	1·16 ± 0·09^{a}						

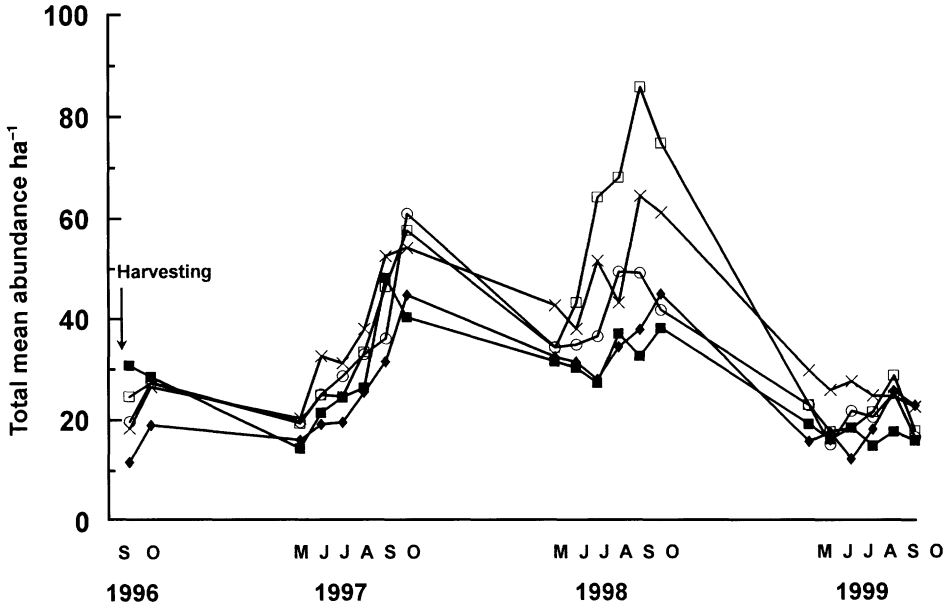

Fig. 1. Total mean ($n = 3$ replicate sites) abundance of small mammals ha^{-1} for the five treatments 1996–99. Clear-cut (open squares); single seed-tree (open circles); group seed-tree (crosses); patch-cut (diamonds); uncut forest (closed squares).

pooled together showed a significant ($F_{4,10} = 5{\cdot}60$; $P < 0{\cdot}01$) difference among sites, with the highest mean density on clear-cut and seed-tree sites in 1997 and 1998 (DMRT; $P = 0{\cdot}05$; Fig. 3). The clear-cut *Microtus* populations were, on average, 6·3 times and 113·0 times higher than those on the patch-cut (1·8 ha^{-1}) and uncut (0·1 ha^{-1}) forest sites, respectively. There appeared to be a peak population of *Microtus* in 1998, particularly on the clear-cut sites (Fig. 3).

The abundance of *C. gapperi* was significantly ($F_{4,10} = 7{\cdot}33$; $P < 0{\cdot}01$) different among sites, with the highest mean numbers occurring in the uncut forest and group seed-tree sites in 1997, and in these two treatments and the patch-cut in 1998 (Table 2 and Fig. 4). Populations of *C. gapperi* were at their highest levels in 1996 and 1997, shortly after harvesting in the clear-cut and seed-tree sites, before declining in 1998 and 1999 (Table 2).

Reproductive performance, as measured by the number of successful pregnancies, was significantly different among sites for *C. gapperi* ($F_{4,10} = 7{\cdot}25$; $P < 0{\cdot}01$) but not for *M. longicaudus* nor *M. pennsylvanicus* (Table 3). Analysis of both species of *Microtus* pooled together was also similar among treatment sites for the mean number of successful pregnancies. *Clethrionomys gapperi* had a higher (DMRT; $P = 0{\cdot}05$) mean number of successful pregnancies in the group seed-tree and uncut forest sites than the single seed-tree in 1997, but was similar to the clear-cut and patch-cut sites (Table 3). The uncut forest had the highest number of *C. gapperi* pregnancies in 1998, and this trend continued in 1999 but with the group seed-tree and patch-cut sites at similar numbers as the uncut forest (Table 3).

Recruitment of new voles was similar among sites for *M. pennsylvanicus* and *M. longicaudus*. However, recruitment with both species pooled together was significantly ($F_{4,10} = 6{\cdot}30$; $P < 0{\cdot}01$) different among sites, with a declining gradient from clear-cut to uncut forest sites in 1997–99 (Table 4). Recruitment of *C. gapperi* was also significantly ($F_{4,10} = 12{\cdot}97$; $P < 0{\cdot}01$) different among sites, with the highest (DMRT; $P = 0{\cdot}05$) mean number of recruits in the uncut forest and group seed-tree sites in 1997. This pattern continued in 1998 and 1999, with the highest number of recruits in the uncut forest and then a declining gradient from patch-cut to clear-cut sites (Table 4).

Mean estimates of J–S survival of *M. longicaudus*, *M. pennsylvanicus* and *C. gapperi* were similar among sites during summer and winter periods (Table 5).

HABITAT VARIABLES

Linear regression analysis indicated that mean abundance of *Microtus* spp. was inversely ($r = 0{\cdot}63$; $P = 0{\cdot}01$) related and that of *C. gapperi* positively ($r = 0{\cdot}75$; $P < 0{\cdot}01$) related to the basal area of residual trees (Fig. 5). Similar relationships were recorded for the density of residual trees and the mean abundance of *Microtus* spp. ($r = 0{\cdot}57$; $P = 0{\cdot}03$) and *C. gapperi* ($r = 0{\cdot}66$; $P < 0{\cdot}01$) (Fig. 5). The mean abundance of *Microtus* spp. was inversely related to percentage cover ($r = 0{\cdot}64$; $P = 0{\cdot}01$) and crown volume index ($r = 0{\cdot}63$; $P = 0{\cdot}01$) of residual trees (Fig. 6). The mean abundance of *C. gapperi* was not related to cover ($r = 0{\cdot}49$; $P = 0{\cdot}07$) nor to crown volume index ($r = 0{\cdot}49$; $P = 0{\cdot}06$). There was no relationship between vole abundance and volume of fallen wood for either *Microtus* spp. ($r = 0{\cdot}38$; $P = 0{\cdot}16$) or *C. gapperi* ($r = 0{\cdot}12$; $P = 0{\cdot}66$).

