

POPULATION AND HABITAT USE CHARACTERISTICS OF FOREST-DWELLING
SMALL MAMMALS IN RELATION TO DOWNED WOOD

by

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Abstract

Downed wood has long been considered an important habitat component for small mammals, although studies to date have generated equivocal results. To examine this relationship in an experimental manner, I removed and added downed wood on areas within two seral stages and two ecosystems, and monitored the population-level response of: a habitat generalist, the deer mouse (*Peromyscus maniculatus*), early seral specialists (meadow voles, *Microtus pennsylvanicus* and long-tailed voles, *M. longicaudus*) and an old seral specialist (southern red-backed vole, *Clethrionomys gapperi*). I also studied fine-scale habitat associations of red-backed voles on the treatment areas using radio-telemetry to determine how relationships with downed wood and other habitat components changed with the removal of downed wood from an area. This study was part of two multi-disciplinary silvicultural systems research projects in southern British Columbia. The first was the Opax Mountain Silvicultural Systems Project area, located in a Douglas-fir-lodgepole pine forest in a warm and dry ecosystem in the interior of British Columbia. The second was the Sicamous Creek Silvicultural Systems Project area located in a high-elevation cold, wet Engelmann spruce- subalpine fir forest.

My study generated several unexpected results that have not been reported in the correlational studies published to date. The relationships of small mammals with downed wood and vegetation varied by species, as well as with ecosystem. At the Opax site, deer mouse populations responded positively to harvesting but not to downed wood manipulations. The highest densities were found on clear-cuts at the Opax site where downed wood had been removed. Within forested areas, higher densities were found in stands with lower canopy cover and higher shrub cover. At Sicamous, deer mice did not respond to harvest treatments nor downed wood manipulations on forested areas. Lower survival rates and higher rates of capture

of mice on the edge of *low* treatment areas suggested that deer mice on clear-cuts might have been negatively affected by the removal of downed wood. Microclimate, and likely the amount of ground covered by vegetation, influenced patterns in abundance on both clear-cut and forested areas.

Meadow voles were strongly associated with clear-cuts at Opax but did not respond to downed wood treatments. This was expected because meadow voles are typically found in grassland habitats, which normally do not have large quantities of downed wood. Unexpectedly, meadow voles were more abundant on sites with higher shrub cover. Long-tailed voles at Sicamous responded positively to the number of pieces of downed wood on clear-cuts. This study and other work suggested that downed wood is an important habitat component for long-tailed voles, regardless of the amount of vegetation on the area.

Downed wood was particularly important for red-backed voles at Opax, but less so at Sicamous, where abundant shrubs likely served a similar role as downed wood in providing cover. Retaining downed wood on Opax clear-cuts mitigated some of the initial effects of harvesting on red-backed voles. Downed wood at Sicamous did not serve the same function, probably because of the sparse vegetation on clear-cuts. Radio-telemetry of red-backed voles on forested areas at Opax indicated that voles were closely associated with downed wood at both the home range and the microhabitat scale.

The abundance of vegetation was an important variable for many small mammal species studied, although there were instances where relationships with downed wood were strong and independent of vegetation. The response to habitat components by small mammals may vary with site conditions (climate, seral stage, disturbance), the spatial scale of investigation, and species.

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Chapter 1. Introduction

1.1 Background

Forests are no longer managed for wood production alone; with increasing information about the potential impacts of intensive harvesting, the maintenance of biodiversity across the managed landscape is of increasing concern (Bunnell *et al.* 1999). Managed forests have very different structural characteristics than old-growth forests (Triska and Cromack 1980, Spies *et al.* 1988, Spies and Franklin 1991, Rosenberg *et al.* 1994, Carey and Johnson 1995), and may provide less suitable habitat for many vertebrate species under intensive management (Bunnell *et al.* 1999). The replacement of old-growth with even-aged younger stands will lead to the loss of important habitat attributes generally associated with old-growth, such as understorey cover, multi-layered forest canopies and large dead or dying trees, or changes in the amount or characteristics of downed wood across the landscape (Hunter 1990, Carey and Johnson 1995, Angelstam 1997, Bunnell *et al.* 1999, Wilson and Carey 2000). Recent research on maintaining biodiversity in managed forests has emphasized the importance of mimicking natural patterns, and maintaining important stand-and landscape-level attributes over space and time (Carey and Johnson 1995, Bunnell *et al.* 1999). To effectively retain old-growth features in managed stands, it is useful to focus on important attributes that are affected by forest management, and can be manipulated (Bunnell *et al.* 1999). Downed wood is one of the structural attributes of forests that meets these criteria (Carey and Johnson 1995, Angelstam 1997, Bunnell *et al.* 1999, Wilson and Carey 2000).

