RELATIONSHIP OF SMALL MAMMAL POPULATIONS

TO UNIFORM EVEN-AGED SHELTERWOOD SYSTEMS

by

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ABSTRACT

This study was designed to test the hypothesis that a shelterwood silvicultural system would reduce small mammal population levels in 30% and 50% basal area removal stands. The benefit of an overstory canopy, or shelterwood, may help reduce the frequent frost problems observed in interior Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca*) plantations, and improve the success of natural regeneration, if seed predation does not threaten the survival of the seed supply. Small mammal population levels, seed fall, seed germination, and seed predation were monitored in order to determine the small mammal population dynamics associated with seed predation in the central interior of British Columbia, Canada. Deer mice (*Peromyscus maniculatus*) and red-backed voles (*Clethrionomys gapperi*) were the most common small mammal species sampled prior to harvesting, and both species continued to be dominant in the first and second year post-harvest. There was no negative effect on small mammal populations due to the different intensities of basal area removal. Seed fall crops were recorded the first and second year post-harvest; the seed crop in the second year post-harvest was substantially larger than the first year post-harvest on treatments and controls. Seed predation varied between 1.4×10^5 and 3.0×10^5 seeds/ha/month, and seemed to fluctuate with the seasonal small mammal population levels (lower in spring and higher in fall) but not with the amount of seed crop available. Germination occurred in 62% to 63% of the seeds that survived overwinter, on the seedbeds created during harvesting. Thus, the regeneration success of the stands, with regard to seed survival and establishment, in 30% and 50% basal area removal stands did not seem to be inhibited by the small mammal communities observed on the sites.

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INTRODUCTION

Difficulties exist in establishing regeneration of interior Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca*) in the central interior region of British Columbia, Canada. Poor survival of planted stock in open clearcuts and increasing public pressure for the integration of non-timber resources in forest management practices has illustrated the need for an alternative silvicultural system on these sites. Stands containing both Douglas-fir and lodgepole pine (*Pinus contorta* Dougl. var. *latifolia*) are especially suited to shelterwood cutting systems (B.C. Ministry of Forests 1991). In a shelterwood system the mature stand is removed with a minimum of two cuts in order to cull the diseased and damaged trees from the stand, and encourage regeneration of the desired species under the protection of a partial canopy. The mature crop is removed in one or more harvests as the regeneration becomes established and requires more growing space. The benefit of an overstory canopy, or shelterwood, may help reduce the frequent frost problems observed in interior Douglas-fir plantations, and improve the success of natural regeneration while retaining the advanced fir regeneration that is usually present (Sutherland 1990).

Within the last 20 - 40 years, the sole reliance on the use of natural regeneration in conifer stands has all but disappeared as planting has generally resulted in more rapid rates of regeneration (Moore 1940; Owston *et al.* 1992; West 1992). The potential delays or failures of the crop trees to establish were too great a risk. However, due to the rising costs of artificial regeneration, the problem of establishing Douglas-fir plantations in clearcuts in the interior region, and public pressure to reduce the amount of clearcut harvesting, there has been a

renewed interest in the natural regeneration which can occur in a shelterwood system. Although one could not expect adequate regeneration from natural seed sources for most conifer species in a given year (West 1992), this does not necessarily hold true for a shelterwood system. Williamson (1973) observed coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) seedlings of all possible ages four years after an initial shelterwood cut, although no appreciable cone crops were predicted during that time. Apparently some regeneration had occurred during years of predicted low seed fall, demonstrating that it is possible for cone and seed production of the remaining trees to be stimulated by a shelterwood cut.

A shelterwood system produces a structurally diverse stand which allows numerous flora and fauna species to coexist. The opening of the canopy combined with the partial cover of the retained mature crop enhances the vertical structure as well as the species composition within a stand. By not prescribing burns after harvest, the coarse woody debris can accumulate and provide cover for small mammal species. In addition to the importance of these small mammal species as a prey base for raptors, furbearers and larger carnivores, these small mammals may significantly help as well as hinder establishment of natural regeneration (Owston *et al.* 1992). Most higher plants have evolved with an obligatory symbiotic relationship with root-inhabiting (mycorrhizal) fungi (Maser *et al.* 1978a). Whereas epigeous mycorrhizal spores are prolific in number and are dispersed primarily by air currents, hypogeous mycorrhizal fungi are dependent upon small mammals such as deer mice (*Peromyscus maniculatus*), voles (*Microtus* spp.), shrews (*Sorex* spp.) and chipmunks (*Eutamias* spp.), all avid mycophagists, as primary vectors of spore dissemination (Maser *et al.* 1978b). The behaviour patterns and habitats used by the different mycophagists determine the extent of spore dispersal: those small mammals which are more

ubiquitous or edge-dwelling may provide mycorrhizal inoculum from forested areas to adjacent nonforested areas. However, harvesting and silvicultural practices may profoundly change small mammal population levels and thereby contribute to their destructive potential in young plantations.

A community of these small mammals exist in established forests and the various species have diverse feeding and habitat preferences. While some species may benefit from, or adapt to harvesting disturbances, the potential impact on more specialized species such as the southern red-backed vole (*Clethrionomys gapperi*) is unknown. Red-backed voles are considered inhabitants of mature forest, and their density may drop precipitously within 1 or 2 years following logging or forest fire disturbance (West *et al.* 1980). Red-backed voles disappeared from a small mammal community following a diameter-limit logging trial (Medin 1986), whereas a study on selective cutting (Medin and Booth 1989) found that a 29% volume removal had no significant effect on red-backed voles. Corn *et al.* (1988) compared coastal Douglas-fir forests of varying age classes (less than 10 years to 450 years of age), and found a positive correlation of red-backed voles with density and basal area of live trees. Red-backed voles were virtually absent from clearcuts whereas deer mice were abundant (Corn *et al.* 1988). Deer mice are known to easily survive harvest operations, and hence are able to rapidly repopulate harvested areas (West 1992). Some studies show that deer mice abound during the early stages of forest succession, particularly when ground cover is disturbed during harvest (Lawrence *et al.* 1961; West 1992), while other findings conclude that numbers of deer mice decrease on logged plots versus unlogged controls (Medin and Booth 1989). In either case, it is necessary to determine how management actions will affect the species capable of damaging regenerating conifers in

order to minimize the risk of seed predation.

Natural regeneration under the partial canopy of seed trees depends upon seed production, survival of the fallen seed until the following growing season, and germination. Both before and after seeds fall from the trees they are likely to be eaten by insects, birds and rodents (Smith 1986). Deer mice, in particular, are primarily granivorous and highly efficient at finding and consuming large quantities of conifer seed (Moore 1940; Smith and Shaler 1947; Sullivan 1979a; Hawthorne 1980; Sullivan and Sullivan 1982); some voles and insectivorous mammals such as shrews (*Sorex* spp.) also consume seeds but are only secondary granivores (Sullivan and Sullivan 1982; West 1992). Seed predation by deer mice and other rodents has contributed to the failure in regenerating cutover forest lands as well as overgrazed range lands (Sullivan 1979b). Seed predation is most severe in years of low seed production; however, animals are not completely efficient at locating seed and are simply incapable of destroying all seed in a good year (West 1992). Emphasis must be put on harvesting strategies that reduce animal damage or seed predation to tolerable levels by allowing regeneration of trees, but discourage the buildup of large populations of potentially damaging species of wildlife (Emmingham *et al.* 1992). To date, there has been little research on the long-term effects of harvesting methods, other than clearcutting, on small mammal populations.

In order to assess the effects of shelterwood harvesting on small mammal species, it is necessary to monitor small mammal population dynamics along with natural seed fall, seed predation, and seed germination in different harvesting treatments to provide some rationale for regeneration, or lack of it, in the years after initial harvest. This study focuses on whether an alternative silvicultural system such as a shelterwood harvest can alleviate frost problems

associated with Douglas-fir regeneration as well as minimize small mammal predation on the natural seed supply.

Objectives

The objectives of this study were to: (1) test the hypothesis that a shelterwood silvicultural system would reduce small mammal population levels in the treated stands; (2) measure natural seed production, seed predation by small mammals and seed germination under uniform, even-aged shelterwood harvesting systems; (3) measure small mammal population dynamics associated with seed predation; (4) use this information to help understand the regeneration success or failure of the various harvesting treatments.

METHODS

Study areas

Three study areas were established within the Cariboo Forest Region, northeast of Williams Lake, British Columbia. The Beaver Valley (Gavin site, 52°29'N; 122°37'W) and the Beedy Creek (Skelton site, 52°33'N; 122°04'W) site were located in the Williams Lake Forest District, and the University of British Columbia's Alex Fraser Research Forest (UBC site, 52°29'N; 122°39'W) was located in the Horsefly Forest District. All sites are in the mesic falsebox (*Paxistima myrsinites*)-sarsaparilla (*Aralia nudicaulis*) ecosystem unit of the dry and

warm Sub-boreal Spruce biogeoclimatic subzone (SBSdw1) (Meidinger and Pojar 1991). The forest cover was primarily mature (107-126 year old) Douglas-fir/lodgepole pine stands with some white spruce (*Picea glauca* (Moench) Voss) interspersed. More spruce was present on the UBC site than on the other two sites, indicating a slightly wetter moisture regime (permesic) in these treatment units (BCMOF 1993a). Topography in the area is flat to gently rolling with elevation ranging from 800 m (Skelton site) to 1050 m (UBC and Gavin sites). The study sites varied in size between 20 and 30 ha. This size accommodated treatment blocks as well as treated buffers and surrounds, and reflected operational cutblock size. In addition, this scale of shelterwood treatments may have been more representative of the potential impact on the mobile small mammal species present, and reflected the effect of the disturbances on these population levels more realistically. Generalist small mammal species such as the deer mouse would not be able to modify their behaviour or home ranges to adjust to the treatments as readily as they may be able to when study sizes are less than their home range size.

Experimental design

The experimental design was a randomized block design with three replicate blocks. Three treatments were interspersed randomly within each block to compare two levels of basal area (BA) removal (30% and 50%) with an unlogged control. The treatment replicates were spatially segregated, thereby ensuring statistical independence (Hurlbert 1984). Treatments were 1.4 ha in size with 20 m buffers. The buffers were treated with 30% BA removal between each treatment in order to minimize any treatment interaction. The location of each of the three

blocks was determined from aerial photographs of the sites.

Block locations were selected according to:

i)   uniformity of ecosystems, topography, and tree species distribution

ii)   low windthrow hazard

iii)   available access and location

The target tree species distribution was between 60/40% to 40/60% Douglas-fir/lodgepole pine. Lodgepole pine was selected over Douglas-fir for removal, as Douglas-fir was the preferred species to regenerate. The southwest corners of each block were permanently marked on a Douglas-fir tree. This acted as a tie point for all corners and block centres. Mechanical falling with a feller-buncher and large skidders was used to create wide skid trails which would mimic current industrial operations. Trees were not marked prior to cutting, but the logging contractors were shown how to use prisms to select stems to meet the 30% and 50% basal area removal criteria. The shelterwood cuts were completed between July and early September, 1991. The 30% BA removal treatments were considered to be preparatory cuts (Smith 1986), removing most of the trees from the lower crown classes, whereas the 50% removal treatments were considered to be seed cuts and removed trees in the overtopped and intermediate crown classes along with all or part of the codominants (BCMOF 1993a). Pre-harvest BA/ha in the stands ranged from 58.2 to 64.1 m^2/ha (490 to 653 m^3/ha). Residual BA's in the 30% removal treatments ranged from 37.9 to 46.2 m^2/ha (369 to 495 m^3/ha) and 31.8 to 33.1 m^2/ha (293 to 356 m^3/ha) in the 50% removal stands.

Small mammal population sampling

Small mammals were captured in Longworth live-traps baited with oats and a slice of carrot. Raw cotton was placed in each trap for bedding. A 1-ha (6 x 8 trap stations) checkerboard sampling grid was established on each treatment area on each block, with a live-trap at each of the 48 trap-stations. Trap-stations were set at 14.3-m intervals and pre-baited with oats at least one week prior to initial sampling each year. Pre-baiting encouraged familiarization with the traps and helped maximize trappability of the species present. Pre-treatment small mammal populations were monitored from June to August, 1991, to ensure that initial base-line populations were similar between treatments within replicate blocks. Post-harvest sampling continued at 3-week intervals from September to October, 1991, May to October, 1992, and May to October, 1993, on each of the treatments.

During trapping periods, traps were set in the afternoon of day 1, checked in the morning and afternoon of day 2, and checked and locked open in the morning of day 3. They remained locked open and accessible during the weeks between trapping periods. Animals captured were marked with serially-numbered, metal ear-tags, with each series being unique to a treatment area. Upon capture, species identification, body mass (to $\pm$ 0.5 g on a Pesola spring balance), sex, breeding condition, and location of capture were recorded for each animal. The reproductive condition for males was noted according to palpation of testes, if not obviously scrotal or abdominal. Females were considered to be in breeding condition if they were obviously pregnant (high body mass and a distended lower abdomen), lactating (verified through palpation), or had developed nipples and mammae showing signs of nursing, such as matted fur

(Krebs *et al*. 1969). All animals were released at point of capture immediately following data collection. These live-traps sampled deer mice, voles, yellow-pine chipmunks (*Eutamias amoenus*), shrews and other less common small mammal species.

Demographic parameters

To assess the effects of the different intensities of overstory removal, various population parameters were monitored. Population density (number of animals/ha), body mass, recruitment, survival, reproduction, and diversity were estimated for the two most common (numerically dominant) small mammal species, deer mice and red-backed voles, and for the less common species such as meadow voles (*Microtus pennsylvanicus*) and heather voles (*Phenacomys intermedius*) when sufficient data were available. Due to the difficulty in differentiating between the less common species in the field, the values obtained for the meadow and heather voles were combined for analysis.

Density

The accuracy of the population parameters of mark-recapture techniques is determined by the probability of an individual animal's capture, or trappability (Krebs and Boonstra 1984). Trappability was calculated as the number of marked individuals trapped/Jolly-Seber population estimate (Seber 1982). Population density was estimated by the Jolly-Seber (J-S) model for reasons indicated by Jolly and Dickson (1983). J-S estimates may be unreliable or impossible

to calculate when sample sizes of the marked population are very small, despite incorporation of the small sample correction factor of Seber (1982) in the calculations (Krebs 1991). Therefore, direct enumeration of minimum number of animals known to be alive (MNA) (Krebs 1966) was calculated in order to distinguish between actual population trends and the creation of artifacts, if any. Those J-S values which seemed biologically unreasonable were substituted with MNA counts before seasonal or treatment density averages were calculated. Small mammal population analysis and seed results were compared for various time periods (Table 1). Data collection was carried out from June 1991 to October 1993, during the snow-free months of the year. Population density was estimated for pre-and-post-harvest 1991, summer 1992, summer 1993, and the overall post-harvest density. Pre-treatment density estimates include only one or two sampling sessions. Therefore, the density analysis was restricted to post-harvest treatment comparisons rather than pre-and-post-treatment analysis.

TABLE 1. Breakdown of time periods for analysis

Time Period	Date
Pre-treatment 1991	June to August 1991
Post-treatment 1991	September to October 1991
Winter 1991	November 1991 to April 1992
Summer 1992	May to September 1992
Winter 1992	October 1992 to April 1993
Summer 1993	May to October 1993
Overall period of study (post-harvest)	September 1991 to October 1993

Survival

Further demographic comparisons and statistical tests incorporated the J-S density

estimates for reasons indicated by Jolly and Dickson (1983), Nichols and Pollock (1983), and

Efford (1992). Survival estimates indicate the disappearance of individuals from the marked

population, due to either emigration or mortality. Mean monthly survival was obtained by a

geometric mean of the observed survival rates during various time periods (Krebs 1991).