The mean number of lodgepole pine cones per ha was significantly ($F_{3,11} = 4{\cdot}74$; $P = 0{\cdot}03$) different among sites, with the clear-cut ($52{\cdot}7 \times 10^5$) and single

Table 2. Mean ($n = 3$ replicate sites) ± SE abundance ha^{-1} of small mammal species for the five treatments during 1996–99 and results of RM-ANOVA. Mean values followed by different letters are significantly different by DMRT. F-values identified by * were calculated using an H–F correction factor, which decreased the stated degrees of freedom due to correlation of data among repeated measures (years)

						Overall analysis					
						Treatment		Time		Treatment × time	
Species and year	Clear-cut	Single seed-tree	Group seed-tree	Patch-cut	Uncut forest	$F_{4,10}$	P	$F_{3,30}$	P	$F_{12,30}$	P
Peromyscus maniculatus						0·93	0·48	18·17	< 0·01	4·04	< 0·01
1996	10·0 ± 0·0	7·5 ± 0·4	2·5 ± 0·1	5·0 ± 0·3	13·3 ± 1·2						
1997	11·0 ± 3·1	10·2 ± 3·9	7·7 ± 1·8	7·5 ± 2·5	6·1 ± 2·7						
1998	27·7 ± 4·2	16·4 ± 1·6	16·4 ± 3·8	12·3 ± 1·4	10·0 ± 1·3						
1999	8·1 ± 0·6	4·7 ± 1·0	10·4 ± 0·8	7·0 ± 2·1	3·5 ± 1·0						
Tamias amoenus						4·70	0·02	8·69*	< 0·01	1·59*	0·17
1996	4·3 ± 0·3^{a}	6·1 ± 0·9^{a}	4·3 ± 0·5^{a}	4·9 ± 0·5^{a}	3·4 ± 0·1^{a}						
1997	4·1 ± 0·4^{bc}	9·0 ± 0·9^{ab}	10·1 ± 2·1^{a}	7·9 ± 1·5^{abc}	2·1 ± 0·6^{c}						
1998	7·3 ± 1·8^{bc}	11·9 ± 1·5^{ab}	15·1 ± 1·7^{a}	8·4 ± 1·7^{bc}	3·3 ± 0·5^{c}						
1999	5·9 ± 1·1^{ab}	8·6 ± 1·9^{a}	8·9 ± 2·0^{a}	4·4 ± 1·2^{ab}	2·2 ± 0·7^{b}						
Phenacomys intermedius						3·74	0·04	8·41	< 0·01	1·8	0·09
1996	0·0^{b}	0·7 ± 0·4^{a}	0·0^{b}	0·0^{b}	0·0^{b}						
1997	0·7 ± 0·2^{a}	0·7 ± 0·5^{a}	0·2 ± 0·1^{a}	0·3 ± 0·1^{a}	0·0^{a}						
1998	1·0 ± 0·2^{a}	1·0 ± 0·4^{ab}	0·5 ± 0·2^{abc}	0·3 ± 0·2^{bc}	0·0^{c}						
1999	0·3 ± 0·2^{ab}	0·8 ± 0·2^{a}	0·3 ± 0·3^{ab}	0·1 ± 0·1^{b}	0·0^{b}						
Microtus longicaudus						0·92	0·49	8·99*	< 0·01	0·91*	0·54
1996	0·3 ± 0·0	0·5 ± 0·1	0·2 ± 0·1	0·0	0·0						
1997	2·4 ± 1·3	6·5 ± 2·2	0·2 ± 0·2	0·8 ± 0·8	0·2 ± 0·1						
1998	9·3 ± 4·2	7·3 ± 2·3	7·5 ± 3·2	2·3 ± 0·6	0·2 ± 0·2						
1999	4·1 ± 1·0	3·9 ± 0·8	3·5 ± 0·7	1·6 ± 0·3	0·0						
Microtus pennsylvanicus						3·03	0·07	4·95*	0·02	3·74*	< 0·01
1996	0·3 ± 0·3	0·0	0·3 ± 0·0	0·7 ± 0·5	0·0						
1997	6·6 ± 3·0	0·1 ± 0·1	0·4 ± 0·1	0·5 ± 0·3	0·0						
1998	13·6 ± 2·8	1·1 ± 0·5	1·1 ± 0·3	0·5 ± 0·2	0·0						
1999	1·4 ± 0·5	0·8 ± 0·2	0·1 ± 0·1	0·1 ± 0·1	0·0						

Table 2. *Continued*

						Overall analysis					
						Treatment		Time		Treatment × time	
Species and year	Clear-cut	Single seed-tree	Group seed-tree	Patch-cut	Uncut forest	$F_{4,10}$	P	$F_{3,30}$	P	$F_{12,30}$	P
Clethrionomys gapperi						7·33	< 0·01	32·97	< 0·01	7·42	< 0·01
1996	10·8 ± 1·0^{ab}	8·3 ± 2·4^{ab}	14·8 ± 2·5^{a}	2·9 ± 0·2^{b}	13·0 ± 0·3^{a}						
1997	8·6 ± 1·7^{b}	4·7 ± 0·9^{b}	19·0 ± 4·2^{a}	7·0 ± 0·9^{b}	20·2 ± 4·3^{a}						
1998	1·7 ± 0·7^{b}	1·2 ± 0·8^{b}	7·7 ± 2·3^{a}	8·6 ± 2·1^{a}	18·7 ± 2·6^{a}						
1999	0·1 ± 0·1^{d}	0·3 ± 0·1^{cd}	1·7 ± 0·1^{c}	4·8 ± 0·6^{b}	10·8 ± 1·4^{a}						
Sorex monticolus						3·92	0·04	3·05	0·04	1·21	0·32
1996	0·5 ± 0·3^{ab}	2·0 ± 0·3^{a}	1·2 ± 0·9^{ab}	0·8 ± 0·6^{ab}	0·0^{b}						
1997	0·6 ± 0·2^{a}	0·7 ± 0·4^{a}	0·5 ± 0·1^{a}	0·5 ± 0·3^{a}	0·1 ± 0·1^{a}						
1998	1·6 ± 0·3^{a}	1.1 ± 0·3^{ab}	1.6 ± 0·6^{a}	0·4 ± 0·1^{ab}	0·3 ± 0·3^{b}						
1999	0·9 ± 0·3^{a}	0·7 ± 0·5^{a}	0·7 ± 0·3^{a}	0·1 ± 0·1^{a}	0·1 ± 0·1^{a}						
Sorex cinereus						0·83	0·54	9·76*	< 0·01	2·23	0·04
1996	0·8 ± 0·6	0·8 ± 0·2	0·2 ± 0·2	0·5 ± 0·0	0·0						
1997	0·2 ± 0·1	0·1 ± 0·1	0·1 ± 0·1	0·0	0·1 ± 0·1						
1998	0·2 ± 0·1	0·3 ± 0·1	0·3 ± 0·3	0·2 ± 0·1	0·3 ± 0·2						
1999	0·0	0·0	0·1 ± 0·1	0·0	0·2 ± 0·1						
Mustela erminea						0·49	0·74	1·00*	0·39	1·10*	0·40
1996	0·0	0·0	0·0	0·2 ± 0·2	0·0						
1997	0·0	0·1 ± 0·1	0·0	0·1 ± 0·1	0·1 ± 0·1						
1998	0·1 ± 0·1	0·3 ± 0·2	0·1 ± 0·1	0·1 ± 0·1	0·1 ± 0·1						
1999	0·1 ± 0·1	0·4 ± 0·4	0·0	0·0	0·1 ± 0·1						