Downed wood has long been recognized as an integral component of the forest ecosystem. Elton (1966) noted that:

“...dying and dead wood provides one of the two or three greatest resources for animal species in a natural forest, and ... if fallen timber and slightly decayed trees are removed the whole system is gravely impoverished of perhaps more than a fifth of its fauna.”

Downed wood is central to many processes of energy flow and nutrient cycling in forest ecosystems, and is important as a habitat component for a wide variety of species. Up to 45% of above-ground organic matter is stored in downed logs and snags which is returned to the ecosystem as the wood decays (Harmon *et al.* 1986). The input of these nutrients to the forest ecosystem is important for maintaining long-term site productivity (Harmon *et al.* 1986). After a tree or other woody debris falls to the forest floor, the decomposition process begins (if not already, as in the case of snags) with the formation of a community of microbes, fungi, and invertebrates (Maser *et al.* 1979, Harmon *et al.* 1986). The moist microclimate associated with decaying logs is an important attribute that provides suitable habitat for a diverse group of organisms including mycorrhizal fungi, salamanders, and invertebrates (Harmon *et al.* 1986, Amaranthus *et al.* 1989, Butts and McComb 2000). The invertebrates and fungi in turn are food for a wide variety of vertebrates, from shrews and salamanders, to bears and woodpeckers (Harmon *et al.* 1986, Bunnell *et al.* 1999, Butts and McComb 2000). Decaying wood provides a suitable growth substrate for many species of plants, including tree seedlings (Harmon *et al.* 1986). The role of downed wood as a habitat component changes over time as it decays. At different periods, logs provide important resting, nesting, travelling routes, security cover, and foraging areas for many invertebrate and vertebrate species (Maser *et al.* 1979, Maser and Trappe 1984, Bartels *et al.* 1985, Harmon *et al.* 1986, Hayes and Cross 1987, Bunnell *et al.* 1999, Butts and McComb 2000). Because of its diverse functions, the loss of downed wood

from the forest ecosystem through intensive forest management as described by Angelstam (1997), would likely cause the disruption of, or loss of, integral processes and species in the managed landscape over time.

My study addresses one aspect of the role of downed wood in forests: as a habitat component for small mammals. Species that are most likely to be affected by the loss of, or changes in the characteristics of, downed wood would be those less vagile species, such as small mammals, that rely on downed wood to satisfy some aspect of their requirements, such as nesting, travelling, or foraging (Thomas 1979, Harmon *et al.* 1986, Carey and Johnson 1995, Bunnell *et al.* 1999, Wilson and Carey 2000). Many small mammals such as shrews and deer mice (*Peromyscus maniculatus*) eat invertebrates that associate with downed wood (Harmon *et al.* 1986). Southern red-backed voles (*Clethrionomys gapperi*) and deer mice also eat truffles (mycorrhizal fungi) that are closely associated with downed wood (Amaranthus *et al.* 1994, Pyare and Longland 2001). Downed wood is an important structural component that provides protected travel routes (Hayes and Cross 1987) and structure in the subnivean layer, which is important for over-winter survival of small mammals (Schlegl-Bechtold 1980, West *et al.* 1980, Pruitt 1984). Although downed wood is considered an important habitat component for many small mammal species, critical issues for management, such as the existence minimum requirements or substitutable resources, remain uncertain.

Small mammals play an important role in the forest ecosystem. Some small mammal species such as southern red-backed voles and deer mice disperse spores of mycorrhizal fungi, which are an important component in coniferous forests (Merritt and Merritt 1978, Martell 1981, Ure and Maser 1982, Rhoades 1986). Small mammals constitute the majority of the diet of many species (*e.g.*, American marten [*Martes americana*], coyotes [*Canis latrans*], owls and other

raptors; Pearson 1985, Korpimäki and Norrdahl 1989, 1991, Boutin *et al.* 1995) and, therefore, are important for the maintenance of local biodiversity. Small mammals can also create problems in forests by damaging seedlings and other vegetation, and by eating seeds (Martell 1981, Sullivan and Sullivan 1982, Von Treba *et al.* 1998, Sullivan *et al.* 2001).