Thus, the survival rates were weighted according to the number of individuals recorded in

the designated time periods. Survival estimates may, at times, exceed unity due to the

peculiarity of the J-S density values. As in the comparisons of the density estimates,

biologically unreasonable J-S survival estimates (>1.00) were compared with minimum

survival estimates (based on MNA population enumeration values) for determining the lower

limit of the survival.

Animals which were able to establish themselves as residents of the sampled

populations were defined as recruits. All animals captured for the first time were categorized

as newcomers; those animals which were captured for a minimum of two consecutive

trapping sessions (i.e. they were present in the area for a minimum of three to six weeks)

were considered residents and classified as recruits (Klenner and Krebs 1991).

Body mass and sexual maturity

The mean adult body mass at which more than 50% of the animals captured were sexually mature was used to distinguish juvenile and adult age categories. Body mass at sexual maturity was derived from a breakdown of weight classes for each sex and each species. Mean body masses from each grid were averaged to obtain the mass at sexual maturity for deer mice and red-backed voles for the entire period of study. Spatial and temporal comparisons of body mass were based on the mean mass of the resident adult males recorded on the grids, and were averaged over the three replicates to analyse treatment differences. Only male body mass was used in the analysis to avoid complications of undetected pregnancies in female data.

Reproduction

Two measures were calculated to evaluate reproductive rate and condition: (i) length of the breeding season, and (ii) proportion of adults in breeding condition during the trapping seasons. Length of breeding season (in weeks) was estimated for 1992 and 1993 trapping years only, as sampling sessions were concurrent across the replicates and sampling was continuous for the duration of the snow-free portion of these years only. The start of the breeding season was defined as the time of capture of the first scrotal male or lactating female and the end of breeding was the week in which the last lactating female was recorded. In the event that no lactating females were captured in the last few weeks of trapping, the

breeding season was assumed to be 3 weeks longer than the last recorded capture of a

pregnant female. Comparisons of the proportions of adult males and females in breeding

condition were based on 1992 and 1993 trapping sessions and averaged over the three

replicates for analysis. Trappability, population density, recruitment, survival rates, and

reproduction estimates were calculated using *Small Mammal Programs for Mark-Recapture*

Data Analysis (Krebs 1991).

Small mammal diversity

Spatio-temporal alpha (within ecosystem) diversity comparisons of small mammal

species were analysed between treatments and controls in the SBSdw biogeoclimatic zone of

B.C. over the course of three trapping years. In this study, species diversity was measured

in terms of richness (number of species present) and evenness (the relative abundance of each

species in the community). The mathematical indices used, Simpson's D index and the

Shannon-Wiener (S-W) H' statistic, are measures of heterogeneity and incorporate richness

and evenness in their calculations (Magurran 1988). Conventionally, maximum evenness is

considered to be the most diverse even though maximum evenness is not generally observed

in natural systems (Kohler 1993). High evenness could be considered either less diverse, if

greater differences among species is considered to be most important (Wood 1994), or more

diverse because of less dominance by any one species. For the purpose of this study, the

greater the value of evenness, the greater the diversity was assumed to be.

Shannon-Wiener's H' statistic and Simpson's D index are both based on proportional abundances of species and may be subject to bias caused by fluctuations in abundance of dominant or rare species. The Shannon-Wiener function is most sensitive to changes in the abundance of rare species in the community sample (Pielou 1966). The larger the value of H', the greater the uncertainty of correctly predicting the species of the next individual collected in the sample and the greater the diversity. Simpson's index is biased towards dominance, and thereby shows greater sensitivity to changes in abundance of the most dominant species in the sample. Simpson's index (1-D) is related to the probability that two individuals picked at random belong to the same species and ranges from 0 (lowest diversity) to almost 1 (Simpson 1949). Comparisons of diversity were analysed using the mean values for the 1992 and 1993 trapping periods and included only the species which were marked.

Seed parameters

Seed fall traps were placed at 10 randomly selected small mammal trap station locations on each of the treatments and controls to measure natural seed fall. The traps consisted of a 0.37 m² frame box covered with 1-cm mesh hardware cloth and window screen on the bottom. This design permitted seeds to fall into the traps while keeping seed predators out. Traps were placed onto the sites in late August 1992 and sampled in October 1992 and 1993. Samples were dried and Douglas-fir and white spruce seeds separated from the other litter. Cutting tests were performed to identify sound seeds (those containing an embryo and thus potentially able to germinate). The number of sound seeds was represented

as a total value and as a percentage of seeds per hectare to use in further comparisons and calculations.

To determine the suitability of the microclimate for seedling growth under the partial shelterwood canopy, 10 rodent-proof exclosures were placed at the same locations as the seed fall traps on each block in October 1992. The exclosures were 0.37 m² in area, and were covered with 0.8-cm mesh hardware cloth which extended 5 cm into the ground on all sides. This exclosure also provided an indication of invertebrate seed predation. Ten stratified Douglas-fir seeds were scattered randomly on the seedbed within each exclosure (the litter layer was not removed) and seed locations were marked with toothpicks. The total number of seeds placed in the germination exclosures was 270 270 seeds/ha (10 seeds/0.37 m² x 10 000 m²/ha). Germination success was recorded in the following growing season (June 1993) as the percentage of seeds which germinated per ha.

Ten 0.37-m² seed predation quadrats were installed in the vicinity of the seed fall and seed germination exclosures. Ten Douglas-fir seeds were distributed in each of the quadrats in mid-fall, 1992. Seed locations were marked with wooden toothpicks placed approximately 0.5 cm from the seed. Quadrats were sampled every three weeks during the snow-free portion of 1993 to observe whether or not the seeds had been removed from the plots or eaten. Remains of eaten Douglas-fir seeds were removed at each sampling session and replaced with whole seeds. The predation rate was calculated as the rate of disappearance of the seeds in the quadrats per day. This method has been used successfully by Sullivan (1979a) to quantify predation rate and to identify seed predators. The predation rate per quadrat was extrapolated to the total number of seeds eaten or removed per hectare per

month. The seeds may have been eaten by seed-eating birds. This would have been apparent by the nature of the seed destruction.

Statistical analysis

Despite the correlation between population measurements taken on the same individuals when animals were captured repeatedly in successive trapping sessions, the analysis concentrated on the comparison of treatment means during certain time periods of the study. Thus, an analysis of variance (ANOVA) was performed on the means of various time periods to examine possible treatment effects. Pre-and-post-harvest 1991 sampling sessions were examined for biological significance but were not used in the statistical analysis because of the unbalanced sampling sessions between the blocks. The data collected in 1991 were not collected in simultaneous sampling sessions, and the number of sampling sessions varied between the replicate treatments. The use of these data to represent replicated treatments and to test these results for significance would have ensued in temporal replication. The statistical analysis was restricted to first and second year post-treatment (1992 and 1993) contrasts rather than pre-and-post treatment comparisons. An overall post-harvest analysis of some parameters incorporated the final trapping week of 1991, and all of the 1992 and 1993 trapping sessions. For the deer mouse population density analysis, MNA values were substituted for one biologically infeasible J-S value in the UBC replicate (Appendix A) and for three J-S values in the Gavin replicate (Appendix B) prior to analysis. One MNA value was substituted for an unrealistic J-S density estimate of red-backed voles in

the UBC replicate (Appendix C).

The balanced sampling design with three different harvesting intensities was analysed for treatment differences with an analysis of variance (ANOVA). An ANOVA was carried out on the mean values obtained from each grid for the first and second year post-treatment in order to detect significant differences between treatments, blocks, and time periods. Arcsine transformations were performed on proportional data to fit the binomial proportions to a normal distribution before proceeding with the analysis. When the results between the interactions were significant, multiple contrasts using Bonferroni t-tests of differences between means (Schlotzhauer and Littell 1987) were used to identify which of the means were significantly different from each other. Confidence intervals (95%) compared differences in percent trappability and percent survival of the various small mammal populations. Mean values and comparisons were based on three replicates for each treatment. For comparisons between treatments, the replicates were pooled and the cumulative numbers of the first and second years post-harvest were analysed. Statistical analysis was conducted using the SAS statistical analysis package (Schlotzhauer and Littell 1987). In all statistical comparisons the level of significance was set at $P=0.05$.

RESULTS

Deer mice and red-backed voles were the most abundant small mammals on the grids and the majority of the analysis concentrated on these two species. Two less common microtines, heather voles and meadow voles, were recorded on each of the nine grids but in low numbers (Table 2). Heather voles and meadow voles were combined for demographic analysis because of the low numbers of individuals captured and the difficulty of differentiating the species in the field. Very low numbers of yellow-pine chipmunks were captured on most of the grids (less than 6 individuals per grid), with one exception (50% removal treatment at the Gavin site) where 15 individuals were recorded. Two species of shrews, *Sorex cinereus* and *Sorex monticolus* were recorded on the majority of the grids. Shrews often did not survive capture, and were not marked if they did. Thus, the shrew data are presented in Table 2 but further population analysis was not possible.

TABLE 2. Total captures of individuals of less common microtines, chipmunks and shrews in the 1991, 1992, and 1993 trapping sessions.

SPECIES		UBC Ctrl	30%	50%	GAVIN Ctrl	30%	50%	SKELTON Ctrl	30%	50%
Microtines	Pre-trtmt '91	3	0	0	2	2	0	1	1	1
	Post-trtmt '91	0	5	0	0	1	1	18	5	3
	1992	6	12	3	1	1	0	2	1	5
	1993	1	10	3	0	7	3	1	1	0
	Total	**10**	**27**	**6**	**3**	**11**	**4**	**22**	**8**	**9**
Chipmunks	Pre-trtmt '91	0	0	0	1	2	3	0	0	0
	Post-trtmt '91	0	0	0	0	0	0	0	0	1
	1992	0	0	0	2	0	6	1	0	1
	1993	0	1	0	1	3	6	0	1	2
	Total	**0**	**1**	**0**	**4**	**5**	**15**	**1**	**1**	**4**
Shrews	Pre-trtmt '91	0	0	0	0	0	0	0	0	0
	Post-trtmt '91	0	0	0	1	4	2	10	9	8
	1992	0	4	4	10	26	3	6	3	6
	1993	2	0	1	7	11	2	2	3	17
	Total	**2**	**4**	**5**	**18**	**41**	**7**	**18**	**15**	**31**

Pre-harvest 1991: n=1 to 2
Post-harvest 1991: n=2 to 4
Summer 1992: n=8
Summer 1993: n=8
Total: n=17

Trappability

Trappability (based on the J-S density model) was calculated for deer mice, red-backed voles and the less common microtines for three different time periods: (1) overall trappability during the entire period of study, (2) trappability during each of summer 1992 and summer 1993. Overall trappability of deer mice and red-backed voles was generally high throughout the duration of the study (deer mice: $61.2 \pm 19.7\%$ to $90.6 \pm 9.3\%$; red-backed voles: $70.1 \pm 19.3\%$ to $90.7 \pm 7.2\%$), whereas less common microtines such as heather voles and meadow voles exhibited a far lower trappability overall ($10.2 \pm 0.1\%$ to $47.2 \pm 21.6\%$). Deer mouse and red-backed vole trappability overall seemed higher in the 30% basal area removal stands but this difference was not significantly different (overlapping 95% confidence limits). There was no difference in trappability of deer mice, red-backed voles or other microtines in relation to the intensity of basal area removal between the first and second year post-treatment (1992 and 1993).

TABLE 3. Jolly trappability estimates for deer mice, red-backed voles, and less common microtine populations. Values shown are the average percent trappability (number caught/Jolly-Seber population estimate) $\pm$ 95% confidence limits.

	Overall *	Summer '92	Summer '93
Deer mice			
UBC - Ctrl	61.2 (41.5 - 80.8)	60.2 (25.5 - 95.0)	72.5 (44.9-100.1)
30%	90.6 (81.4 - 100.0)	91.9 (82.0 - 101.8)	85.9 (63.2 - 108.6)
50%	82.9 (67.6 - 98.2)	100.0 (100.0 - 100.0)	71.9 (44.9 - 98.8)
Gavin - Ctrl	64.6 (50.3 - 78.9)	79.0 (61.4 - 96.6)	45.6 (23.8 - 67.4)
30%	78.2 (64.4 - 92.1)	88.4 (74.7 - 102.1)	71.0 (43.3 - 98.7)
50%	69.8 (58.4 - 81.2)	80.3 (65.3 - 95.2)	76.4 (65.2 - 87.5)
Skelton - Ctrl	76.5 (66.3 - 86.7)	72.8 (52.9 - 92.6)	86.5 (75.4 - 97.6)
30%	89.9 (84.2 - 95.5)	94.0 (89.6 - 98.4)	81.6 (68.4 - 94.8)
50%	88.4 (81.7 - 95.1)	92.9 (87.5 - 98.2)	85.8 (75.5 - 96.0)
Red-backed voles			
UBC - Ctrl	84.2 (70.6 - 97.7)	80.0 (47.8 - 112.2)	86.6 (70.0 - 103.2)
30%	82.8 (68.5 - 97.2)	81.9 (51.2 - 112.5)	87.4 (67.7 - 107.1)
50%	70.1 (50.8 - 89.4)	76.3 (53.3 - 99.2)	52.8 (10.1 - 95.4)
Gavin - Ctrl	90.7 (83.5 - 97.8)	91.6 (78.6 - 104.6)	94.1 (84.8 - 103.4)
30%	87.1 (79.0 - 95.2)	93.0 (82.0 - 104.0)	86.0 (69.6 - 102.4)
50%	76.8 (64.9 - 88.7)	78.6 (50.0 - 107.3)	67.9 (50.3 - 85.4)
Skelton - Ctrl	72.2 (54.8 - 89.5)	69.0 (30.8 - 107.2)	94.8 (82.3 - 107.2)
30%	86.0 (78.4 - 93.5)	94.8 (82.3 - 107.2)	76.0 (63.0 - 89.3)
50%	85.0 (75.8 - 94.2)	91.9 (78.9 - 104.9)	83.0 (65.8 - 100.2)
Other microtines			
UBC - Ctrl	31.6 (8.6 - 54.6)	50.0 (5.3 - 94.7)	12.5 (-17.1 - 42.1)
30%	47.2 (25.6 - 68.7)	54.1 (12.1 - 96.1)	32.9 (3.9 - 61.8)
50%	21.1 (0.9 - 41.2)	25.0 (-13.7 - 63.7)	25.0 (-13.7 - 63.7)
Gavin - Ctrl	14.3 (-2.0 - 30.6)	12.5 (-17.1 - 42.1)	0.0 (0.0 - 0.0)
30%	33.3 (11.3 - 55.3)	12.5 (-17.1 - 42.1)	37.5 (-5.8 - 80.8)
50%	10.2 (0.0 - 0.2)	0.0 (0.0 - 0.0)	13.1 (-0.2 - 0.4)
Skelton - Ctrl	36.9 (14.8 - 58.9)	37.5 (-5.8 - 80.8)	0.0 (0.0 - 0.0)
30%	42.9 (19.8 - 65.9)	50.0 (5.3 - 94.7)	12.5 (-17.1 - 42.1)
50%	38.1 (15.4 - 60.7)	62.5 (19.2 - 105.8)	0.0 (0.0 - 0.0)

* entire post-harvest period (September 1991 - October 1993)

Population density

The different intensities of basal area removal had no effect on deer mouse population levels (Fig. 1). Deer mouse population levels were not different between treatments and controls in immediate post-harvest (1991: $F_{2,2}=0.92$, $P=0.47$), one year post-harvest (1992: $F_{2,2}=1.12$, $P=0.41$), or two years after harvest (1993: $F_{2,2}=2.54$, $P=0.19$). A slight decrease in density between pre-treatment and post-treatment 1991 was observed in the unlogged controls as well as in the treated stands (10% to 50% lower density post-harvest) in two of the three replicates (Table 4). However, there were no significant differences in population trends or density levels between the first or second year post-harvest ($F_{1,2}=0.00$, $P=1.00$). Deer mouse populations appeared to increase on two of three replicates in 1992, but the differences were not significant ($F_{2,2}=0.08$, $P=0.93$). The increase in density in the 50% treatment (Gavin replicate) in 1992 seemed to be greater than that of the other treatments or controls but this trend was not repeated on other replicates or in the following trapping year. There were no detectable differences between deer mouse population densities in any of the controls or treatments by the second year post-harvest. Mean numbers of deer mice ranged from 5.6 - 12.8 animals/ha in the overall post-harvest period.