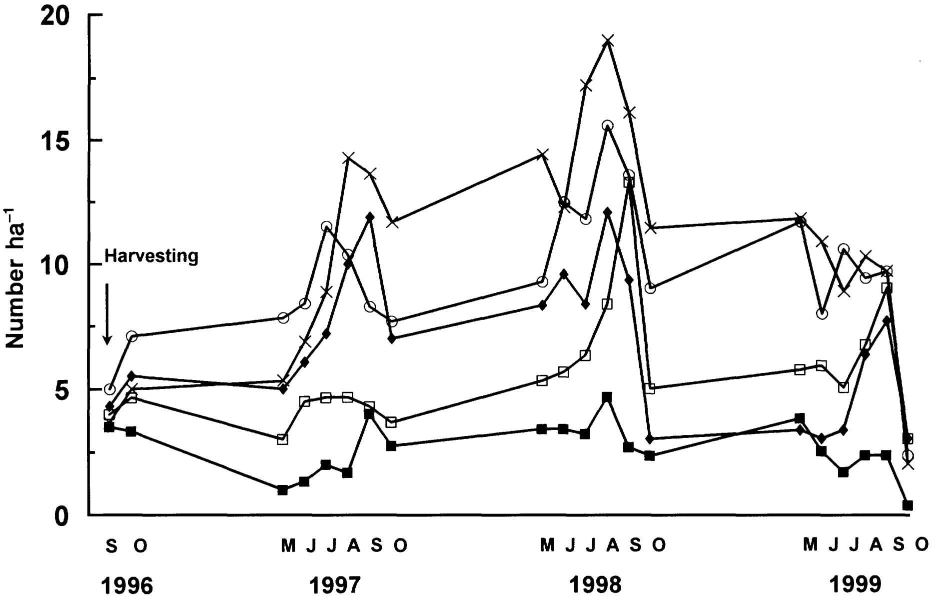

Fig. 2. Mean (n = 3 replicate sites) population density (Jolly–Seber) of *Tamias amoenus* for the five treatments 1996–99. Symbols as for Fig. 1.

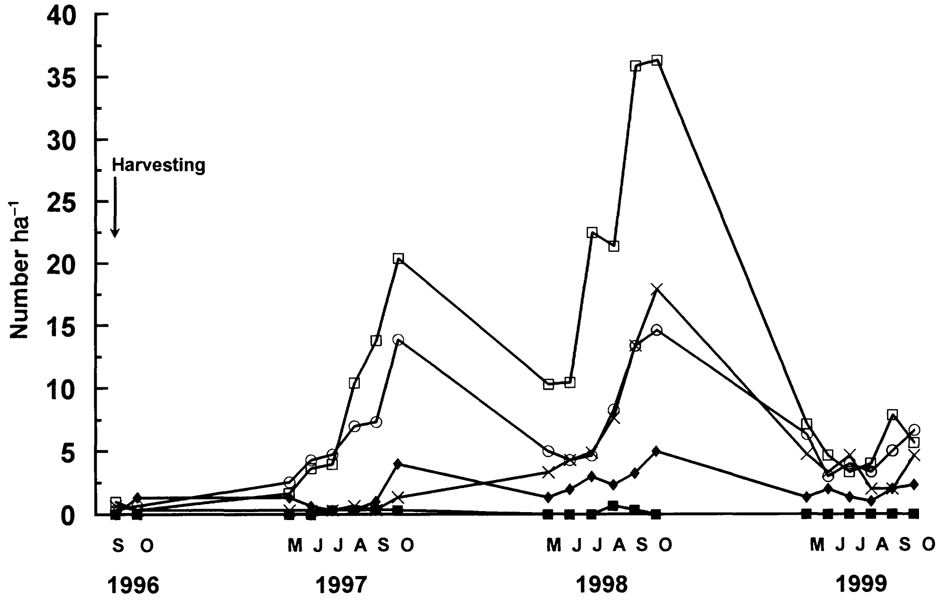

Fig. 3. Mean (n = 3 replicate sites) population density (Jolly–Seber) of *Microtus* spp. for the five treatments 1996–99. Symbols as for Fig. 1.

seed-tree ($50{\cdot}8 \times 10^5$) sites having more cones than the group seed-tree ($14{\cdot}7 \times 10^5$) and patch-cut sites ($2{\cdot}2 \times 10^5$) (DMRT; $P = 0{\cdot}05$). Mean abundance of *Microtus* spp. was significantly ($r = 0{\cdot}63$; $P = 0{\cdot}03$) related to the number of cones, whereas that of *C. gapperi* was not ($r = 0{\cdot}38$; $P = 0{\cdot}22$).

There were no significant relationships between the mean abundance of *Microtus* spp. nor *C. gapperi* and the total crown volume index of herbs, shrubs, mosses and lichens. Mean abundance of *Microtus* spp. was not ($r = 0{\cdot}47$; $P = 0{\cdot}08$) related to crown volume index of herbs in 1998, when both *Microtus* populations peaked and herbaceous vegetation had increased significantly on treatment sites (Sullivan, Sullivan & Lindgren 2001). Abundance of *C. gapperi* also was not related to herb volume ($r = 0{\cdot}12$; $P = 0{\cdot}66$).