Research on small mammal habitat associations has concentrated on retrospective, correlative studies that identify habitat characteristics associated with capture locations of individuals (*e.g.*, Goodwin and Hungerford 1979, Kaufman *et al.* 1983, Hayes and Cross 1987, Ribble and Samson 1987, Bowman *et al.* 2000) or population size (Snyder and Best 1988, Corn *et al.* 1988, Rosenberg and Anthony 1993, Bowman *et al.* 2000). Habitat components identified during these studies provide an important baseline of information about the types of habitats that are important; however, they suffer from the potential confounding effects of existing environmental conditions.

Although downed wood is generally considered to be an important, and perhaps a critical habitat feature for small mammals, the results of studies to date have been contradictory (references above, Mills 1995, Loeb 1999, Bowman *et al.* 2000, Moses and Boutin 2001). To answer some of the questions about the relationship between downed wood and small mammals, I conducted a study where I manipulated the amount of downed wood on both forested and harvested (clear-cut) areas in two ecosystems (low-elevation dry forest and high-elevation wet forest). I studied the relationship between downed wood and deer mice, meadow (*Microtus pennsylvanicus*) and long-tailed voles (*M. longicaudus*), and southern red-backed voles by experimentally removing and adding downed wood to treatment areas, and by studying the response of populations of these species with an intensive mark-recapture study.

Microhabitat relationships may not be evident at a macrohabitat scale (Morris 1987, Wiens *et al.* 1993, Bunnell *et al.* 1999). As well, some relationships cannot be studied with trapping data, such as activity patterns, or the location and attributes of nest sites. To explore the microhabitat associations of a habitat specialist, the red-backed vole, I used radio-telemetry to determine whether they associated with downed wood or other habitat components, and whether other habitat components substituted for downed wood when it was removed from an area.

This study design enabled me to examine the response of a habitat generalist (deer mouse), as well as early seral (meadow vole, long-tailed vole) and late seral specialists (red-backed vole) to the availability of downed wood on forested and clear-cut areas. Conducting the experiment in two different ecosystems allowed me to explore the patterns of response of these species to downed wood across an environmental gradient.

In Chapter 3, I report the results of a study on deer mouse populations on clear-cut and forested areas where the level of downed wood was manipulated. Deer mice are considered to be habitat generalists (Thomas 1979). They are omnivorous, regularly eating seeds, lichens, fungi, and insects (Thomas 1979, Martell 1981, Rhoades 1986) and are abundant in both clear-cut and forested habitat (Martell and Radvanyi 1977, Martell 1983, Kirkland 1990, Gilbert and Krebs 1991, Sullivan and Boateng 1996, Sullivan *et al.* 1999a). Deer mice have a well-documented relationship with downed wood at the microhabitat scale, using it for nesting, travelling, and foraging (Graves *et al.* 1988, Barnum *et al.* 1992, Planz and Kirkland 1992, McMillan and Kaufman 1995, McCay 2000), although responses at the population level are not as clear (Loeb 1999, Moses and Boutin 2001).

Meadow voles and long-tailed voles are generally not considered forest-dwelling species, but both are commonly found in clear-cut, early seral habitat (Van Horne 1982, Kirkland 1990,

Krupa and Haskins 1996). The abundance of long-tailed voles, but not meadow voles, has been related to downed wood (Van Horne 1982, Moses and Boutin 2001). I report the results of a study of the population dynamics of these voles on clear-cut areas where downed wood was added or removed, in Chapter 4.

Of the four species I studied, the southern red-backed vole is considered the most dependent on downed wood. The red-backed vole is associated with old seral forest (Merritt 1981), and forages on fungi and lichens, which are often associated with downed wood (Harmon *et al.* 1986, Clarkson and Mills 1994, Waters *et al.* 1997, Carey *et al.* 1999, Gagné *et al.* 1999, Pyare and Longland 2001). In Chapter 5, I report the results of a mark-recapture study of red-backed voles on clear-cut and forested areas where downed wood was manipulated. To investigate microhabitat associations of red-backed voles that could not be identified by trapping, I radio-tracked female red-backed voles on areas where downed wood was manipulated. The results of the radio-telemetry study are presented in Chapter 6.