Thirty and fifty percent basal area removal intensities did not negatively affect the overall red-backed vole populations (Fig. 2). A substantial increase in red-backed voles/ha was recorded immediately post-harvest 1991 in the controls and treatments (Table 4). Mean number of red-backed voles post-harvest 1991 escalated to 40.9 animals/ha in the controls, 61.3 animals/ha in the 30% removals, and 62.2 animals/ha in the 50% removals.

TABLE 4. Average Jolly-Seber population density estimates of deer mice and red-backed voles. Values shown are mean J-S estimates for the time periods indicated. Overall time period is the entire post-harvest period of study (September 1991 - October 1993). The number of sampling sessions (n) varied between blocks pre- and post-harvest 1991.

	Pre-harvest 1991 (n=1 to 2)	Post-harvest 1991 (n=2 to 4)	Summer 1992 (n=8)	Summer 1993 (n=8)	Overall (n=17)
Deer mice					
UBC - Ctrl	15.0	2.0	7.1	5.1	5.6
30%	5.0	2.0	10.6	4.9	7.1
50%	5.0	2.3	11.6	10.4	10.0
Gavin - Ctrl	15.5	7.2	9.6	9.4	9.1
30%	12.5	3.7	7.9	8.5	7.5
50%	18.7	8.9	14.0	12.3	12.5
Skelton - Ctrl	3.0	11.0	10.0	13.1	11.4
30%	5.0	12.1	11.5	14.6	12.8
50%	3.0	7.6	9.4	13.6	10.7
Red-backed voles					
UBC - Ctrl	26.0	36.0	4.6	8.8	9.9
30%	31.0	48.1	6.6	10.2	12.8
50%	22.0	48.5	5.7	5.2	10.2
Gavin - Ctrl	10.5	47.0	7.0	9.4	14.4
30%	26.8	70.4	8.0	14.8	20.7
50%	14.5	76.4	8.5	11.8	20.6
Skelton - Ctrl	9.0	39.7	4.3	2.4	10.6
30%	10.0	65.4	9.0	10.4	20.8
50%	30.9	61.6	7.9	5.9	17.8

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FIGURE 1. Jolly-Seber estimate of deer mouse population size on unlogged controls, 30% and 50% basal area removal stands. Vertical solid line indicates the time of harvesting.
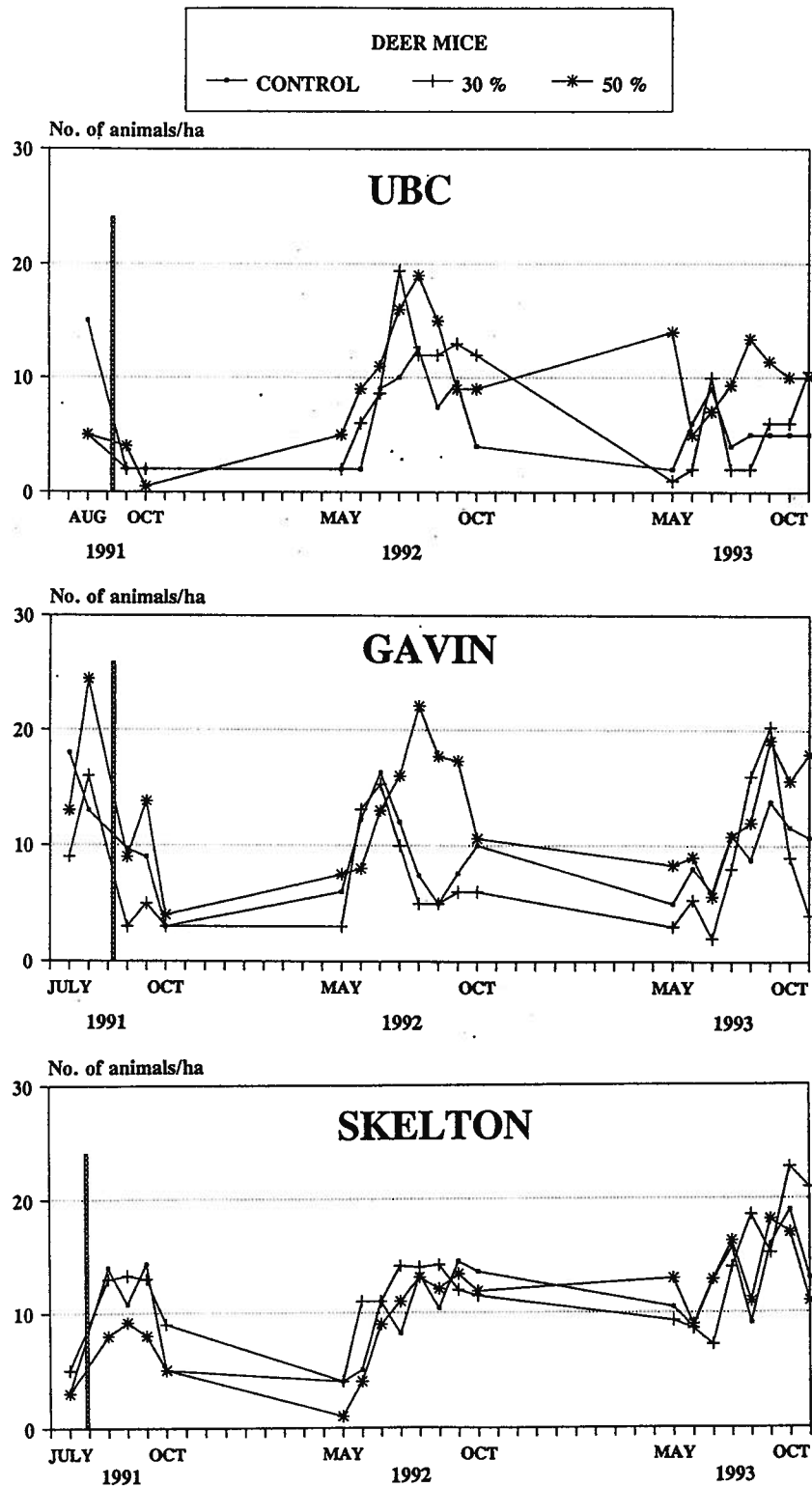
FIGURE 2. Jolly-Seber estimate of red-backed vole population size on unlogged controls, 30% and 50% basal area removal stands. Vertical solid line indicates the time of shelterwood harvesting.
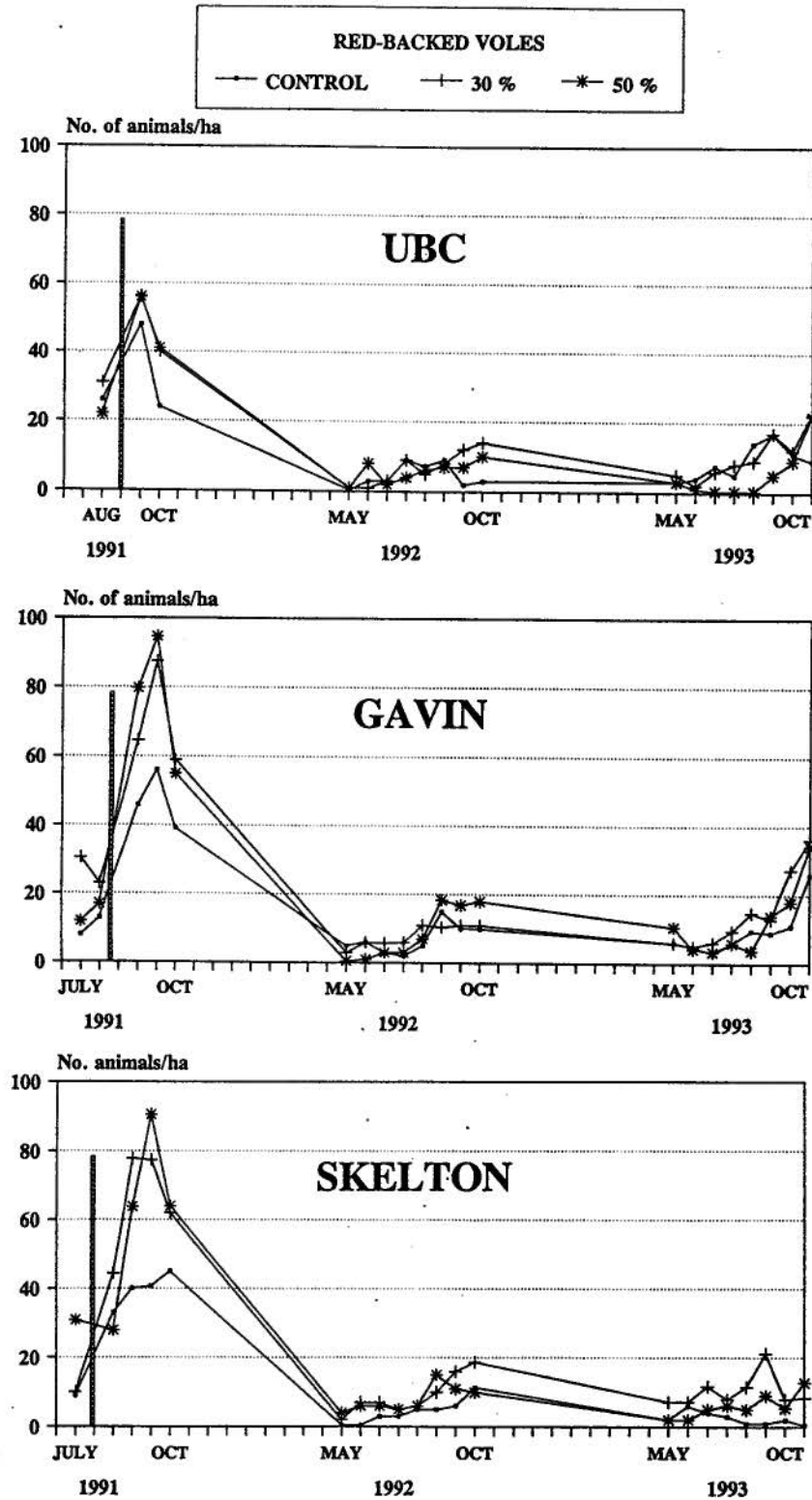
Post-harvest 1991 red-backed vole density values were 7.3-fold to 12.6-fold greater than 1992 population levels. Although the increases in density in 1991 (post-harvest) were notable on the controls as well as the treatments, the mean number of animals/ha was 1.5 times greater on the treatment areas than the controls. An analysis of variance between treatments for one trapping session (the final trapping week in 1991 was balanced in all three replicates) indicated that the treatment population densities differed significantly from the control populations ($F_{2,2}=108.30$, $P=0.00$) and each of the replicate blocks was significantly different from each other ($F_{2,2}=137.82$, $P=0.00$). The increases observed immediately post-harvest were temporary, and by 1992, red-backed vole populations had declined in the controls and treatments and had reached similar densities (4.6 to 9.0 animals/ha). There were no significant differences between treatments (1992: $F_{2,2}=5.35$, $P=0.07$) or between the replicate blocks (1993: $F_{2,2}=3.72$, $P=0.12$) within the first year post-harvest.

The population trend of red-backed voles exhibited in 1993 was similar to that of 1992: treatment populations remained at control levels. There was no difference between treatments ($F_{2,2}=4.74$, $P=0.09$) or between the replicate blocks ($F_{2,2}=5.88$, $P=0.06$) two years post-harvest. A comparison of pooled treatments between 1992 and 1993 detected no significant differences in red-backed vole density between the two post-harvest treatment years ($F_{1,2}=1.77$, $P=0.31$). Sampling years reflected seasonal fluctuations in population levels (lower after the winter months and higher in the fall at the end of the breeding season), but no significant treatment differences during the overall period of study.

Animal survival

Jolly-Seber survival of deer mice and red-backed voles was estimated for the winter

and summer of the first and second year post-treatment as well as for the entire post-harvest

period of study (Table 5). Comparisons of the means did not result in any survival values

greater than 1.00, thus it was not necessary to calculate minimum survival rates in addition

to the Jolly survival rates. Overall survival of deer mice post-treatment was not significantly

different between unlogged controls and treatments (controls mean monthly survival rate:

0.84; 30% removal: 0.74; 50% removal: 0.80). Mean deer mouse survival appeared to

decline between first and second year post-harvest, but no significant treatment effect was

detected (based on overlapping confidence limits). In both trapping years, there was no

significant difference in mean deer mouse over-winter survival. Mean survival rates in the

second year post-harvest (summer 1993) were significantly lower than mean over-winter

survival (winter 1992-93) estimates on treatments and controls on one of the three replicates

blocks (Skelton). There was no significant difference between deer mouse and red-backed

vole overall survival on the treatment and control stands. No treatment effect was detected

between mean over-winter survival and summer survival between the two post-harvest

trapping years (Table 5).

TABLE 5. Mean monthly Jolly survival of deer mice and red-backed voles. Values represent mean estimates $\pm$ 95% confidence limits of different sampling periods.