FEEDING DAMAGE TO TREE SEEDLINGS

The mean percentage of planted lodgepole pine seedlings eaten by voles was similar across sites in the 1997–98 ($F_{3,8} = 3{\cdot}33$; $P = 0{\cdot}08$) and 1998–99 ($F_{3,8} = 2{\cdot}83$; $P = 0{\cdot}11$) winters (Table 6). However, it may be biologically significant that the patch-cut sites (18·3% and 13·5% in the two winters) appeared to have the highest loss of seedlings from vole feeding. From a practical perspective, these patch-cut sites were surveyed and found to be unsatisfactorily restocked with

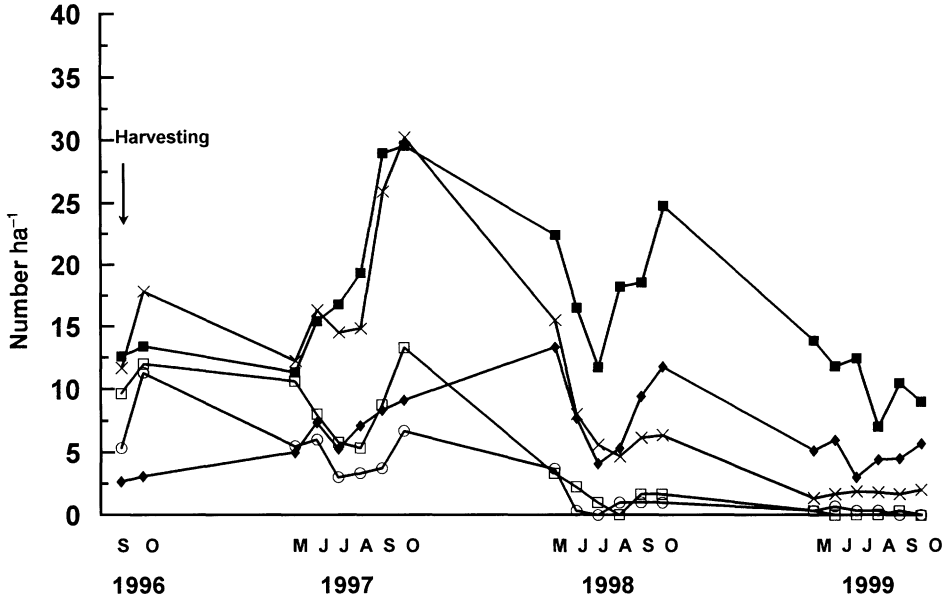

Fig. 4. Mean ($n = 3$ replicate sites) population density (Jolly–Seber) of *Clethrionomys gapperi* for the five treatments 1996–99. Symbols as for Fig. 1.

coniferous seedlings, thereby necessitating a spot planting programme.

Discussion

SMALL MAMMAL COMMUNITIES

Our study is the first detailed investigation of the diversity and population dynamics of small mammals over a range of variable retention harvests in replicate sites of mixed Douglas fir–lodgepole pine original forest. The forest-floor small mammal communities were sufficiently diverse (10 species) in our study area that simple generalizations regarding their responses to variable retention harvests were unlikely. Thus, hypothesis (i), that abundance and diversity of small mammals will decline with decreasing levels of tree retention, needs to be evaluated on a species-specific or species-group basis. The prevalence of early successional small mammal species across our harvested sites resulted in higher levels of both species richness and diversity on those sites.

A habitat generalist such as *Peromyscus maniculatus* was common in all sites, with the highest numbers reached on clear-cuts in 1998. This result was typical for *Peromyscus* as reported in other forestry clear-cutting and habitat studies (Baker 1968; Hooven & Black 1976; Sullivan 1979; Martell 1983; Morrison & Anthony 1989; Sullivan, Lautenschlager & Wagner 1999). *Tamias amoenus* was also a habitat generalist with respect to our harvested sites, which fits the reported affinities of this species (Sutton 1992; Hayes, Horvath & Hounihan 1995). *Sorex monticolus* also followed this pattern, as did *M. longicaudus*, and a strong preference for clear-cut sites was also displayed by *M. pennsylvanicus*. *Clethrionomys gapperi* was the major species occupying our uncut forest sites and its persistence in the group seed-tree sites, albeit at lower abundance than in the uncut forest, suggested that aggregated retention of green trees might maintain this species on harvested sites. Thus, the prediction by Lehmkuhl *et al.* (1999) that those small mammal species associated with early successional habitats and habitat generalists will increase, or have no change in abundance, with decreasing levels of tree retention, is supported by our results.

Responses of forest-floor small mammals to variable retention levels of trees represented spring to autumn seasons, and may not have been the same during winter months. Overwinter changes in abundance were presumably most dramatic during 1998–99, when peak populations of *Microtus* declined. Species richness and diversity measurements may also have been affected overwinter by this decline.

VOLE POPULATIONS AND HABITAT

Microtus longicaudus, *M. pennsylvanicus* and *C. gapperi* were the principal components of the forest-floor small mammal communities on our sites. Voles of the genus *Microtus* clearly preferred 'open' homogeneous habitats generated by clear-cutting and seed-tree harvest methods. Conversely, *C. gapperi* was most abundant in group seed-tree, patch-cut and uncut forests. Thus, in terms of hypothesis (ii), that abundance of *Microtus* spp. will be inversely related to, and abundance of *C. gapperi* positively related to, basal area and density of residual trees after harvest, significant linear relationships appeared to support this part of the hypothesis.

Several other habitat variables were investigated but only percentage ground cover and crown volume index of residual trees showed linear relationships similar to

Table 3. Mean (n = 3 replicate sites) ± SE number of successful pregnancies for *Microtus longicaudus*, *Microtus pennsylvanicus* and *Clethrionomys gapperi* for the five treatments during 1997–99 and results of RM-ANOVA. Mean values followed by different letters are significantly different by DMRT. F-values identified by * were calculated using an H–F correction factor, which decreased the stated degrees of freedom due to correlation of data among repeated measures (years)