In the rest of this chapter, I describe the two study areas in which my research took place. In Chapter 2, I report on the downed wood manipulations, and the resulting downed wood and habitat characteristics on the treatment areas.

1.2 Study Areas

My project was part of two large silvicultural systems experimental research projects established in the Interior of British Columbia (B.C.). The Opax Mountain Silvicultural Systems project was a co-operative venture between the B.C. Ministry of Forests and the local Small Business Forest Enterprises program. It was designed to investigate the influence of harvesting and silvicultural techniques in a dry, fir-pine forest on a wide range of biotic (such as small mammal populations, regeneration and windthrow) and abiotic (such as snow

accumulation and growing season temperatures) factors (Vyse *et al.* 1998). The Sicamous Creek Silvicultural Systems Project was established by the B.C. Ministry of Forests as a long-term research study in a high-elevation system (Kamloops Region, Hollstedt and Vyse 1997, Vyse 1999). The project was also designed to examine the effect of silvicultural treatments including harvest prescriptions and site-preparation on various aspects of forest regeneration, floral, and faunal response.

1.2.1 Opax Mountain Silvicultural Systems Project

The Opax Mountain study area (hereafter “Opax” study area) was located approximately 15 km northwest of Kamloops, British Columbia (50° 48' N, 120° 27' W), in a dry, Douglas-fir-lodgepole pine forest (the Interior Douglas-fir, IDF, biogeoclimatic zone; Meidinger and Pojar 1991; Fig. 1). Parts of the study area had been partially harvested with a limited-diameter partial-cut in 1956 to 1957; other areas were unharvested (Bealle-Statland 1998). The site was at least partially covered in up to 0.5 m of snow for five to six months of the year (Huggard *et al.* 1998).

The research site was initially divided into twelve, 20-25-ha harvest treatment areas; six at each of the Mud Lake (1000 m elevation) and Opax Mountain blocks (1100 m elevation). The following treatments were randomly assigned to the six harvest treatment areas within each block (Fig. 2a, Klenner and Vyse 1998):

1. control (no harvest), harvest treatment areas D and I
2. 20% volume removal by individual tree selection, F and L
3. 50% volume removal by individual tree selection, B and G
4. 20% volume removal in patches of 0.1 ha, 0.4 ha, and 1.6 ha, C and K
5. 50% volume removal in patches of 0.1 ha, 0.4 ha, and 1.7 ha, E and J
6. 50% volume removal with 30% left as uncut reserves, A and H.