	Winter 1991	Summer 1992	Winter 1992	Summer 1993	Overall *
Deer mice					
UBC - Ctrl	1.00	0.72	0.83	0.68	0.82
	(0.75 - 1.25)	(0.32 - 1.12)	(0.63 - 1.02)	(-0.89 - 2.26)	(0.45 - 1.19)
30%	0.84	0.76	0.65	0.34	0.64
	(0.58 - 1.10)	(0.6 - 0.92)	(-0.26 - 1.58)	(-0.81 - 1.48)	(0.16 - 1.13)
50%	1.00	0.75	0.92	0.49	0.81
	(0.75 - 1.25)	(0.68 - 0.83)	(0.85 - 1.00)	(-1.07 - 2.04)	(0.34 - 1.28)
Gavin - Ctrl	1.04	0.63	0.91	0.75	0.85
	(0.84 - 1.23)	(0.55 - 0.7)	(0.83 - 0.99)	(-1.13 - 2.63)	(0.46 - 1.23)
30%	1.00	0.57	1.00	0.51	0.73
	(0.75 - 1.25)	(0.4 - 0.74)	(0.75 - 1.25)	(-0.33 - 1.36)	(0.50 - 0.97)
50%	1.02	0.62	0.90	0.55	0.79
	(0.79 - 1.24)	(0.5 - 0.74)	(0.81 - 0.99)	(0.38 - 0.73)	(0.71 - 0.87)
Skelton - Ctrl	0.89	0.81	0.94	0.67	0.84
	(0.33 - 1.45)	(0.69 - 0.93)	(0.89 - 0.99)	(0.53 - 0.81)	(0.67 - 1.01)
30%	0.87	0.73	0.96	0.78	0.84
	(0.76 - 0.97)	(0.56 - 0.89)	(0.91 - 1.00)	(0.66 - 0.89)	(0.79 - 0.90)
50%	0.81	0.80	0.92	0.61	0.80
	(-0.21 - 1.84)	(0.67 - 0.93)	(0.85 - 0.99)	(0.48 - 0.74)	(0.48 - 1.12)
Red-backed voles					
UBC - Ctrl	0.61	0.39	0.77	0.62	0.59
	(0.61 - 0.61)	(-0.23 - 1.00)	(-0.68 - 2.21)	(0.43 - 0.82)	(0.21 - 0.98)
30%	0.57	0.68	0.77	0.37	0.60
	(-9.44 - 1.58)	(0.36 - 1.00)	(0.64 - 0.91)	(0.16 - 0.57)	(-2.68 - 3.88)
50%	0.57	0.75	0.73	0.46	0.62
	(0.57 - 0.57)	(0.66 - 0.84)	(0.54 - 0.91)	(-0.81 - 1.73)	(0.31 - 0.94)
Gavin - Ctrl	0.63	0.47	0.73	0.51	0.59
	(-5.25 - 0.65)	(0.27 - 0.67)	(0.54 - 0.91)	(0.31 - 0.71)	(-1.15 - 2.34)
30%	0.59	0.51	0.79	0.72	0.65
	(0.59 - 0.59)	(0.36 - 0.67)	(0.65 - 0.93)	(0.56 - 0.89)	(0.59 - 0.71)
50%	0.55	0.76	0.81	0.57	0.66
	(0.55 - 0.55)	(0.42 - 1.10)	(0.67 - 0.95)	(0.37 - 0.77)	(0.58 - 0.75)
Skelton - Ctrl	0.56	0.64	0.81	0.36	0.59
	(0.56 - 0.56)	(0.22 - 1.07)	(0.74 - 0.88)	(-0.78 - 1.50)	(0.24 - 0.94)
30%	0.64	0.57	0.85	0.69	0.69
	(0.64 - 0.64)	(0.35 - 0.78)	(0.81 - 0.88)	(0.56 - 0.82)	(0.63 - 0.75)
50%	0.59	0.59	0.66	0.62	0.61
	(0.59 - 0.59)	(0.42 - 0.76)	(0.41 - 0.91)	(0.41 - 0.82)	(0.53 - 0.70)

* entire post-harvest period (September 1991 - October 1993)

Recruitment

Recruitment of deer mice was not affected by the intensity of the shelterwood treatments in the first (1992) or second (1993) year post-disturbance. Cumulative post-harvest recruitment of individual deer mice appeared to be greater in the highest intensity of basal area removal and lowest in the unlogged controls (Fig. 3). However, recruitment in the various intensities of basal area removal was not significantly different in the first and second year after disturbance (treatments 1992: $F_{2,2}=1.44$, $P=0.34$; 1993: $F_{2,2}=3.50$, $P=0.13$). Recruitment of deer mice was noticeably lower prior to treatment and immediately post-treatment 1991 (Fig. 4). Differences between the means of the replicate blocks were not significant within trapping years (treatments 1992: $F_{2,2}=2.66$, $P=0.18$; 1993: $F_{2,2}=2.49$, $P=0.20$).

There were no significant differences in recruitment of red-backed voles between the different intensities of shelterwood treatments in the first or second year after logging (1992: $F_{2,2}=0.39$, $P=0.70$; 1993: $F_{2,2}=2.27$, $P=0.22$) (Fig. 4). The number of red-backed voles recruited into the sample populations exhibited an opposite pattern to deer mouse recruitment immediately post-harvest: mean recruitment (cumulative) increased substantially on controls and treatments in the months immediately post-harvest (1991) and increased with intensity of disturbance on all three replicates (Table 6). Cumulative recruitment per sampling year appeared to return to pre-treatment levels by the first year post-harvest and began to increase marginally, on controls and treatments, by the second year post-harvest.

FIGURE 3. Cumulative post-harvest (1991-1993) number of deer mouse and red-backed vole recruits, as observed over three replicates: unlogged controls, 30% basal area removal shelterwood treatments, and 50% basal area removal shelterwood treatments.

DEER MICE

■ Control   ▨ 30% removal   ▢ 50% removal

Number of recruits

RED-BACKED VOLES

■ Control   ▨ 30% removal   ▢ 50% removal
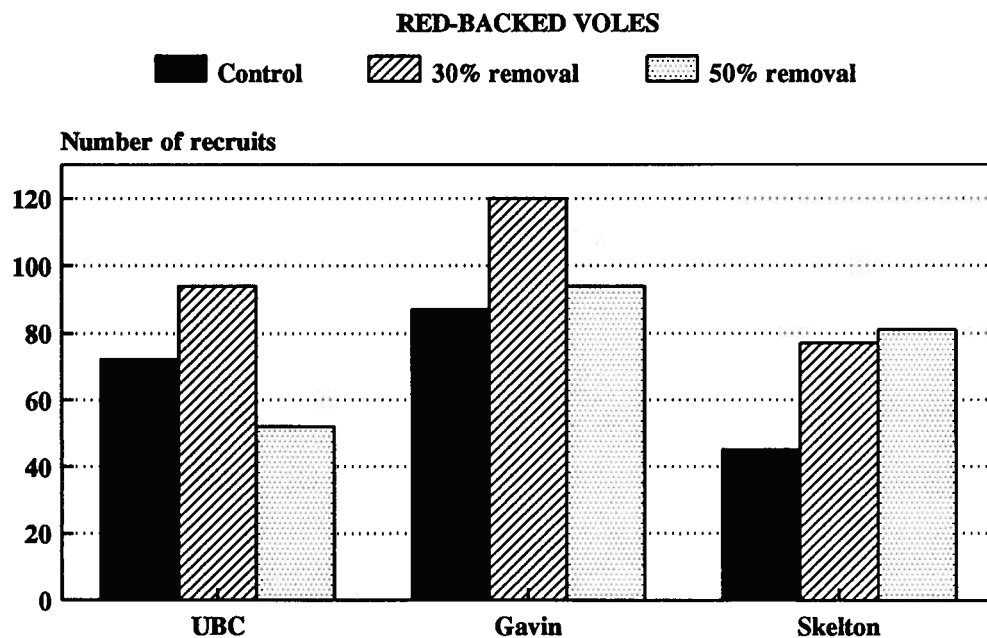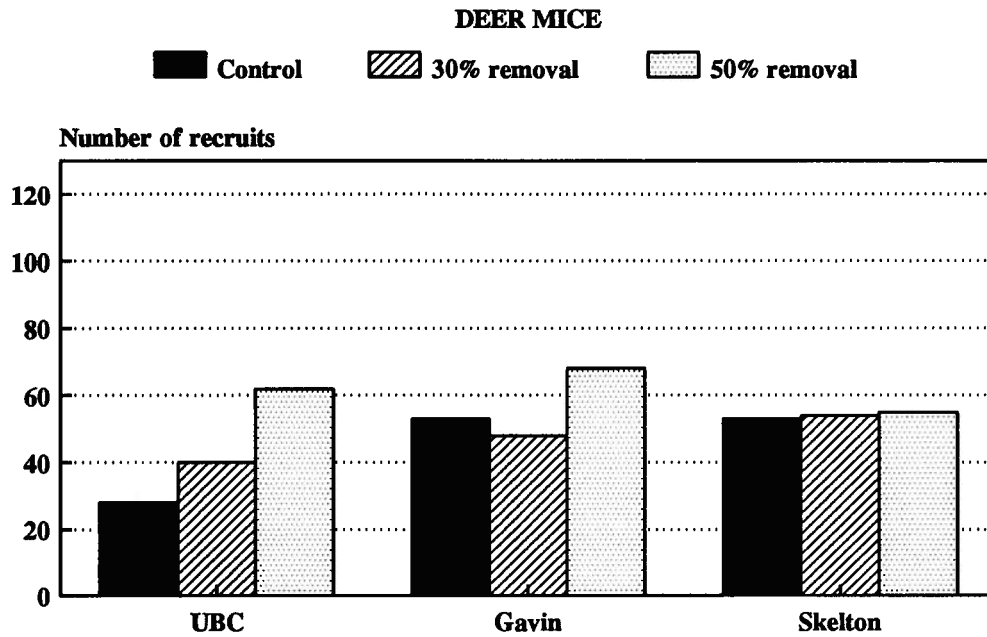
Number of recruits

FIGURE 4. Cumulative number of deer mouse and red-backed vole recruits throughout various periods of study: pre-treatment 1991, post-treatment 1991, summer 1992, summer 1993. Values represent means of pooled treatments and controls.

DEER MICE

Controls 30% removals 50% removals

RED-BACKED VOLES

Controls 30% removals 50% removals
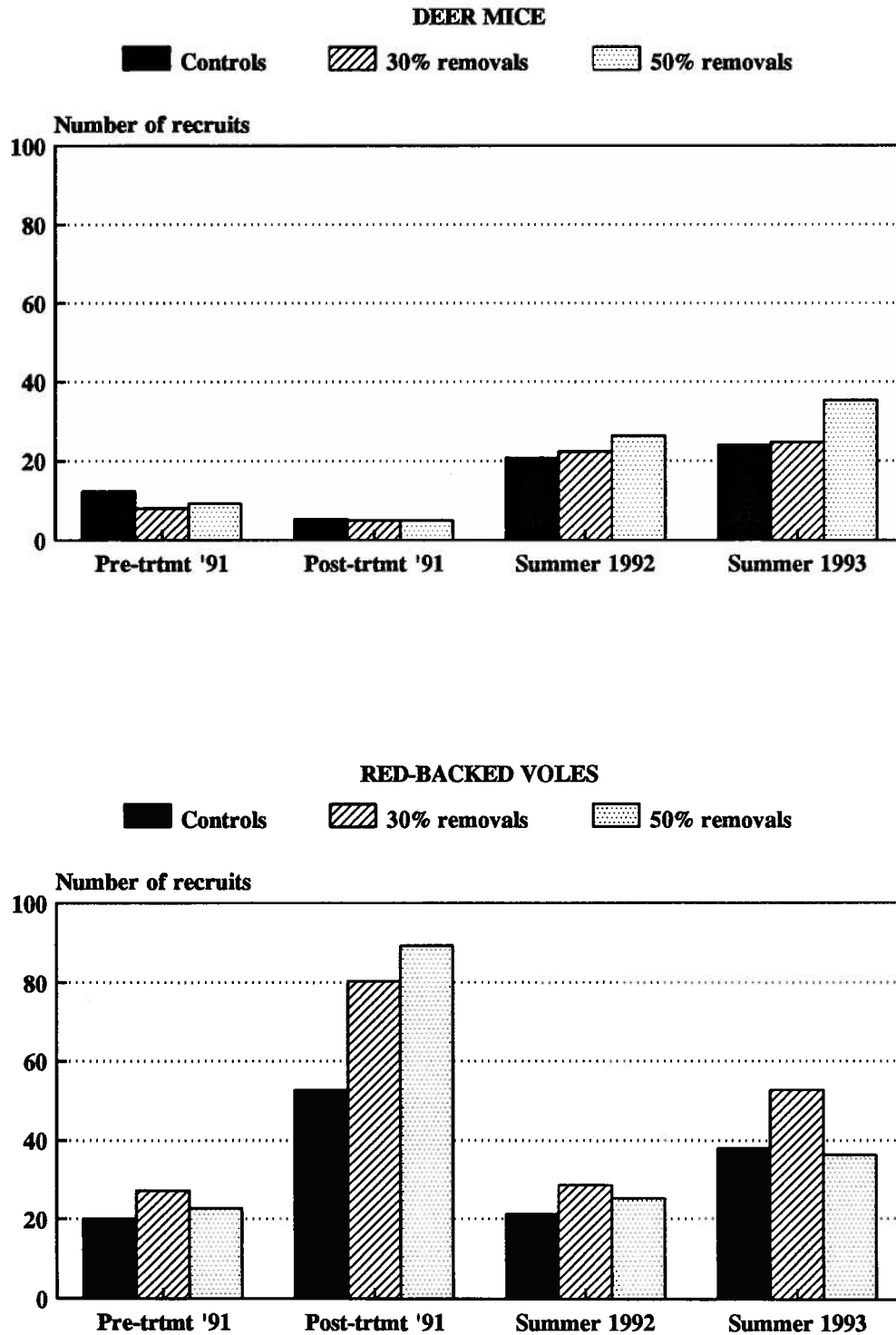
TABLE 6. Cumulative number of deer mouse and red-backed vole recruits per ha during pre-treatment and post-treatment periods of study (1991-1993).

	UBC			GAVIN			SKELTON		
	Ctrl	30%	50%	Ctrl	30%	50%	Ctrl	30%	50%
Deer mice									
Pre-trtmt 1991	15	5	6	19	13	19	3	6	3
Post-trtmt 1991	0	0	1	3	3	3	13	12	11
Summer 1992	15	23	25	26	23	34	21	21	20
Summer 1993	13	17	37	27	25	34	32	32	35
Overall	28	40	62	53	48	68	53	54	55
Red-backed voles									
Pre-trtmt 1991	35	35	26	19	35	26	6	12	16
Post-trtmt 1991	34	59	59	59	82	100	65	100	109
Summer 1992	20	24	17	28	32	31	16	30	28
Summer 1993	42	52	23	57	71	51	15	35	35
Overall	72	94	52	87	120	94	45	77	81

Number of sampling sessions per site:
Pre-treatment 1991: UBC=2, Gavin=3, Skelton=2
Post-treatment 1991: UBC=2, Gavin=3, Skelton=4
Summer 1992: all sites = 8
Summer 1993: all sites = 9
Overall post-harvest = 18

Reproduction

Mean adult body mass at which 50% or more of the individuals captured were at sexual maturity was averaged over all grids for each sex and species (Table 7). Males of both species were sexually mature at a lower body mass than females (deer mice: 16.8 g for males vs 20.2 g for females; red-backed voles: 20.8 g for males vs 22.2 g for females). Deer mice reached sexual maturity at a lower body mass than red-backed voles.

There was little difference in the length of the deer mouse or red-backed vole breeding seasons between treatments within trapping years (Table 8). However, both species showed a considerable increase in breeding season length in the second year post-harvest (1993) versus the first year post-harvest (1992). For the majority of the grids, the red-backed vole breeding season seemed marginally longer than that of the deer mouse: from mid- to late-May to the end of September (1992) or October (1993) for red-backed voles whereas deer mice had, at times, finished breeding as early as the beginning of July (1992) or on occasion as late as the end of October (1993). In 1992, the length of the deer mouse breeding season ranged from 6.0 to 15.0 weeks (average 11.0); in 1993 the breeding season was 12.0 to 24.0 (average 20.3) weeks long. Red-backed voles were in breeding condition from 9.0 to 21.0 weeks (average 14.3) in 1992 and for 18.0 to 24.0 (average 21.3) weeks in 1993. Thirty and 50% shelterwood removals did not have a significant effect on the length of the breeding season in either of the trapping years for red-backed voles or deer mice (ANOVA, treatment, deer mice, 1992: $F_{2,2}=0.43$, $P=0.68$; 1993: $F_{2,2}=0.54$, $P=0.62$; red-backed voles, 1992: $F_{2,2}=0.34$, $P=0.73$; 1993: $F_{2,2}=1.00$, $P=0.44$).