						Overall analysis					
						Treatment		Time		Treatment × time	
Species and year	Clear-cut	Single seed-tree	Group seed-tree	Patch-cut	Uncut forest	$F_{4,10}$	P	$F_{2,20}$	P	$F_{8,20}$	P
Microtus longicaudus						0·75	0·58	4·95	0·02	1·82	0·13
1997	1·67 ± 1·2	8·67 ± 7·7	0·00	1·33 ± 0·7	0·33 ± 0·3						
1998	6·00 ± 3·5	9·00 ± 4·7	6·33 ± 4·1	3·33 ± 1·7	0·33 ± 0·3						
1999	4·00 ± 3·1	5·00 ± 4·1	7·33 ± 4·7	1·33 ± 1·3	0·00						
Microtus pennsylvanicus						2·49	0·11	2·72*	0·10	2·09*	0·09
1997	5·00 ± 3·2	0·00	0·00	1·00 ± 1·0	0·00						
1998	11·33 ± 7·3	0·33 ± 0·3	0·33 ± 0·30	0·67 ± 0·7	0·00						
1999	0·67 ± 0·3	0·67 ± 0·3	0·00	0·00	0·00						
Clethrionomys gapperi						7·25	< 0·01	17·49*	< 0·01	1·86*	0·13
1997	9·33 ± 3·4^{ab}	3·00 ± 1·2^{b}	25·00 ± 6·8^{a}	11·00 ± 6·0^{ab}	24·67 ± 7·1^{a}						
1998	0·67 ± 0·6^{c}	0·33 ± 0·3^{c}	6·00 ± 0·0^{b}	8·00 ± 2·9^{b}	15·00 ± 2·3^{a}						
1999	0·33 ± 0·3^{b}	0·67 ± 0·7^{b}	3·00 ± 2·5^{ab}	3·33 ± 2·0^{ab}	7·33 ± 2·0^{a}						

Table 4. Mean ($n = 3$ replicate sites) ± SE number of first captures (recruits) for *Microtus longicaudus*, *Microtus pennsylvanicus* and *Clethrionomys gapperi* for the five treatments and results of RM-ANOVA. Mean values followed by different letters are significantly different by DMRT. F-values identified by * were calculated using an H–F correction factor, which decreased the stated degrees of freedom due to correlation of data among repeated measures (years)

						Overall analysis					
						Treatment		Time		Treatment × time	
Species and year	Clear-cut	Single seed-tree	Group seed-tree	Patch-cut	Uncut forest	$F_{4,10}$	P	$F_{3,30}$	P	$F_{12,30}$	P
Microtus longicaudus						0·86	0·52	12·35*	< 0·01	0·84*	0·60
1996	0·3 ± 0·3	0·7 ± 0·7	0·3 ± 0·3	0·0	0·0						
1997	10·3 ± 8·0	17·0 ± 13·7	1·0 ± 0·6	4·0 ± 1·5	1·0 ± 1·0						
1998	25·7 ± 16·4	20·7 ± 15·0	24·0 ± 14·2	9·3 ± 5·4	0·7 ± 0·7						
1999	11·3 ± 9·4	10·0 ± 7·2	9·3 ± 7·9	4·0 ± 3·5	0·0						
Microtus pennsylvanicus						2·96	0·07	14·78	< 0·01	3·76	< 0·01
1996	0·7 ± 0·7	0·0	0·3 ± 0·3	1·3 ± 1·3	0·0						
1997	21·0 ± 14·2	0·7 ± 0·7	0·3 ± 0·3	2·0 ± 2·0	0·0						
1998	31·7 ± 13·6	5·7 ± 2·0	2·7 ± 1·2	2·3 ± 1·3	0·0						
1999	4·0 ± 2·7	4·3 ± 1·5	1·3 ± 0·7	0·3 ± 0·3	0·0						
Total *Microtus*						6·30	< 0·01	20·42	< 0·01	1·82	0·09
1996	1·0 ± 0·6^{a}	0·7 ± 0·7^{a}	0·6 ± 0·7^{a}	1·3 ± 1·3^{a}	0·0^{a}						
1997	31·3 ± 8·5^{a}	17·7 ± 13·4^{ab}	1·3 ± 0·3^{b}	6·0 ± 2·9^{ab}	1·0 ± 1·0^{b}						
1998	57·4 ± 8·6^{a}	26·4 ± 14·9^{a}	26·7 ± 13·9^{a}	11·6 ± 5·0^{a}	0·7 ± 0·7^{b}						
1999	15·3 ± 7·4^{a}	14·3 ± 6·8^{a}	10·6 ± 8·3^{ab}	4·3 ± 3·3^{ab}	0·0^{b}						
Clethrionomys gapperi						12·97	< 0·01	25·57*	< 0·01	5·44*	< 0·01
1996	15·7 ± 6·3^{ab}	12·3 ± 2·2^{ab}	23·0 ± 5·0^{a}	4·0 ± 2·1^{b}	19·7 ± 3·9^{a}						
1997	17·0 ± 10·6^{b}	13·3 ± 3·9^{b}	45·7 ± 9·2^{a}	15·3 ± 6·0^{b}	66·3 ± 11·1^{a}						
1998	4·3 ± 4·3^{c}	4·3 ± 3·0^{c}	17·3 ± 5·8^{bc}	19·0 ± 3.0^{b}	47·3 ± 4·3^{a}						
1999	0·7 ± 0·7^{c}	0·7 ± 0·7^{c}	3·7 ± 0·9^{b}	8·3 ± 3·2^{b}	26·7 ± 2·3^{a}						

Table 5. Mean ($n = 3$ replicate sites) ± SE estimates of Jolly–Seber 28-day survival for *Microtus longicaudus*, *Microtus pennsylvanicus* and *Clethrionomys gapperi* during summer and winter periods 1996–99 for the five treatments

Species and year	Clear-cut	Single seed-tree	Group seed-tree	Patch-cut	Uncut forest
Microtus longicaudus					
Winter 1996–97	0·92	1·00	–	–	–
Summer 1997	0·61 ± 0·20	0·67 ± 0·01	0·77	0·77	–
Winter 1997–98	0·77 ± 0·01	0·81 ± 0·10	0·88	0·79 ± 0·04	–
Summer 1998	0·85 ± 0·04	0·56 ± 0·06	0·55 ± 0·02	0·49 ± 0·05	–
Winter 1998–99	0·72 ± 0·09	0·84 ± 0·06	0·79 ± 0·01	0·83	–
Summer 1999	0·28	0·63 ± 0·04	0·52 ± 0·04	0·61	–
Microtus pennsylvanicus					
Winter 1996–97	–	–	–	0·77	–
Summer 1997	0·78 ± 0·14	–	–	0·46	–
Winter 1997–98	0·83 ± 0·04	–	–	0·92	–
Summer 1998	0·71 ± 0·14	0·66 ± 0·10	0·58	0·69	–
Winter 1998–99	0·78 ± 0·02	0·82 ± 0·19	0·80	0·77	–
Summer 1999	0·68 ± 0·48	0·49 ± 0·20	0·69	–	–
Clethrionomys gapperi					
Winter 1996–97	0·92 ± 0·05	0·83 ± 0·03	0·87 ± 0·01	0·89 ± 0·04	0·83 ± 0·04
Summer 1997	0·66 ± 0·06	0·45 ± 0·02	0·71 ± 0·06	0·70 ± 0·09	0·64 ± 0·11
Winter 1997–98	0·81 ± 0·06	0·82 ± 0·09	0·86 ± 0·04	0·95 ± 0·05	0·81 ± 0·04
Summer 1998	0·41	0·51 ± 0·01	0·47 ± 0·08	0·52 ± 0·14	0·53 ± 0·12
Winter 1998–99	0·72	0·82 ± 0·07	0·75 ± 0·02	0·88 ± 0·02	0·80 ± 0·04
Summer 1999	0·69	0·69	0·75 ± 0·12	0·78 ± 0·11	0·61 ± 0·03