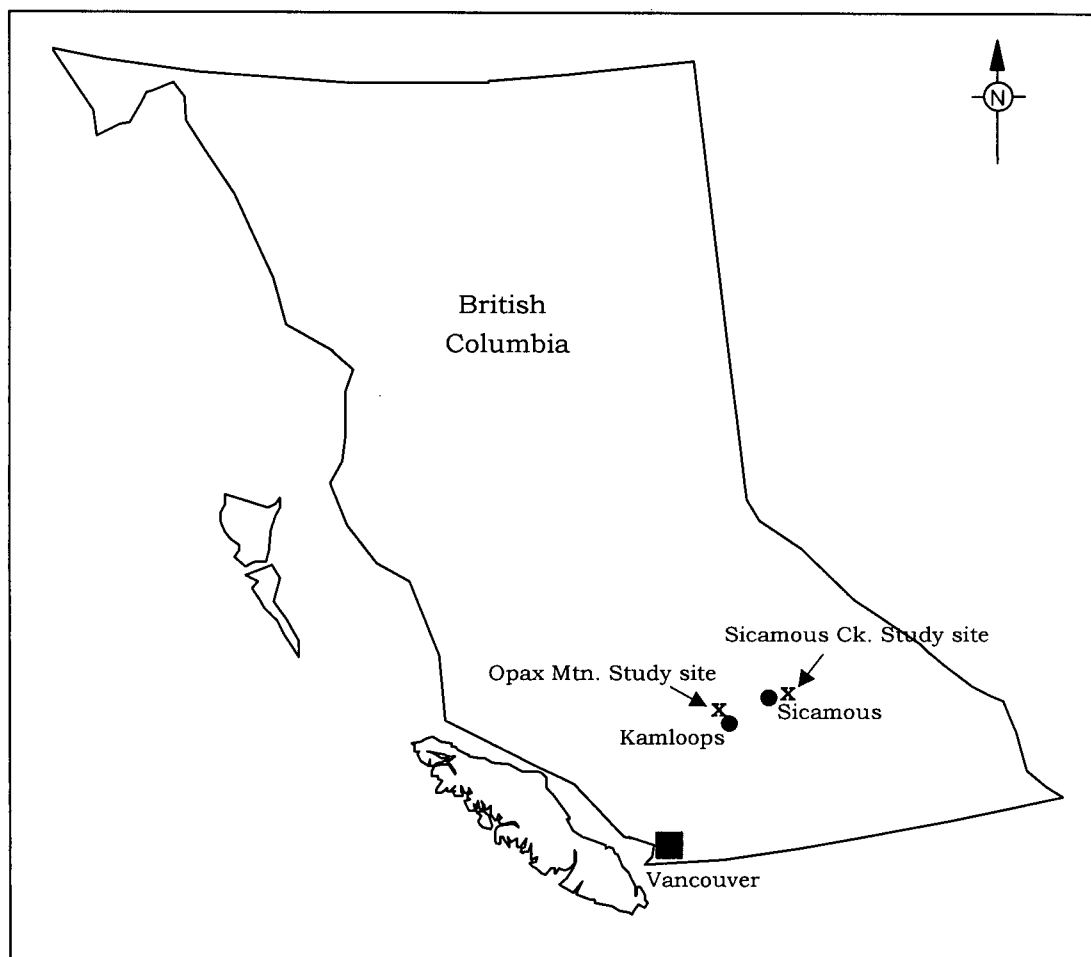
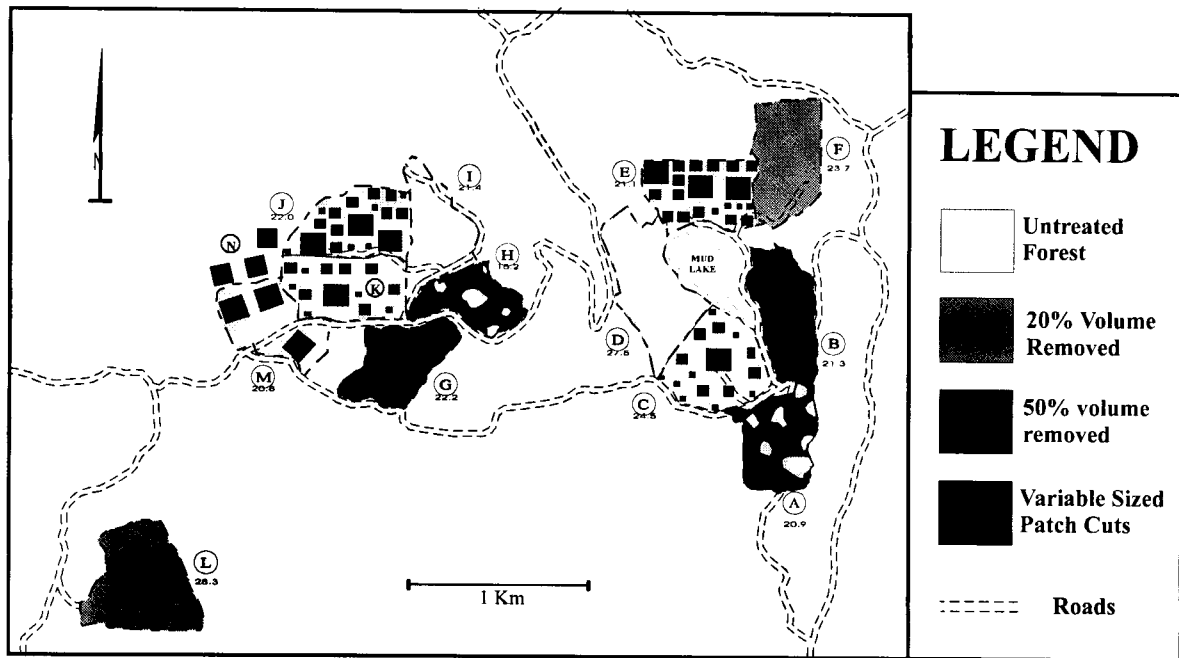


Figure 1. Map of British Columbia illustrating the location of the Opax Mountain and Sicamous Creek study areas.