TABLE 7. Mean body mass (in grams) at sexual maturity for male and female deer mice and red-backed voles. Averages were taken from each of the nine grids and are based on the entire period of study.

	Male	Female
Deer mouse	16.8	20.2
Red-backed vole	20.8	22.2

TABLE 8. Length of breeding season in weeks. The start of the breeding season is the time of capture of the first scrotal male or lactating female. The end of the breeding is the week in which the last lactating female was recorded.

	Deer mice		Red-backed voles	
	1992	1993	1992	1993
UBC				
Control	6	12	15	18
30% removal	15	18	18	21
50% removal	9	21	15	24
Gavin				
Control	12	24	15	24
30% removal	9	18	9	24
50% removal	15	21	12	24
Skelton				
Control	12	21	9	18
30% removal	15	24	21	21
50% removal	6	24	15	18
	1992	1993	1992	1993
Pooled replicates				
Controls	10	19	13	20
30% removals	13	20	16	22
50% removals	10	22	14	22

The overall percentage of male deer mice in breeding condition ranged from 59.0% to 92.6% and the percentage of females in breeding condition ranged from 66.7% to 100.0% (Table 9). The percentage of adult male red-backed voles in breeding condition ranged from 50.0% to 90.0% (Table 10) and females ranged from 44.4% to 87.3%. The low percentages of adult red-backed voles breeding may have been due to the high influx of animals immediately after logging (Table 10).

TABLE 9. Numbers and proportions of adult deer mice in breeding condition on three replicates throughout the study period (n=number of individuals sampled).

	CONTROLS				30% REMOVALS				50% REMOVALS			
	M*	n	F*	n	M	n	F	n	M	n	F	n
UBC												
Pre-trtmt '91	0.00	2	0.00	3	0.00	0	0.00	0	0.00	0	1.00	1
Post-trtmt '91	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
Summer 1992	0.75	8	1.00	7	0.60	5	1.00	8	1.00	6	1.00	8
Summer 1993	0.89	9	0.71	7	1.00	4	1.00	6	0.90	21	0.91	11
Overall	0.82	17	0.86	14	0.78	9	1.00	14	0.93	27	0.95	19
GAVIN												
Pre-trtmt '91	0.43	7	0.71	7	0.00	0	0.67	6	0.67	3	0.57	7
Post-trtmt '91	0.00	6	0.00	3	0.00	1	0.00	0	0.00	0	0.00	0
Summer 1992	0.89	9	1.00	1	1.00	6	0.88	8	1.00	2	0.86	22
Summer 1993	1.00	15	1.00	5	0.86	7	1.00	8	0.86	14	0.81	16
Overall	0.77	30	0.67	9	0.86	14	0.94	16	0.88	16	0.84	38
SKELTON												
Pre-trtmt '91	0.25	4	0.00	0	1.00	1	0.50	2	1.00	2	0.00	0
Post-trtmt '91	0.00	3	0.00	1	0.00	0	0.00	0	0.00	1	0.00	2
Summer 1992	0.64	11	1.00	7	1.00	1	0.70	10	0.54	13	1.00	2
Summer 1993	0.64	25	1.00	15	0.88	25	0.74	31	0.82	22	0.88	17
Overall	0.59	39	0.96	23	0.88	26	0.73	41	0.69	36	0.81	21

*M = males F = females

TABLE 10. Numbers and proportions of adult red-backed voles in breeding condition on three replicates throughout the study period (n=number of individuals in the sample).

	CONTROLS				30% REMOVALS				50% REMOVALS			
	M*	n	F*	n	M	n	F	n	M	n	F	n
UBC												
Pre-trtmt '91	1.00	6	0.67	12	0.75	4	0.79	19	1.00	4	0.58	12
Post-trtmt '91	0.00	1	0.00	6	0.00	3	0.29	7	0.00	2	0.18	11
Summer 1992	1.00	5	0.92	12	1.00	4	1.00	7	1.00	1	0.73	15
Summer 1993	0.93	14	0.94	18	0.87	15	0.80	25	1.00	3	0.90	10
Overall	0.90	20	0.78	36	0.77	22	0.74	39	0.67	6	0.61	36
GAVIN												
Pre-trtmt '91	0.63	8	0.75	8	0.46	13	0.53	15	0.56	9	0.63	8
Post-trtmt '91	0.00	5	0.15	13	0.67	3	0.18	11	0.50	4	0.17	12
Summer 1992	1.00	5	0.85	13	0.91	11	0.71	14	1.00	6	1.00	8
Summer 1993	0.94	16	0.78	27	0.86	21	0.82	28	0.85	13	0.75	20
Overall	0.77	26	0.64	53	0.86	35	0.66	53	0.83	23	0.63	40
SKELTON												
Pre-trtmt '91	0.50	4	0.00	0	0.89	9	0.80	5	0.56	9	0.25	4
Post-trtmt '91	0.00	7	0.18	17	0.08	12	0.44	9	0.20	10	0.35	20
Summer 1992	1.00	3	0.75	4	0.86	14	0.92	12	0.83	12	0.94	16
Summer 1993	1.00	4	1.00	6	0.94	17	0.97	34	0.88	8	0.88	17
Overall	0.50	14	0.44	27	0.67	43	0.87	55	0.63	30	0.70	53

M* = males   F* = females

There were no significant treatment effects on the percentage of adult deer mice or

red-backed voles breeding within the 1992 or 1993 trapping years (Table 11). The majority

of the individual red-backed voles captured were juvenile and were never recorded in

breeding condition during the course of this study. Eighty-five percent of the individual male

red-backed voles and 78% of the females captured were juvenile, thus the percentage of

adults in breeding condition reflected only a small proportion of the red-backed vole

populations on the study sites. The majority of the male deer mice captured were adults

(68.9%), but the female deer mice sampled on all treatments were largely juvenile (63.0%).

TABLE 11. Treatment effects on the percentage of breeding adults in the sample populations. Anova F and P values are shown for treatment effects within trapping years. Treatments were pooled across the replicate blocks. Degrees of freedom=2. $P=0.05$.

Species	F statistic	P value
P. maniculatus		
1992 males	0.54	0.62
females	1.80	0.28
1993 males	0.29	0.76
females	0.37	0.71
C. gapperi		
1992 males	1.80	0.28
females	0.22	0.81
1993 males	0.67	0.56
females	1.49	0.33

Body mass

There were no significant treatment differences in the mean body mass of adult, male deer mice within the first and second years post-harvest (ANOVA treatment 1992: $F_{2,2}=1.28$, $P=0.37$; 1993: $F_{2,2}=0.57$, $P=0.61$). The body mass of adult deer mice after the harvesting treatments were uniform across the treatments and ranged from 19.8 to 20.4 g (Table 12). Adult red-backed voles seemed to be heavier than deer mice: male body mass of red-backed voles ranged from 22.5 g to 25.0 g (Table 13). There was no significant treatment difference observed in the mean adult body mass of red-backed voles within the two post-harvest sampling years (ANOVA treatment 1992: $F_{2,2}=2.06$, $P=0.24$; 1993: $F_{2,2}=2.30$, $P=0.22$).

Diversity

Values for the calculation of Shannon-Wiener and Simpson's measures of heterogeneity were obtained from absolute numbers of individuals in the various time periods. Over the course of the study (1991-1993) shrews were observed on each of the nine grids (Table 2) but they were not marked for identification. Hence, it was not possible to determine if shrews were new individuals or repeated captures of the same individuals. Therefore, shrews could not be included in the diversity measurements or comparisons. Suffice it to say they were present in low numbers on each of the grids. The concordance of S-W and Simpson's indices in the patterns of diversity throughout the study periods is illustrated in Figure 5.

TABLE 12. Mean body mass (in grams) of male adult deer mice in treatment and control stands throughout the study period (n=number of individuals recorded during the separate time periods).

	CONTROLS			30% REMOVALS			50% REMOVALS		
	n	Mean	S.E.	n	Mean	S.E.	n	Mean	S.E.
UBC									
pre-trtmt '91	5	20.4	1.5	2	19.5	0.5	2	18.0	1.0
post-trtmt '91	0	0.0	0.0	0	0.0	0.0	1	18.0	0.0
summer 1992	5	21.8	0.6	9	19.2	0.7	10	17.9	0.5
summer 1993	9	19.3	0.7	7	21.3	2.1	18	21.6	0.6
overall	14	20.2	0.6	16	20.1	1.0	28	20.3	0.5
GAVIN									
pre-trtmt '91	9	20.4	0.7	1	17.0	0.0	3	21.0	1.2
post-trtmt '91	1	23.0	0.0	2	21.5	2.5	4	20.0	0.4
summer 1992	9	20.8	1.0	11	20.3	0.8	8	18.8	0.5
summer 1993	11	20.9	0.7	7	20.9	1.3	14	19.6	0.6
overall	20	20.9	0.6	18	20.5	0.7	22	19.3	0.4
SKELTON									
pre-trtmt '91	3	22.3	0.3	2	21.5	1.5	3	23.3	2.6
post-trtmt '91	7	19.3	0.6	4	17.5	0.3	5	19.0	0.8
summer 1992	9	18.9	0.7	4	19.0	1.2	7	19.9	0.8
summer 1993	25	20.1	0.4	16	20.6	0.6	25	20.0	0.6
overall	34	20.1	0.4	21	20.1	0.5	32	19.9	0.5

TABLE 13. Mean body mass (in grams) of male adult red-backed voles in treatment and control stands throughout the period of study (n=number of individuals recorded during the separate time periods).

	CONTROLS			30% REMOVALS			50% REMOVALS		
	n	Mean	S.E.	n	Mean	S.E.	n	Mean	S.E.
UBC									
pre-trtmt '91	5	21.8	0.6	3	24.3	1.5	3	24.0	1.7
post-trtmt '91	1	24.0	0.0	2	21.5	0.5	2	19.5	3.5
summer 1992	2	23.0	2.0	2	24.0	0.0	1	22.0	0.0
summer 1993	6	24.7	0.9	10	25.2	0.8	2	24.0	0.0
overall	9	24.2	0.7	12	25.0	0.7	4	21.5	1.9
GAVIN									
pre-trtmt '91	5	25.4	1.3	6	25.8	1.2	6	24.2	0.9
post-trtmt '91	4	21.5	0.5	1	25.0	0.0	3	22.3	0.7
summer 1992	3	24.3	0.3	6	24.0	0.9	2	22.5	1.5
summer 1993	10	24.2	0.9	10	23.3	0.8	5	22.2	0.6
overall	13	24.2	0.7	16	23.6	0.6	7	22.3	0.5
SKELTON									
pre-trtmt '91	2	26.0	1.0	5	25.0	1.3	6	24.5	0.8
post-trtmt '91	4	22.5	0.7	9	22.7	0.7	5	21.8	0.4
summer 1992	2	22.5	1.5	5	24.4	1.0	4	23.8	0.6
summer 1993	4	29.8	6.8	6	24.5	1.2	4	23.8	0.9
overall	7	26.4	4.0	11	24.5	0.8	8	23.8	0.5

Species richness varied between 1 and 4 species throughout the study years (Table 15). Diversity and evenness was lowest on all grids immediately following the logging disturbance in 1991 (post-treatment 1991), presumably due to the high proportion of red-backed voles present at this time (Table 14). There was no significant difference in diversity due to the logging disturbance detected in the first sampling year post-harvest (ANOVA, Simpson's index, treatment 1992: $F_{2,2}=2.06$, $P=0.24$; S-W index, treatment 1992: $F_{2,2}=0.34$, $P=0.73$). In the second sampling year post-harvest, Simpson's index indicated no treatment differences (ANOVA, Simpson's index, treatment 1993: $F_{2,2}=6.54$, $P=0.05$), whereas the S-W index was significantly greater on the logged treatments (30% and 50% removals had equal diversity in 1993) than on the unlogged controls (ANOVA, S-W index, treatment 1993: $F_{2,2}=7.92$, $P=0.04$) (Fig. 5). S-W and Simpson's evenness seemed highest on all grids the first year after disturbance (summer 1992). Despite the initial decline in evenness immediately post-harvest (fall of 1991, when red-backed voles greatly outnumbered the other species recorded in the traps), no overall differences in species evenness were found to be attributable to the shelterwood treatments by the first and second year post-harvest.

FIGURE 5. Simpson's and Shannon-Wiener indices of small mammal species diversity for different time periods throughout the study. Values represent means of pooled treatments and controls.
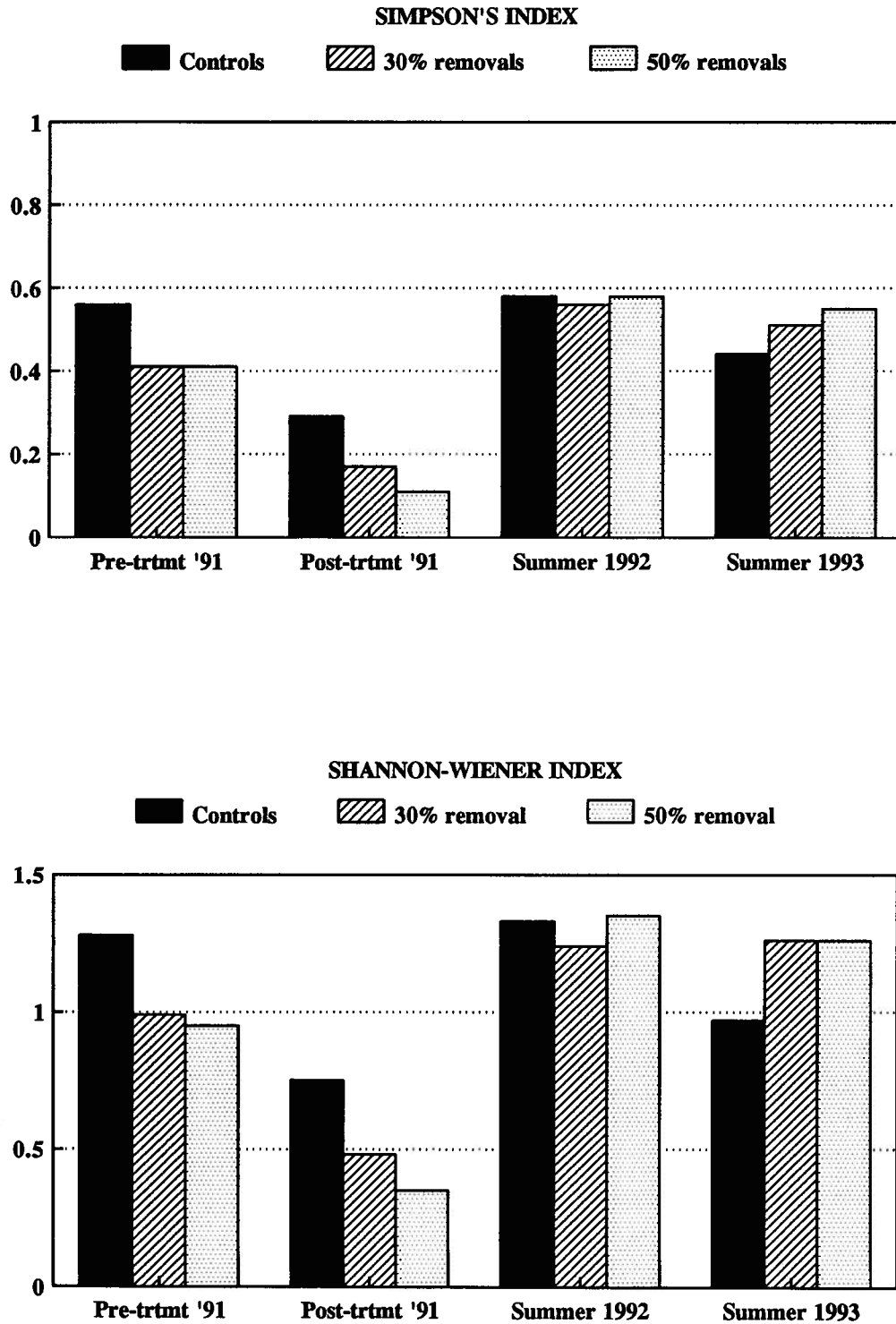