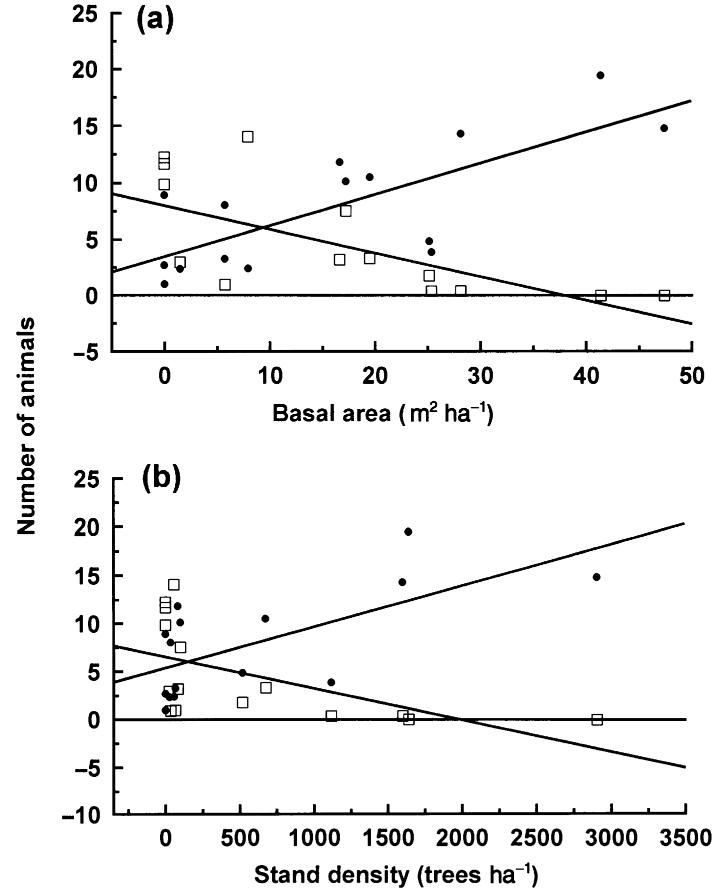

Fig. 5. Linear regression analysis relating mean abundance of *Microtus* spp. (open squares) to (a) basal area ($y = 8{\cdot}00 - 0{\cdot}21x$) and (b) density ($y = 6{\cdot}54 - 0{\cdot}003x$), and *C. gapperi* (closed circles) to (a) basal area ($y = 3{\cdot}46 + 0{\cdot}28x$) and (b) density ($y = 5{\cdot}39 + 0{\cdot}004x$) of residual trees.

basal area and density. As expected, because of the similarity in fallen wood levels among treatment sites (Sullivan, Sullivan & Lindgren 2001), neither *Microtus* spp. nor *C. gapperi* showed any relationship to this variable.

Clethrionomys gapperi prefer mesic habitats in coniferous, deciduous and mixed forests with abundant organic debris composed of stumps, logs and exposed roots (Martell & Radvanyi 1977; Merritt 1981; Yahner

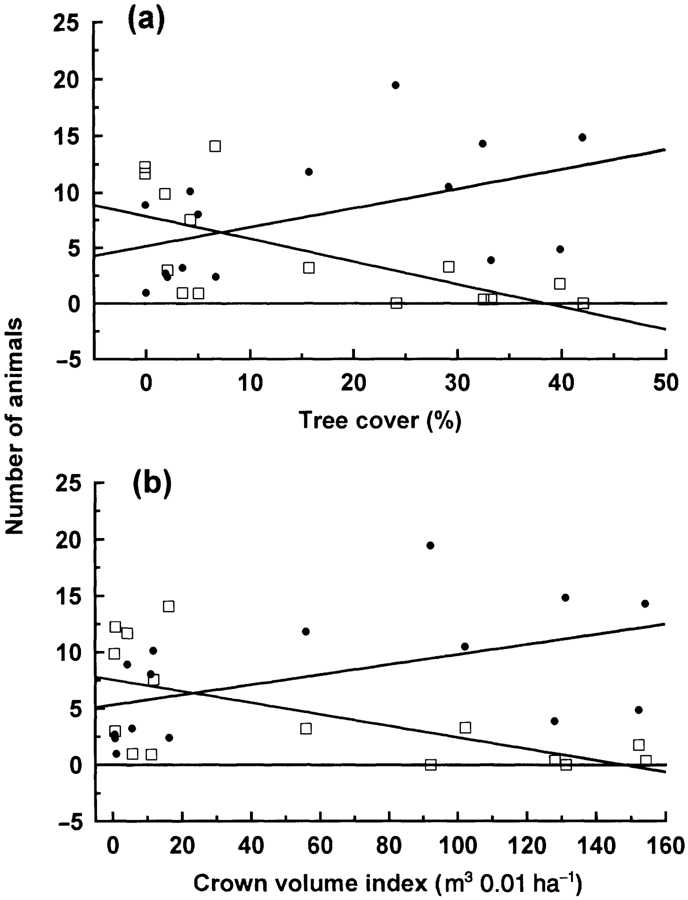

Fig. 6. Linear regression analysis relating mean abundance of *Microtus* spp. (open squares) to (a) percentage cover ($y = 7{\cdot}88 - 0{\cdot}20x$) and (b) crown volume index ($y = 7{\cdot}56 - 0{\cdot}05x$), and *C. gapperi* (closed circles) to (a) percentage cover ($y = 5{\cdot}14 + 0{\cdot}17x$) and (b) crown volume index ($y = 5{\cdot}31 + 0{\cdot}04x$) of residual trees.