To provide three replicates for my study, an additional control (forested, harvest treatment area N) and three, 1.7-ha patch-cuts (harvest treatment area M) were added to the original design (Fig. 2a).

The area has rolling topography, and an open forest canopy of Douglas-fir (*Pseudotsuga menziesii*) with some lodgepole pine (*Pinus contorta*). Aspen (*Populus tremuloides*) and sitka alder (*Alnus sitchensis*) is present in moister areas. The forest is generally multi-storied with locally-dense pockets of shrubs such as birch-leaved spirea (*Spiraea betulifolia*), rose (*Rosa* spp.), and soopolallie (*Sheperdia canadensis*). The low ground vegetation is sparse; where present it is dominated by herbs such as twinflower (*Linnaea borealis*) and racemose pussytoes

a) Opax Mountain



b) Sicamous Creek

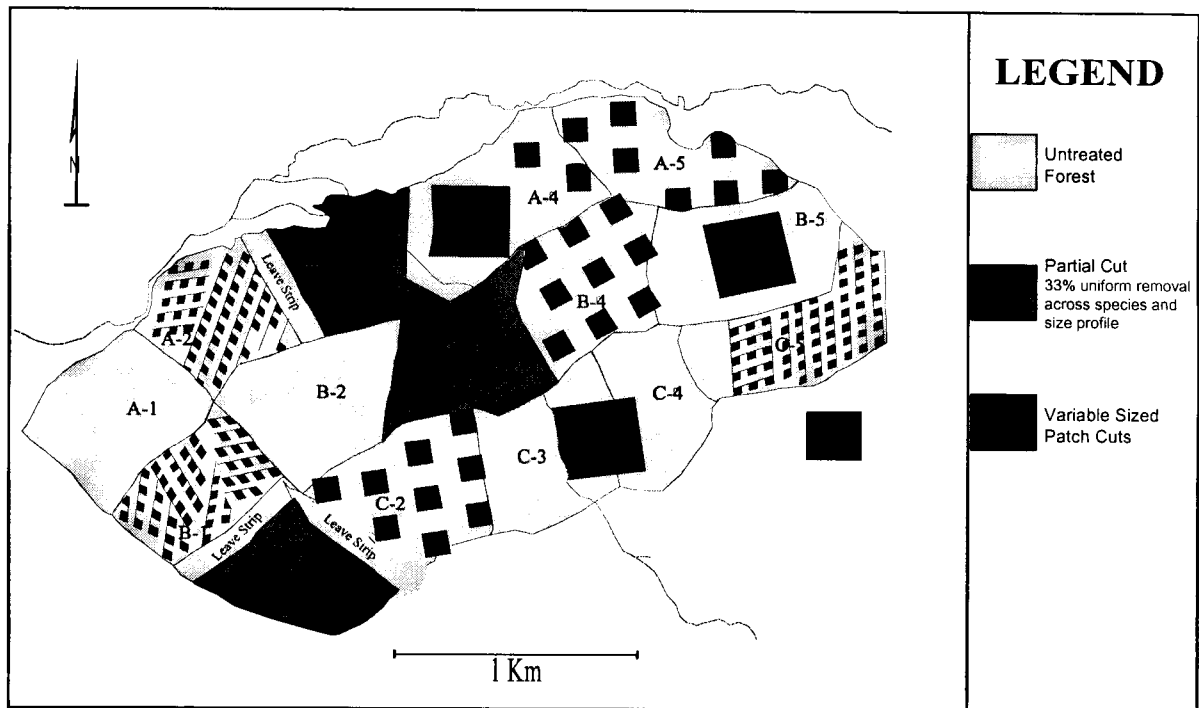


Figure 2. a) Map of the Opax Mountain Silvicultural Systems Project area. The area to the right is the lower-elevation Mud Lake portion (blocks A to F) and the area to the left is the Opax Mountain portion (blocks G to L), and b) Harvesting treatments at the Sicamous Creek Silvicultural Systems site.

(*Antennaria racemosa*), and pinegrass (*Calamagrostis rubescens*). Clear-cut areas were heavily vegetated by two years post-harvest. Clear-cuts were dominated by shrubs (rose, birch-leaved spirea, and common snowberry [*Symphoricarpos albus*]), pinegrass, and herbs (showy aster [*Aster conspicuus*], wild strawberry [*Fragaria virginiana*], and racemose pussytoes).