SIMPSON'S INDEX

SHANNON-WIENER INDEX

TABLE 14. Mean Simpson's and Shannon-Wiener's indices of diversity and evenness for various time periods over three consecutive trapping years.

| PERIODS	UBC Control	30%	50%	GAVIN Control	30%	50%	SKELTON Control	30%	50%
Simpson's index									
Pre-treatment	0.50	0.22	0.32	0.58	0.49	0.56	0.60	0.53	0.35
Post-treatment	0.29	0.15	0.03	0.09	0.09	0.08	0.49	0.26	0.22
Summer 1992	0.62	0.65	0.56	0.54	0.52	0.58	0.58	0.51	0.60
Summer 1993	0.39	0.52	0.53	0.46	0.48	0.58	0.47	0.54	0.53
Overall	0.48	0.58	0.55	0.50	0.48	0.57	0.64	0.54	0.56
Shannon-Wiener									
Pre-treatment	1.16	0.54	0.70	1.37	1.25	1.26	1.30	1.17	0.88
Post-treatment	0.75	0.40	0.12	0.28	0.31	0.27	1.22	0.73	0.66
Summer 1992	1.44	1.53	1.26	1.19	1.10	1.33	1.37	1.10	1.45
Summer 1993	0.90	1.33	1.19	0.99	1.27	1.42	1.03	1.19	1.16
Overall	1.14	1.43	1.23	1.14	1.20	1.40	1.55	1.27	1.38
Simpson's Evenness									
Pre-treatment	0.73	0.44	0.61	0.76	0.64	0.82	0.82	0.75	0.50
Post-treatment	0.46	0.29	0.07	0.18	0.13	0.11	0.73	0.39	0.29
Summer 1992	0.91	0.96	0.82	0.80	0.76	0.86	0.75	0.77	0.78
Summer 1993	0.57	0.69	0.78	0.67	0.64	0.76	0.69	0.70	0.79
Overall	0.71	0.77	0.81	0.67	0.64	0.76	0.85	0.72	0.74
Shannon-Wiener Evenness									
Pre-treatment	0.73	0.54	0.70	0.69	0.62	0.79	0.74	0.75	0.56
Post-treatment	0.53	0.40	0.12	0.28	0.20	0.17	0.77	0.46	0.33
Summer 1992	0.59	0.96	0.80	0.75	0.69	0.84	0.68	0.69	0.72
Summer 1993	0.57	0.67	0.75	0.62	0.63	0.71	0.65	0.59	0.73
Overall	0.72	0.72	0.78	0.57	0.60	0.70	0.77	0.64	0.69

TABLE 15. Species richness, and mean Simpson's and Shannon-Wiener diversity and evenness values pooled for three replicates for the overall study period.

	Pre-treatment 1991	Post-treatment 1991	Summer 1992	Summer 1993	Overall
Species richness					
Controls	3 to 4	1 to 3	3 to 4	3	3 to 4
30% removal	2 to 4	2 to 3	3	4	4
50% removal	2 to 3	2 to 4	3 to 4	3 to 4	3 to 4
Simpson's index					
Controls	0.56	0.29	0.58	0.44	0.54
30% removal	0.41	0.17	0.56	0.51	0.53
50% removal	0.41	0.11	0.58	0.55	0.56
Simpson's evenness					
Controls	0.77	0.46	0.82	0.64	0.74
30% removal	0.61	0.27	0.83	0.68	0.71
50% removal	0.64	0.16	0.82	0.78	0.77
Shannon-Wiener index					
Controls	1.28	0.75	1.33	0.97	1.28
30% removal	0.99	0.48	1.24	1.26	1.30
50% removal	0.95	0.35	1.35	1.26	1.34
S-W evenness					
Controls	0.75	0.53	1.01	0.61	0.69
30% removal	0.63	0.35	0.78	0.63	0.65
50% removal	0.68	0.21	0.79	0.73	0.72

Seed fall

Total seed fall for Douglas-fir and white spruce was recorded in the fall of the first and second year post-treatment (Fig. 6). The 1992 seed crop ranged from 5.4×10^4 to 6.2×10^5 Douglas-fir seeds per hectare, and a negligible amount of white spruce seed was recorded on 6 of the 9 treatment units. There were no detectable treatment differences in total Douglas-fir seed fall in the first year post-harvest (ANOVA, treatment 1992: $F_{2,2}=1.37$, $P=0.78$). The seed crop in the second year post-harvest was considerably larger than that of the first year (Douglas-fir seed crops ranged from 1.6×10^6 to 4.6×10^6 seeds per hectare, and white spruce seed was recorded on all 9 treatments at densities of up to 1.8×10^6 seeds per hectare), but again there was no identifiable pattern of seed fall intensities observed between the treatment units. The number of Douglas-fir seeds recorded in the fall of 1993 appeared to be greatest on the unlogged controls and lowest on the 50% basal area removal stands (3.6×10^6 seeds/ha vs 3.0×10^6 seeds/ha), but there was no significant treatment effect detected in the amount of seed fall (ANOVA, treatments 1993: $F_{2,2}=1.17$, $P=0.40$).

FIGURE 6. Total number of Douglas-fir and white spruce seeds collected per ha. Distribution of seed rain shown for unlogged controls, 30% and 50% removal treatments in the first and second year post-treatment. Samples collected in fall of 1992 and 1993.
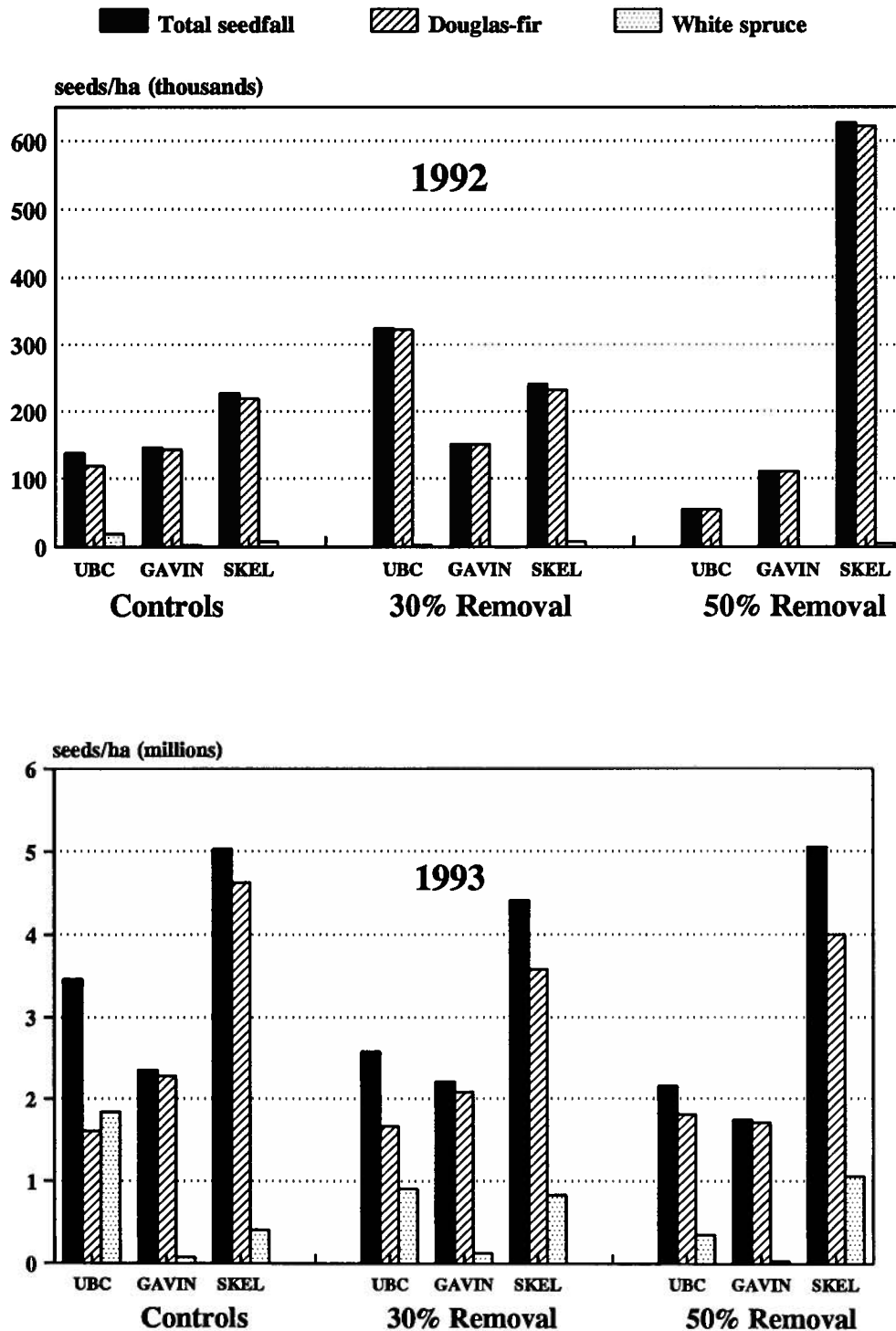
The percentage of sound Douglas-fir seeds varied between the two sampling years: 36.5% to 42.0% of the seeds collected in the first year post-harvest were sound, and 71.0% to 78.0% of the seeds collected in the second year post-harvest were sound (Table 16). The viability of the seeds seemed to increase with the larger seed crop. The percentage of sound seeds did not vary significantly between treatment units within either of the two post-harvest sampling years (ANOVA, treatments 1992: $F_{2,2}=0.08$, $P=0.92$; treatments 1993: $F_{2,2}=2.61$, $P=0.19$).

TABLE 16. Mean number of Douglas-fir seeds/ha and number of sound Douglas-fir seeds/ha. Seed fall samples were collected in the first and second year post-harvest (1992 and 1993, respectively).

	Total seed fall	No. sound seeds	Percentage sound
1992			
controls	160 360	58 558	36.5
30% removal	235 135	72 973	31.0
50% removal	262 162	109 910	41.9
1993			
controls	2 838 738	2 213 513	78.0
30% removal	2 443 243	1 756 757	71.9
50% removal	2 504 504	1 802 702	72.0

Seed germination

Seed germination exclosures were placed on the grids in the fall of 1992 and sampled

in June 1993. Not all of the seeds survived in the germination exclosures until the sampling

period, thus two values are presented: 1) the percent germination of the total number of

seeds placed in the germination exclosures, and 2) the percent germination of the number of

seeds which survived until the following spring (Table 17). The percentage of seeds which

survived in the exclosures and germinated was presumed to be the actual germination
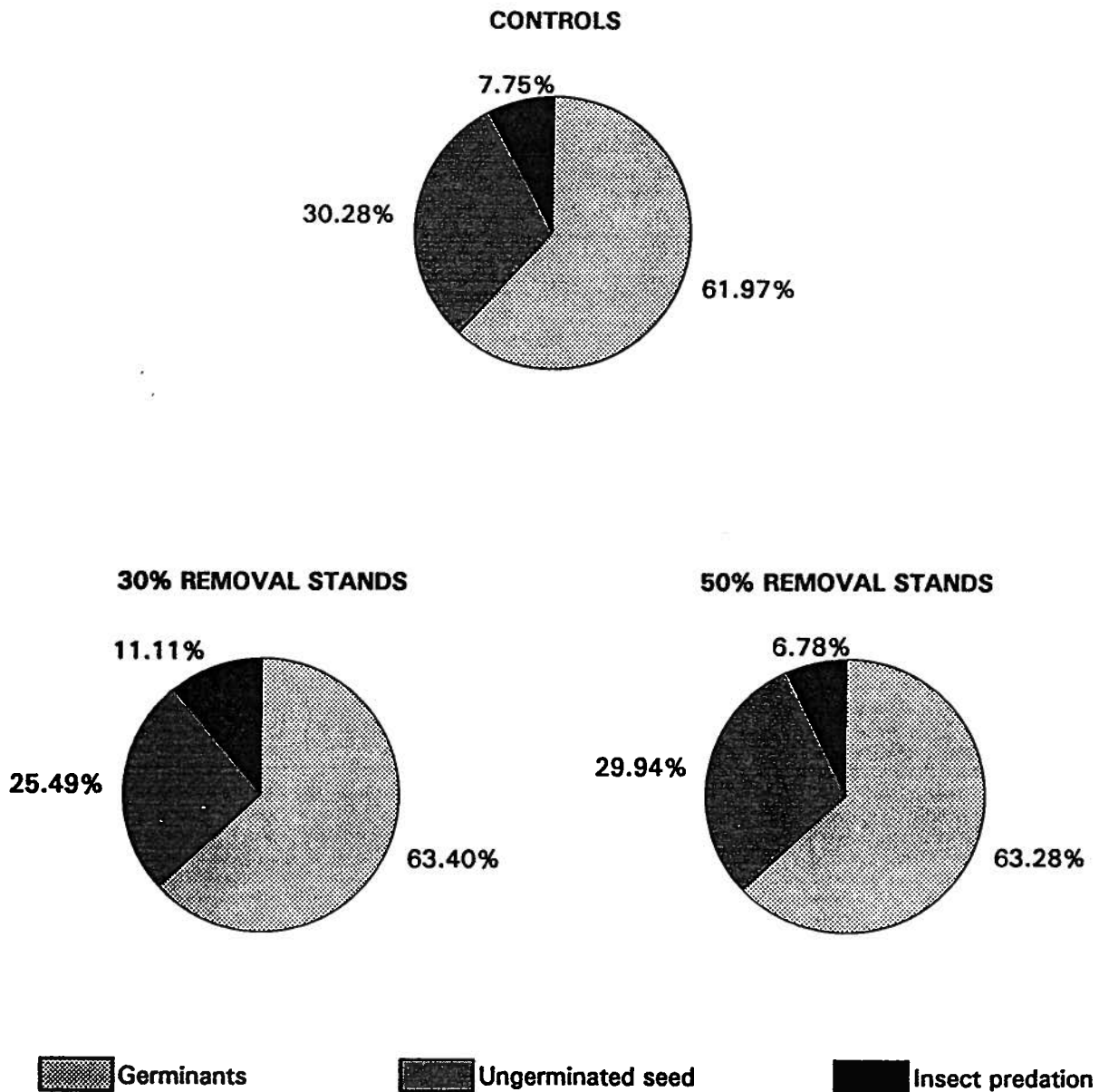
potential of the sites.

TABLE 17. Survival and germination results of Douglas-fir germination trials.
Shown are the mean values of three replicated unlogged controls, 30% and 50% basal
area (BA) removal treatments.