Table 6. Mean (n = 3 replicate sites) ± SE percentage of lodgepole pine seedlings eaten by voles on the four harvested sites during the overwinter periods of 1997–98 and 1998–99

					Analysis	
Year	Clear-cut	Single seed-tree	Group seed-tree	Patch-cut	$F_{3,8}$	P
1997–98	0·4 ± 0·4	4·0 ± 3·5	0·4 ± 0·4	18·3 ± 8·7	3·33	0·08
1998–99	3·0 ± 1·6	2·9 ± 1·5	3·9 ± 2·5	13·5 ± 2·2	2·83	0·11

1986). These habitat conditions provide a substrate for maintenance of hypogeous ectomycorrhizal fungi, which are a major food supply for *C. gapperi* (Maser, Trappe & Nussbaum 1978; Ure & Maser 1982). Presumably, as reviewed by Hayward, Henry & Ruggiero (1999) and Sullivan, Lautenschlager & Wagner (1999), a reduction in moisture and insufficient coniferous tree cover result in extirpation of *C. gapperi* from recent clear-cuts. This pattern was evident in our study where *C. gapperi* declined to very low numbers or disappeared on the clear-cut and single seed-tree sites.

Persistence of *Clethrionomys* spp. in forests subjected to selection, patch and shelterwood cutting has been reported by several authors (Ramirez & Hornocker 1981; Scott, Crouch & Whelan 1982; Martell 1983; Medin & Booth 1989; Steventon, MacKenzie & Mahon 1998; Von Trebra, Lavender & Sullivan 1998). In addition to aiding in dispersal of mycorrhizal fungi, *C. gapperi* are also important prey for several carnivores (Hayward & Verner 1994; Ruggiero *et al.* 1995). Thus, maintenance of *C. gapperi* in variable retention harvest forests will also have potentially favourable impacts on predator populations (Garton, Hayward & Hayward 1989).

The preference of *M. longicaudus* and *M. pennsylvanicus* for the early successional habitats of the clear-cut and seed-tree sites may be explained by the abundance of herbs and grasses providing food and cover (Reich 1981; Getz 1985). The occurrence of *M. longicaudus* on clear-cut and seed-tree sites, and to some degree on patch-cut sites, fits the variety of habitats

Table 7. Summary of responses of small mammal abundance (overall mean values, $n = 20$ trapping periods) to variable retention harvests 1996–99

Parameter	Clear-cut	Single seed-tree	Group seed-tree	Patch-cut	Uncut forest
Mean abundance ha^{-1}					
Clethrionomys gapperi	4·20	2·68	10·00	6·42	16·20
Microtus longicaudus	4·77	5·40	3·37	1·41	0·12
Microtus pennsylvanicus	6·48	0·58	0·50	0·38	0·00
Peromyscus maniculatus	14·73	10·14	10·60	8·54	7·23
Tamias amoenus	5·64	9·47	10·66	6·72	2·61
Phenacomys intermedius	0·62	0·82	0·30	0·20	0·00
Zapus princeps	0·00	0·00	0·00	0·00	0·02
Sorex monticolus	0·92	0·75	0·83	0·33	0·12
Sorex cinereus	0·15	0·15	0·15	0·10	0·13
Mustela erminea	0·07	0·22	0·02	0·07	0·07
Total	37·58	30·21	36·43	24·17	26·50

occupied by this vole (Halvorson 1982; Van Horne 1982; Morris 1984; Smolen & Keller 1987). Habitats with some open areas and shrub and sapling cover at 7–10 years after clear-cutting appeared optimum for *M. longicaudus* in Alaska (Van Horne 1982). Later seral stages with less understorey vegetation and thick canopies had lower densities of long-tailed voles (Van Horne 1982), which fits the pattern found in our study. Both species of voles consume lodgepole pine seeds and the very high abundance of seeds on the clear-cut and single seed-tree sites is likely to have contributed to population increases.

Although multi-annual population fluctuations in *M. pennsylvanicus* are well documented, population changes in *M. longicaudus* appear to be annual (Van Horne 1982; Taitt & Krebs 1985). However, the population changes of *M. longicaudus* in our study appeared to have a multi-annual fluctuation in abundance, with a peak year in 1998 which was synchronous with populations of *M. pennsylvanicus*. Longer-term data than recorded in this study are needed to determine if *M. longicaudus* also has a cyclic fluctuation in abundance. These data would have considerable significance in terms of knowing when this species would be abundant and likely to feed on tree seedlings, particularly during the winter of peak numbers.

The decline in *C. gapperi* on clear-cut and seed-tree sites occurred during the peak numbers of *M. pennsylvanicus* in 1998 and suggested the possibility of competitive displacement (Iverson & Turner 1972; Morris & Grant 1972). However, *C. gapperi* also declined on some sites (one replicate of each of the clear-cut, single seed-tree and group seed-tree) where *M. pennsylvanicus* was absent or at very low density. Similarly, *M. longicaudus* also appears subordinate to *M. pennsylvanicus* based on behaviour studies (Colvin 1973). This pattern of competitive displacement may have occurred on our clear-cut sites where the overall mean density on replicates 1, 2 and 3 was 3·00, 11·31 and 0·00 for *M. longicaudus* and 6·87, 0·35 and 12·25 for *M. pennsylvanicus*, respectively. Without experimental verification, these differences could be attributed to site-specific habitat features as well.

GRADIENT OF DEMOGRAPHIC PARAMETERS

Another prediction of hypothesis (ii), that reproduction and survival of *Microtus* and *C. gapperi* will follow reciprocal gradients across the five treatment sites, was partially supported. In terms of abundance (overall mean numbers ha^{-1}) the combined *Microtus* spp. did, indeed, follow a gradient of clear-cut (11·3) > single seed-tree (6·0) > group seed-tree (3·9) > patch-cut (1·8) > uncut forest (0·1) (Table 7). Reproductive performance of *Microtus* spp. based on number of new voles (recruits) also followed this pattern. However, survival rates did not follow a gradient for either species.