The study area was harvested during the winter of 1993-1994. Operational site-preparation (spot screefing with an excavator) in spring 1994 was followed by planting of tree seedlings on cut-over areas. In summer of 1994 I manipulated downed wood within three, 1.7-ha areas in each control and three, 1.7-ha areas in the 50% removal with patch-cuts harvest blocks, to provide a range in the amount of downed wood on the site.

In summer of 1995 I manipulated the amount of downed wood on 1.7-ha treatment areas within forested (control) blocks to provide a range in the amount of downed wood (methods described below). In total, I had 18 downed wood treatment areas on the study area.

1.2.2 Sicamous Creek Silvicultural Systems Project

The Sicamous Creek study area was located near the town of Sicamous, B.C. (50° 50' N, 119° 50' W, Fig. 1), approximately 150 km northeast from the Opax Mountain study area (Hollstedt and Vyse 1997). The site was located in the high-elevation Engelmann spruce-subalpine fir (ESSF, Meidinger and Pojar 1991) biogeoclimatic zone. It ranged from 1530 to 1830 m in elevation and was on a north-facing slope that was dominated by old-growth subalpine fir (*Abies lasiocarpa*), with some Engelmann spruce (*Picea engelmannii*) present. The oldest trees on the site were approximately 340 years old (Parish 1997). The understory was dominated by white rhododendron (*Rhododendron albiflorum*), black huckleberry (*Vaccinium membranaceum*) and oval-leaved blueberry (*V. ovalifolium*). Clear-cuts remained sparsely vegetated throughout the study; dominant vegetation included shrubs: white

rhododendron and black huckleberry, and herbs: sitka valerian (*Valeriana sitchensis*) and one-leaved foamflower (*Tiarella unifoliata*). Snow levels vary from approximately 1 m to 2.5 m on the site. Snow generally begins falling in October, and the snowpack is usually melted by the end of June. The study area was blocked by elevation (Fig. 2b), resulting in three strata (A, B, and C). Harvest treatments were randomly assigned to each of the five, 30-ha blocks within each stratum, and were designed to remove approximately 30% of the standing volume on the block (including skid trails and roads):

1. Single 10-ha clear-cut (A4, B5, C4 in Fig. 2b)
2. Array of nine, 1.0-ha patch cuts (A5, B4, C2)
3. Array of 65, 0.1-ha patch cuts (A2, B1, C5)
4. Uniform individual tree selection harvest (A3, B3, C1)
5. Uncut control (A1, B2, C4).

The study area was harvested during winter of 1994-1995. Operational site preparation, involving soil mounding with an excavator followed by planting, was conducted in the harvested zones. I manipulated downed wood levels on three, 1.7-ha areas within 10-ha clear-cut harvest blocks during harvest and summer 1995. Downed wood was manipulated on three 1.7-ha treatment areas within each forested block (uncut control) in summer 1996. As at Opax, I had 18 downed wood treatment areas on the study area.

Chapter 2. Downed Wood and Habitat Characteristics

2.1 Introduction

Although downed wood is often reported to be an important habitat component for small mammals, little population-level manipulative research has been conducted. Loeb (1999) reported that cotton mouse (*Peromyscus gossypinus*) abundance and survival was higher on areas where a tornado had created a large amount of downed wood in a 45 year-old forest. Moses and Boutin (2001) studied the response of small mammals to the removal of downed wood from clear-cuts in a 60-80 year-old boreal mixedwood forest. They reported that all of the small mammal species studied were similarly abundant on clear-cuts without downed wood, and areas where downed wood was retained. My study is the first to experimentally examine the relationship between small mammals and downed wood in older forests. I studied deer mouse, meadow and long-tailed vole, and southern red-backed vole population dynamics on both forested areas and on clear-cuts (forest openings), where I manipulated the amount of downed wood. The experimental design was replicated in two forest types. For a description of the study areas, see Chapter 1.

In this chapter, I describe the downed wood treatments, and the resulting amounts of downed wood and habitat characteristics on the treatment areas.