SEEDS	CONTROLS	30% REMOVALS	50% REMOVALS
No. sown	100	100	100
No. recovered	47.3	51.0	59.0
No. germinated	29.3	32.3	37.3
No. consumed by insects	3.7	5.7	4.0

Only 47% to 59% of the seeds sown in the germination trials were actually located in

the spring sampling session. Germination occurred on all treatments and on all sampled

seedbeds. The percentage of seeds that germinated was highly uniform between the

treatments: 62.0% of the seeds that were found on the controls and 63.4% of the seeds found on the 30% and 50% basal area removal treatments germinated in the following growing season (Fig. 7). There was no significant treatment effect detected in the germination results, but the three replicate blocks were significantly different (ANOVA, treatments: $F_{2,2}=0.28$, $P=0.77$; blocks: $F_{2,2}=11.29$, $P=0.02$). Insect predation was observed on 6.8 to 11.1% of the seeds which survived in the germination sampling plots, but it was not possible to distinguish between pre-dispersal insect predation from the nursery seed and on-site insect predation. Survival of the seeds in the germination exclosures was jeopardized by various unforeseen hazards: some of the protective covers were trampled by moose or deer, and others were punctured by falling branches or windfall, thereby exposing the seeds to small mammal or bird predation. Still other seeds may have been lost in the litter layers, as the seeds were carried down through the forest profile during the winter months.

FIGURE 7. Fates of the Douglas-fir seeds which were recovered in the germination trials. Seeds were sown in fall 1992 and results were recorded in June 1993. Values shown are the mean values of three pooled replicates.


CONTROLS

7.75%

30.28%

61.97%

30% REMOVAL STANDS

11.11%

25.49%

63.40%

50% REMOVAL STANDS

6.78%

29.94%

63.28%

Germinants   Ungerminated seed   Insect predation

Seed predation

Mean monthly seed predation rates in the second year post-disturbance averaged
1.4×10^5 seeds/ha/month on the controls, and 1.9×10^5 seeds/ha/month on the 30% and 50%
removal areas. Mean monthly seed predation rates throughout the snow-free months were
not significantly different between treatments (ANOVA, treatments, 1993: $F_{2,2}=2.98$, $P=0.06$)
(Fig. 8). The highest seed predation rates were recorded in the fall of 1992 (controls:
1.6×10^5 seeds/ha/month; 30% removals: 2.7×10^5 seeds/ha/month; 50% removals: 2.1×10^5
seeds/ha/month) but these values were based on a single sampling session and may have a
high human error factor as it was the first time the seed predation plots were sampled.
Overwinter mean monthly seed predation was noticeably lower than predation during the
snow-free months, but again no treatment effect was discernable in the winter predation rates
(controls: 2.6×10^4 seeds/ha/month; 30% removals: 3.4×10^4 seeds/ha/month; 50% removals:
2.8×10^4 seeds/ha/month). Some seeds remained in the sampling plots throughout the winter
months and were identified in the following spring.

An increase in predation rates was observed in the early fall of 1993 on all grids, but
this increase subsided during the last two sampling sessions of the year. The increase in
predation during the fall was larger on the 30% and 50% removal treatments than on the
unlogged controls, but there was no significant treatment effect on the overall seed predation.

FIGURE 8. Douglas-fir seed predation per ha per month on the controls and treatments. Values shown are the number of seeds consumed per month in October, 1992, overwinter 1992/93 (o/w) and May to October, 1993. Treatment means are pooled across the three replicates.
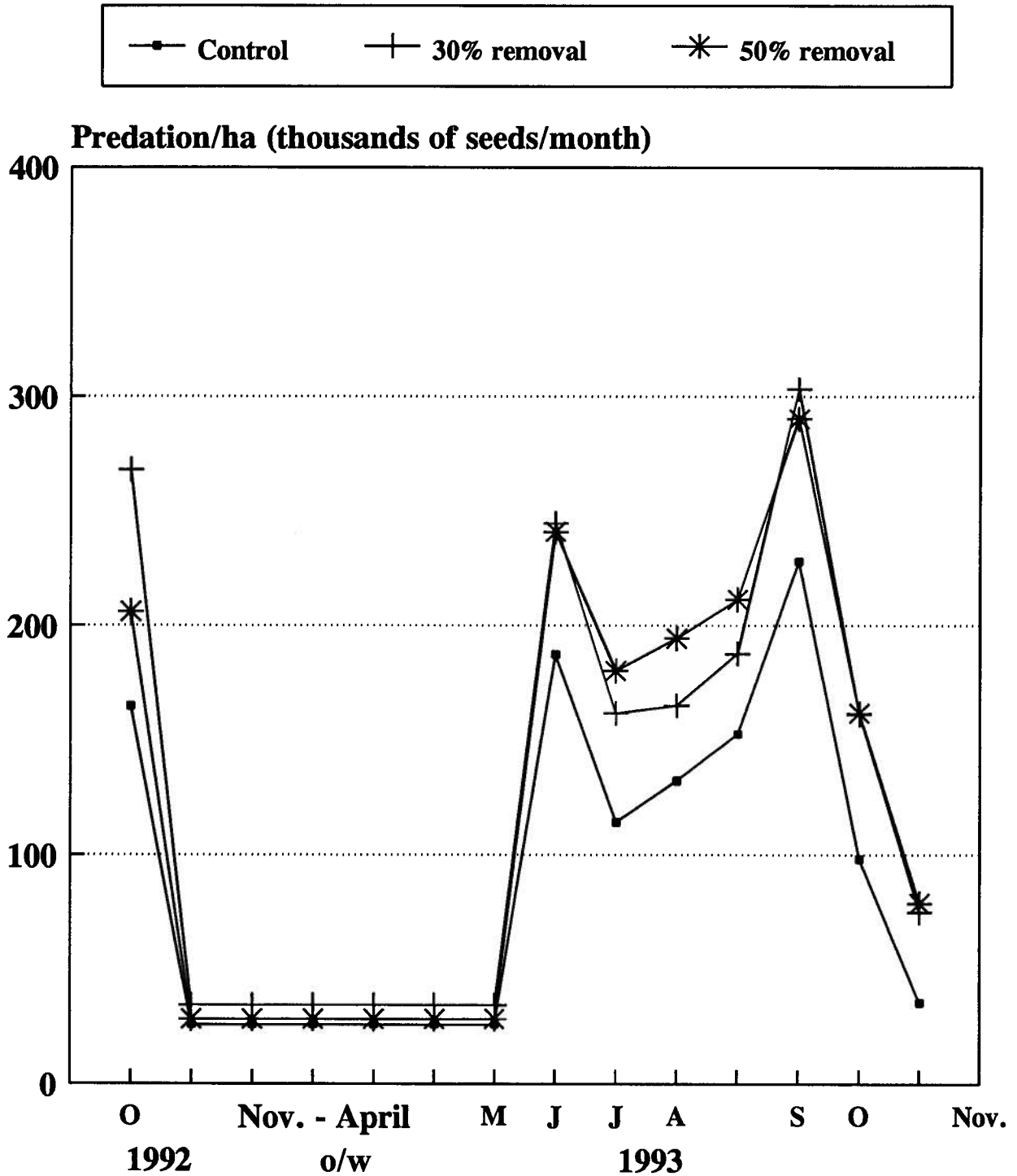
The number of seeds placed in the seed predation quadrats was less than the total number of seeds collected in the seed fall traps per hectare on all grids. Thus, it was assumed that the seed predation quadrats did not encourage any additional predation or attract additional animals onto the sites. On average, 32 to 35% of the total seeds consumed within the sampling quadrats were eaten by small mammals, but 65 to 67% of the predation could not be attributed to a specific group of seed eaters, as the seeds were removed from the sample plots. It is probable that a combination of seed-eaters was responsible for the total predation, as seed-eating birds such as the dark-eyed juncos (*Junco hyemalis*) were also observed on the sites.

DISCUSSION

Experimental design

The random interspersion of the three treatment replicates within each of the three blocks (study sites) ensured statistical independence of the replicates, appropriate testing of the hypotheses in question, and avoidance of pseudoreplication (Hurlbert 1984). The increased sample size provided by additional replicates may have increased the precision of these results, and possibly improved the power of the statistical tests, but additional replicates may not have been economically justifiable. The control treatments may not have been entirely effective in providing an indication of undisturbed population trends or densities. The movement of animals between the treatment units within the replicate blocks and the disturbance by researchers during the intense sampling and data collection on the sites may have jeopardized the validity of the controls. The sites were sampled during the snow-free portions of the year (May to October) only, but there was considerable activity on the study sites during these months. In addition, the removal of trees in order to minimize further pest problems (some trees were removed from buffer zones in an attempt to contain a Douglas-fir beetle (*Denroctonus pseudotsugae*) attack) may have sacrificed the soundness of some of the buffer zones between the treatments.

Burton (1994) conducted a survey of surface materials in the fall of 1993 to estimate the relative abundance of seedbed materials in the control and treatment stands. Disturbance was recorded on the harvesting treatments as well as on the unlogged controls, but the

disturbance was understandably greater on the harvested areas (2% on the unlogged controls, 10% on the 30% BA removals, and 12% on the 50% BA removals) (Burton 1994). There was reasonable uniformity in site characteristics and no significant block differences in population levels of small mammals between the treatments in the first or second year post-treatment, and little indication that the soundness of the treatments was compromised. The logistics of the logging operation required that the harvesting be staggered over a number of weeks across the sites, and thus the sampling sessions during the treatment year were irregular between the replicates. In addition, the pre-treatment sampling sessions were not balanced in number or timing across the replicates. The results of the pre-and post-treatment data in 1991 were notable biologically but could not analysed statistically. Greater emphasis on synchronizing the number and timing of the sampling sessions across the replicates would have enabled the pre-treatment and immediate post-treatment results to be interpreted with more confidence. Extending the duration of this study to two years post-treatment provided comparatively long-term results of the effects of the shelterwood harvests on small mammal populations and seed parameters, but follow-up sampling is recommended to observe small mammal population and seed fall responses throughout the second and final shelterwood passes.

Demographic responses of small mammals

The results of the population analysis of the small mammal species present on the study sites indicated that, other than the initial influx of red-backed voles immediately post-harvest (which may have been attributable to a population cycle), the first pass of the shelterwood system did not significantly affect small mammal population levels or dynamics in the treated stands. It was presumed that chipmunks, shrews, and the less common microtines did not constitute a large component of the small mammal community in the partially logged stands during the first two years post-harvest, and played a minor role in seed predation at that time. The less common microtines were only occasionally recorded during the trapping sessions and, as a result, the trappability of these species was very low (10.2 to 47.2%). The trappability of the predominant species (deer mice and red-backed voles) was consistently high (ranging from 61.2 to 90.7%) throughout the time of study and across the treatments. Thus, the accuracy and reliability of the additional demographic parameters calculated for these common species was presumed to be high.

The habitat requirements of the deer mice and red-backed voles appeared to be met, at least initially, with the habitat created within a shelterwood system. It is plausible that the demographic responses of the less common species to these treatments were similar to those of the deer mice and red-backed voles, and also may not have been negatively affected by the removal treatments. Throughout the post-harvest period of study, the mean number of deer mice ranged from 6 to 13 animals/ha. As deer mice tend to be more common on recently

cut areas or early successional stages than in mature forest (Tevis 1956; Gashwiler 1970; Krefting and Ahlgren 1974; Sullivan and Krebs 1981; Gunther *et al.* 1983; Scrivner and Smith 1984; Medin 1986; Walters 1991), they have imposed a serious threat to natural regeneration on clearcut areas. On the contrary, the habitat alterations resulting from the partial cuts did not appear to attract additional deer mice to the sites or cause a great increase in density of seed-eater populations.

Red-backed voles are known to collect, cache, and presumably consume conifer seed (Askham 1992) and seemingly fare well in a partially logged environment. Results from this study showed dramatic increases in red-backed vole population levels immediately post-harvest 1991, on the treatments as well as on unlogged controls: 3-fold increase from pre-harvest levels on the controls and 50% removal treatments, and 4-fold increases from pre-harvest levels on the 30% removal treatments. This increase in density was temporary, and by the first year post-harvest, the average population levels had subsided from a range of 41 to 62 voles/ha to a range of 6 to 10 voles/ha.

Discrepancies exist with regard to the periodicity and duration of small mammal cycles, but fluctuations in small mammal populations are common and are presumed to occur every 3-4 years (Krebs 1966). Thus, it is possible that the 1991 "super-populations" of red-backed voles may have reflected a vole peak. Whereas red-backed vole densities of 5 to 15 individuals per hectare are common (Medin, 1986; Medin and Booth 1989), our study showed as many as 70 individuals per hectare on some sites in October 1991.

As the high population levels in the fall of 1991 were positively correlated with the intensity of harvesting disturbance (density levels on the 30% and 50% removal sites were 1.5 times greater on the treated areas than the controls), the initial shelterwood removal may have affected the red-backed vole habitat in various ways:

a) by providing a temporary increase in local forage and/or cover with the falling of selected trees. This may have provided increased insect and/or seed availability by dislodging them from the canopy or exposing them in the duff;

b) by providing a more readily available food source for rodents. The soil disturbance associated with the removal of felled trees may have exposed hypogeous fungi to a greater extent than was naturally present;

c) by increasing thermal and security cover for small mammal species by leaving coarse woody debris on the sites after logging. In addition, the undisturbed ground cover remaining after harvesting (as indicated by the low post-harvest soil disturbance levels) may have contributed to suitable overwintering sites for the red-backed voles (West *et al.* 1980).

These habitat alterations may explain the magnitude of post-treatment population densities encountered in 1991. It is important to note that this increase in vole density occurred to a varying extent on the unlogged controls as well as on the treatment sites, as did

the overwinter (1991-1992) population decline. Therefore, the oscillating population trends and the poor over-winter survival of red-backed voles cannot be wholly attributable to the effects of harvesting and instead must be reflecting some sort of cycle. Red-backed voles continued to exhibit seasonal population fluctuations (lower after winter, higher in the fall) despite the surge in density in the fall of 1991. Thus, the populations were merely present in lower numbers in the first and second year post-harvest, as would be expected following a cyclical peak, but were not displaced by the harvesting treatments.

The seasonal variation in deer mouse survival may have been a result of the habitat variety created by the partially-cut stands. The habitat alterations created with shelterwood harvesting were apparently favourable for a variety of predator species. Pine marten (*Martes americana*), red fox (*Vulpes fulva*), wolves (*Canis lupus*), and raptors were observed in the controls and treatment stands throughout the study. As deer mice are active year round, the winter snow cover may have provided greater protection from predators and enabled higher survival in the winter than could be expected during the snow-free months, but no data were collected for such an analysis as it was beyond the scope of this study. The two major species showed no significant difference in survival on the controls or basal area removal treatments for the entire post-harvest period of the study. There was no significant seasonal difference observed in the survival of red-backed voles.

Recruitment of deer mice showed no difference between the first and second year post-harvest, and there was no detectable treatment effect between the stands. Recruitment of deer mice was lowest immediately following the disturbance (post-harvest 1991) but increased in subsequent years, possibly indicating that the deer mice can rapidly repopulate

disturbed areas. Recruitment of red-backed voles was greatest immediately after logging (post-harvest 1991), and exhibited a positive correlation of recruitment with residual basal area in the stands. This correlation paralleled the growth in red-backed vole population levels at this time. The post-harvest 1991 increase could not be analysed statistically because of the unbalanced sampling sessions during this time period, and the observed increase in recruitment at this time had subsided to pre-treatment levels by the first year post-treatment (summer 1992).