Abundance (overall mean numbers ha^{-1}) of *C. gapperi* did not follow a gradient: clear-cut (4·2), single seed-tree (2·7), group seed-tree (10·0), patch-cut (6·4) and uncut forest (16·2) (Table 7). Reproduction and survival followed a similar pattern, with no clear gradient across treatments. The group seed-tree harvest method may provide 'islands' of mature forest habitat that allow *C. gapperi* to persist for a longer period post-harvest than on clear-cut and single seed-tree sites. Although not sampled in our study, the 'clear-cut areas' adjacent to the group of residual trees on group seed-tree sites probably supported *C. gapperi* in a similar manner to the clear-cut and single seed-tree sites. The persistence of *C. gapperi* on patch-cut sites was similar to the results reported by Hayward, Henry & Ruggiero (1999) in their patch-cuts in a 'perforated' forest landscape, but not to the results of Mills (1995) where the California red-backed vole *C. californicus* was negatively impacted by widespread forest fragmentation.

HABITAT HETEROGENEITY AND FOREST REGENERATION

We investigated habitat heterogeneity across a range of variable retention harvests in the context of vole population dynamics and the impact on forest regeneration. Hypothesis (iii), that habitat heterogeneity generated by our harvest methods would limit population size of *Microtus* spp. but not *C. gapperi*, seemed to be supported for *Microtus* spp. The homogeneous clear-cut habitats presumably provided suitable habitat for *M. pennsylvanicus* to increase and undergo a typical population fluctuation. This pattern was also evident for *M. longicaudus* in the clear-cut and both seed-tree sites, which were considerably more homogeneous early successional habitats than either of the patch-cut or uncut forest sites (see Figs 1–3 in Sullivan, Sullivan & Lindgren 2001). The patch-cut sites averaged 0·70 ha in area, which was apparently not enough habitat for either species of *Microtus* to begin a population build-up leading to peak numbers. As reviewed by Krebs (1996), both predation and food supply may be extrinsic factors that drive the cyclic population dynamics of *Microtus* spp.

Habitat alteration from forest harvesting creates landscape configurations ranging from undisturbed habitat to a matrix of disturbed habitat surrounding scattered fragments of original habitat. Because of the interaction of many factors, theoretical predictions suggest that the response of wildlife populations to increasing levels of habitat alteration is probably non-linear (Andrén 1994; Wiens 1997). However, our results for *Microtus* spp. indicated a reasonably clear linear gradient of improved habitat for these two vole species with reduced cover and basal area of trees. Thus, the prediction by Emmingham, Holthausen & Vomocil (1992) appears plausible in that alternative silvicultural systems to clear-cutting, which leave residual trees and small opening sizes, should prevent growth of *Microtus* populations to levels that could damage forest regeneration. However, feeding damage to seedlings by *Microtus* spp. on clear-cut and seed-tree sites in our study was minor (≤ 4·0% mortality), whereas that on patch-cut sites ranged from 13·5% to 18·3% over the two winters.

Clearly, these results do not support the second part of hypothesis (iii) that habitat heterogeneity would limit feeding damage to seedlings. Because *C. gapperi* was the primary vole species, averaging 7 animals ha^{-1} (with *Microtus* spp. at 1·3 animals ha^{-1}), on patch-cut sites in 1997, the majority of seedling damage during overwinter 1997–98 was presumably caused by this species. Similarly, numbers of *Microtus* spp. averaged 2·8 ha^{-1} and *C. gapperi* 8·6 ha^{-1} on patch-cut sites in 1998 prior to the second overwinter period of damage. Again, unless *Microtus* spp. moved onto the patch-cuts during winter months when we could not sample them, the majority of feeding damage was caused by *C. gapperi*. This observation of damage to seedlings by *C. gapperi* was also reported in north-western British Columbia (T. Zimmerling & L. Zimmerling, unpublished data).

A possible explanation for the lack of feeding damage to seedlings on clear-cut and seed-tree sites by *Microtus* spp., particularly during the 1998–99 winter of peak numbers, relates to time of planting. Seedlings planted in spring 1997 had been in the field for two growing seasons by that time and may have lost some of the effects of nursery fertilization. Voles will feed preferentially upon nursery-raised seedlings, which tend to have elevated levels of nitrogen and related nutrients (Sullivan & Martin 1991).

CONCLUSIONS

Contrary to hypothesis (i), abundance, species richness and diversity of small mammals were maintained on all harvested sites, primarily because of habitat generalist and early successional species. Late-successional forest species such as *C. gapperi* and the early successional, but mycophagist, *T. amoenus* persisted on the group seed-tree harvested sites. Our study represents an initial 'snapshot' in time (4 years post-harvest) and future monitoring of these sites over many years will determine if these trends continue.

The results of our study suggest that vole populations will respond to a range of habitat heterogeneity created by variable retention harvests. Basal area and density of residual coniferous trees appear crucial to maintaining *C. gapperi*. Patch-cuts that leave 60–70% basal area of uncut forest and some group seed-tree harvest prescriptions that leave at least 15 $\text{m}^2\ \text{ha}^{-1}$ basal area or 30% of uncut forest in patches of residual trees may allow for persistence of *C. gapperi*. At the same time, they are likely to prevent build-ups of *Microtus* spp. and consequent feeding damage. Such population increases tend to occur with harvest prescriptions leaving less than 5 $\text{m}^2\ \text{ha}^{-1}$ basal area on cutting units ≥ 4 ha, which provide sufficient area of early successional habitat for build-ups and fluctuations of *M. longicaudus* and *M. pennsylvanicus*. Volume of herbaceous plants and provision of seed from lodgepole pine cones may contribute to favourable habitat conditions for *Microtus*.

If feeding damage to planted seedlings is a risk in a given forest management area, then alternative harvest practices to clear-cutting or single seed-tree systems should be considered to avoid build-ups of *Microtus* spp. If management for *C. gapperi* is a priority, because of its ecological roles as a disperser of mycorrhizal fungi and prey source for a variety of forest carnivores, then alternative harvesting systems, such as the group seed-tree and patch-cut which generate habitat heterogeneity, should be implemented. These methods of 'green-tree retention' achieve both aims of *C. gapperi* persistence and prevention of *Microtus* outbreaks. In addition, these harvesting systems are as good for overall small mammal abundance, species richness and diversity as any other.

However, *C. gapperi* also appears to feed on seedlings in some patch-cut situations. The risk of seedling loss needs to be balanced with the ecological functions of *C. gapperi*, which is an indicator species of late-successional forest conditions. Management for *C. gapperi* may provide habitat for many other species that rely on mature and old-growth forest ecosystems.

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