Deer mouse and red-backed vole males were sexually mature at a lower mass (age) than females on all sites. However, adult body mass did not exhibit any discernable differences due to treatment effects for the deer mice or the red-backed voles. The length of the breeding seasons were not significantly different across treatments but were considerably longer, for both species, in the second year post-harvest than the first (mean number of weeks breeding in 1992 versus 1993, deer mice: 11.0 versus 20.3 weeks, respectively; red-backed voles: 14.3 versus 21.3 weeks, respectively). Breeding seasons may be shortened during times of stress in a population, and hence any increase in breeding season length may be favourable in terms of the health of the species.

There was a wide range in the percentage of adults in breeding condition throughout the course of the study, but there were no significant differences attributable to treatment effects. The lowest percentages of red-backed voles in breeding condition was recorded immediately post-harvest, at which time the population densities were escalating to the highest levels recorded in the course of the study. However, a high proportion of the red-backed voles captured during this study were juvenile and were never recorded as sexually

mature. Only 15% of the male red-backed voles and 22% of the females captured during the study were recorded as adults. Thus, the analysis of the adult individuals reflected only a small proportion of the animals present throughout the study. The deer mice populations sampled consisted of predominantly adult males (68.9%), but the females sampled were largely juvenile (63.0%). Grids with lower quality habitat have been known to exhibit high animal densities, but van Horne (1983) noted that this may be due to an irruption of juveniles consisting largely of immigrants which have been forced into lower-quality, or "sink" habitats. The information collected in this study was not sufficient for determining whether the fates of the individuals were attributable to death or dispersal, and high proportions of juveniles were recorded on the controls as well as the treatment units.

Diversity

Despite the debate of whether diversity may or may not be a reasonable objective in natural resources management (Magurran 1988; Hunter 1990; Burton *et al.* 1992), species diversity and evenness was measured to assess treatment effects. Diversity measures and species evenness measures were lowest on all grids immediately following the harvesting operations, presumably due to the great influx of red-backed voles at this time. There appeared to be greater species diversity on the unlogged controls pre-and-post-treatment 1991 and throughout 1992, but the differences between the controls and treatments were not significant. The second year after disturbance, species diversity was greater on the logged treatments than on the unlogged controls.

Seed Parameters

Seed fall measurements indicated that a small Douglas-fir crop was produced in 1992 and a larger crop of Douglas-fir and white spruce was produced in 1993 on all grids. Total seed fall in 1992 was marginally greater in the treatments than the unlogged controls but these differences were not significant. The larger seed crop in 1993 showed only minor differences between treatments but there was a notable increase in the proportion of viable seeds in the seed crop. Surface materials in each of the three study site locations were dominated by organic materials (80 to 90% cover), and this did not change markedly with the harvesting treatments (Burton 1994). There was no detectable treatment effect on the germination potential of the post-disturbance seed beds in the stands.

Seed predation increased dramatically on all sites in the early fall of 1993, at which time deer mouse and red-backed vole populations were at their seasonal peaks. However, there did not seem to be a large influx of new animals at this time, and by late fall seed predation had subsided considerably. This decline in predation in the sampling plots coincided with the timing of the natural seed crop dispersal in the fall. Some Douglas-fir seed survived in the exposed sampling plots throughout the winter months. Snow cover promoted seed survival by concealment, regardless of the small mammal density, and as the vulnerability of the seeds decreased, the rate of seed predation was also reduced. Seed predation due to insects was negligible on all sites. Seeds missing from the plots may have been eaten by various seed-eating birds, but accurate identification of the various birds

observed in the stands was not obtained.

Seed predation varied with the seasonal fluctuations of the seed-eater populations, but the predation rates did not seem to be influenced by the amount of seed available on the sites. There was no observed change in small mammal population parameters or community structure in relation to the amounts of conifer seed available on the sites during the two post-harvest sampling years. The population levels of the most common small mammal species did not vary with the increased seed crop. Seed predation rates reflected seasonal population fluctuations rather than seed fall intensities, i.e. the rate of seed predation per ha per month did not increase with the larger seed crop in the second year after harvesting. Seed predation rates seemed less severe at times when seed-eater populations were at annual low points, such as late winter or early spring. Douglas-fir seeds survived the winter on all grids and had the potential to germinate on the seedbeds available and in the microclimate created with shelterwood harvesting. Thus, the regeneration success of the stands, with regard to seed survival and establishment, in the basal area removal intensities tested during this study did not seem to be inhibited by the small mammal communities recorded during this study.

MANAGEMENT IMPLICATIONS

By examining the habitat requirements of the seed predators and observing their seasonal population fluctuations, this study showed that it may be possible to manage for seed-eaters and still allow natural regeneration to succeed. Changes in habitat due to the shelterwood harvesting did not appear to be severe enough to negatively affect the generalist, rapidly reproducing small mammal species monitored during this study. It is important to recognize that complete elimination of animal damage is neither practical nor necessary (Owston *et al.* 1992). Prevention of severe seed predation can be mitigated by monitoring seed crops and scheduling harvests in years preceding high seed production. Over longer time frames, harvest operations could be scheduled during good seed years when seed production would be sufficient to overcome losses due to seed-eaters (Janzen 1971, Shearer and Schmidt 1971). Comparison of these seed and small mammal results with regeneration data collected by the B.C. Ministry of Forests (Williams Lake) would determine if the regeneration observed during the first two years post-harvest was considered adequate for restocking the harvested areas, or if it was necessary to supplement the natural regeneration with planted stock.

Alternative silvicultural systems such as the shelterwood system are a step towards providing diversity within the managed forest landscape. By combining the maintenance of ecological systems with the extraction of timber, shelterwood systems present an option to the preservation versus timber production stalemate that dominates forest landscapes in B.C.

(Hopwood 1991). By removing the overstory canopy in a series of cuts, forest cover is provided during the establishment of regeneration and the advance growth on the sites is incorporated into the next rotation. Shelterwood systems may increase the component of Douglas-fir in future stands and have the potential to integrate the management of timber values with non-timber values such as wildlife, water supply, range, recreation, and esthetics, which are demanded from these interior sites.

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APPENDIX 1. Comparison of Jolly-Seber estimates and MNA direct enumeration of deer mouse population levels in the control and treated stands of the UBC replicate.
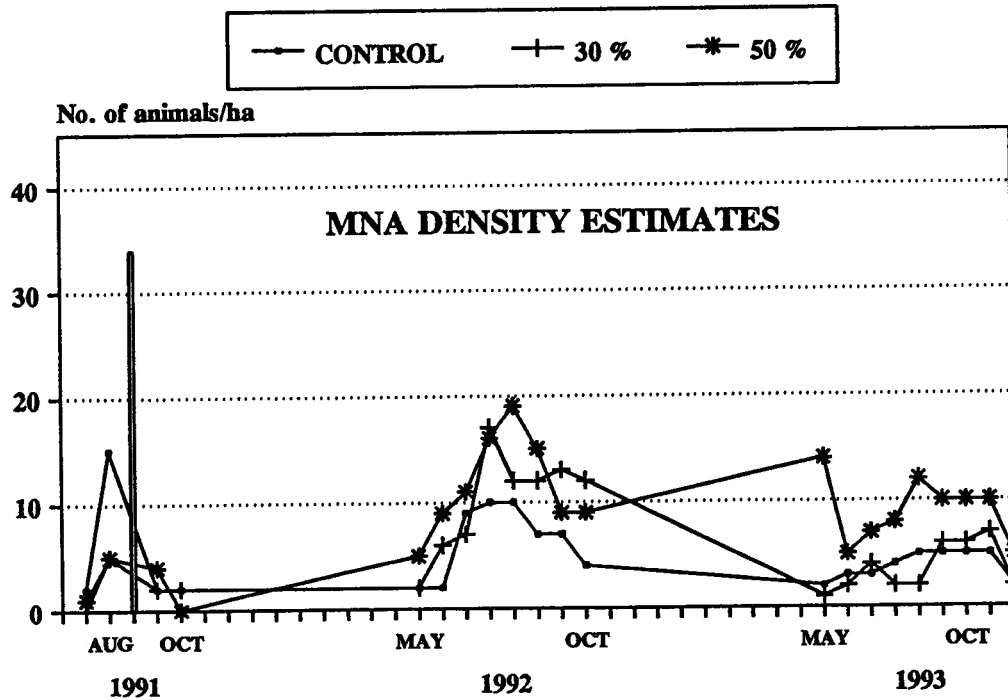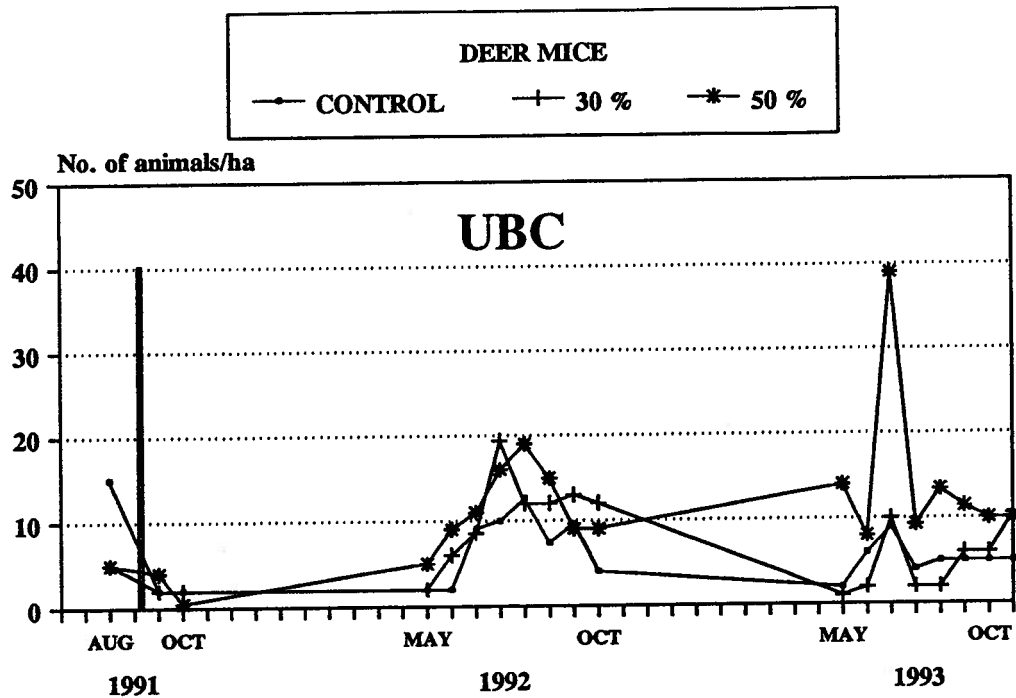
APPENDIX 2. Comparison of Jolly-Seber estimates and MNA direct enumeration of deer mouse population levels in the control and treated stands of the Gavin replicate.
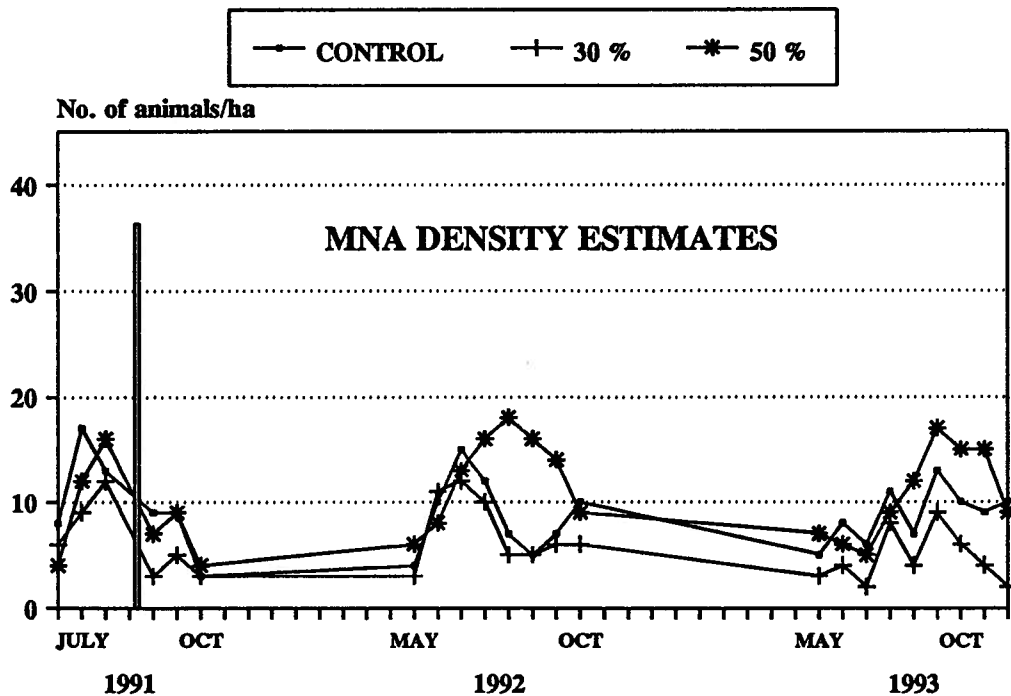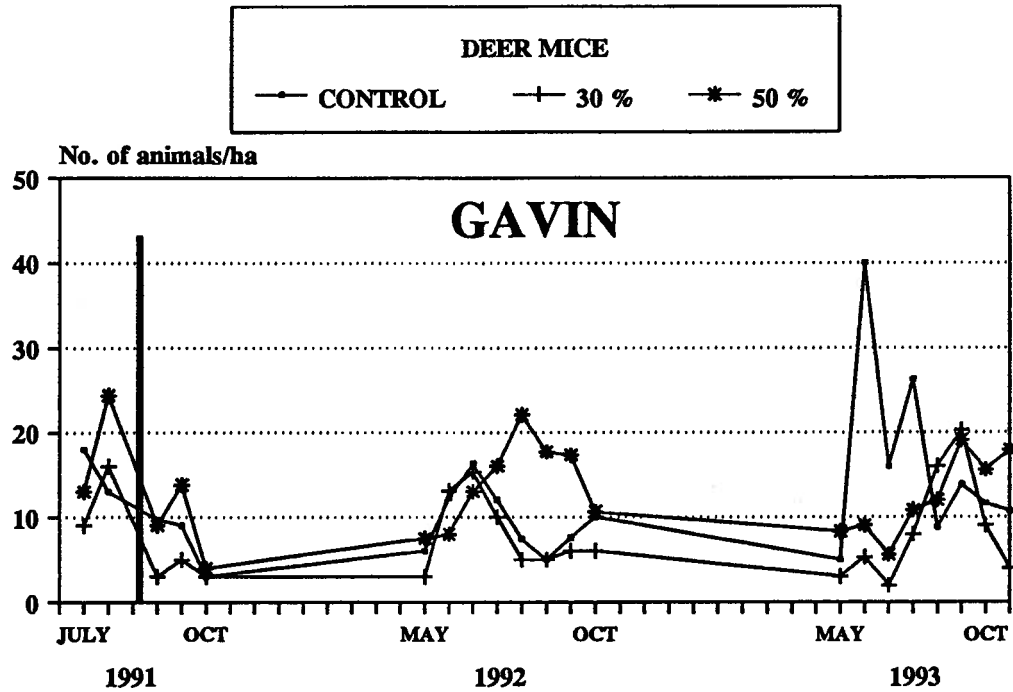
APPENDIX 3. Comparison of Jolly-Seber estimates and MNA direct enumeration of red-backed vole population levels in the control and treated stands of the UBC replicate.