2.2 Methods

2.2.1 Field Methods

2.2.1.1 Downed Wood Treatments

Three 1.7-ha treatment areas were laid out in each patch-cut/clear-cut harvest block (Figs. 3 and 4). Treatments designated as *low*, *medium* (control) or *high* amounts of downed wood were randomly assigned to each treatment area. Downed wood on clear-cuts at both Opax and

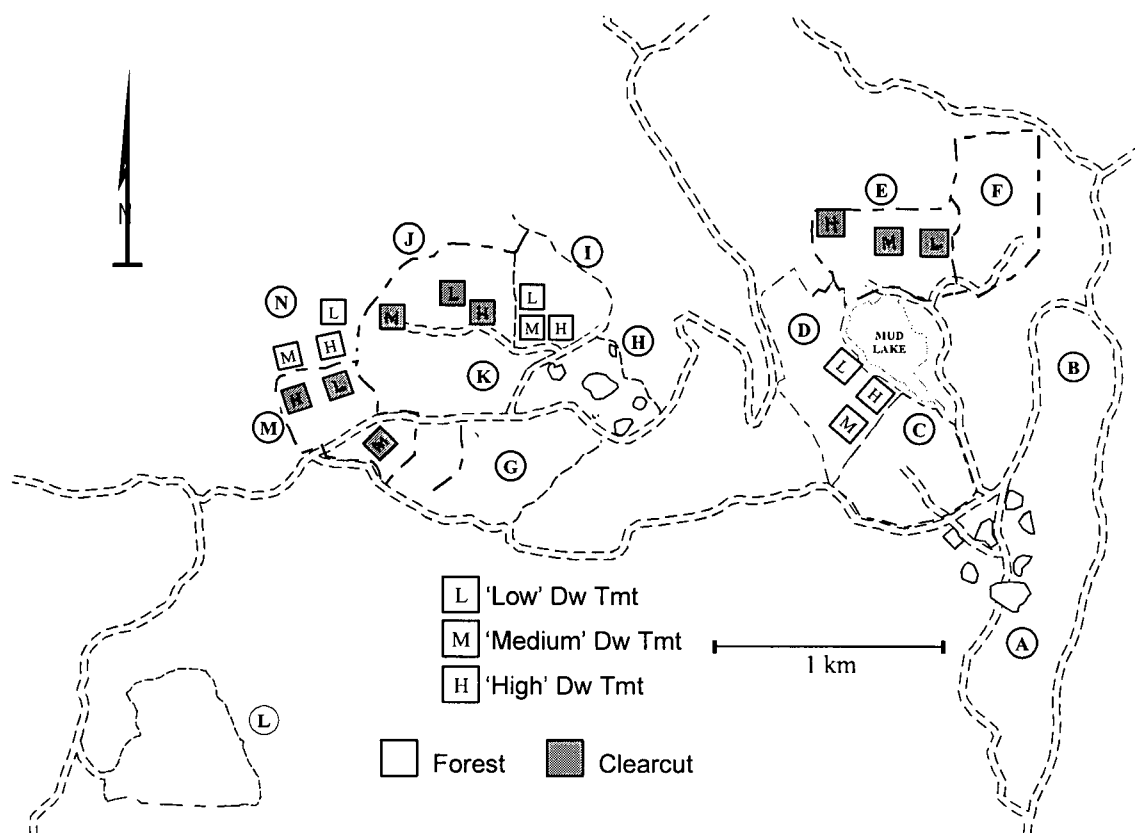


Figure 3. Map showing the placement of the downed wood treatment areas in the Opax Mountain Silvicultural Systems project study area. Detail for other silvicultural treatments illustrated in Fig. 2a was removed for clarity. Downed wood treatment areas were placed in the 1.7-ha cut-blocks in blocks E, J, and M, and in the forested control blocks (D, I, and N).

Sicamous study areas was manipulated following the same procedure. All downed wood >6 cm in diameter was removed from *low* treatment areas during harvesting. The excavator operator removed intact pieces and crushed and scattered logs of decay class 4 or 5 (Maser *et al.* 1979). This prevented small mammals from using tunnels associated with the logs, and altered the log microclimate to reduce insects and fungi associated with decayed downed wood (Harmon *et al.* 1986). Although the excavator was able to remove most of the downed wood on clear-cuts at Opax, downed wood removal at Sicamous was not as complete. Downed wood remaining on *low* clear-cut treatment sites at Sicamous was removed by hand. *Medium* treatments at both study areas were treated in an operational manner; downed wood was not manipulated beyond

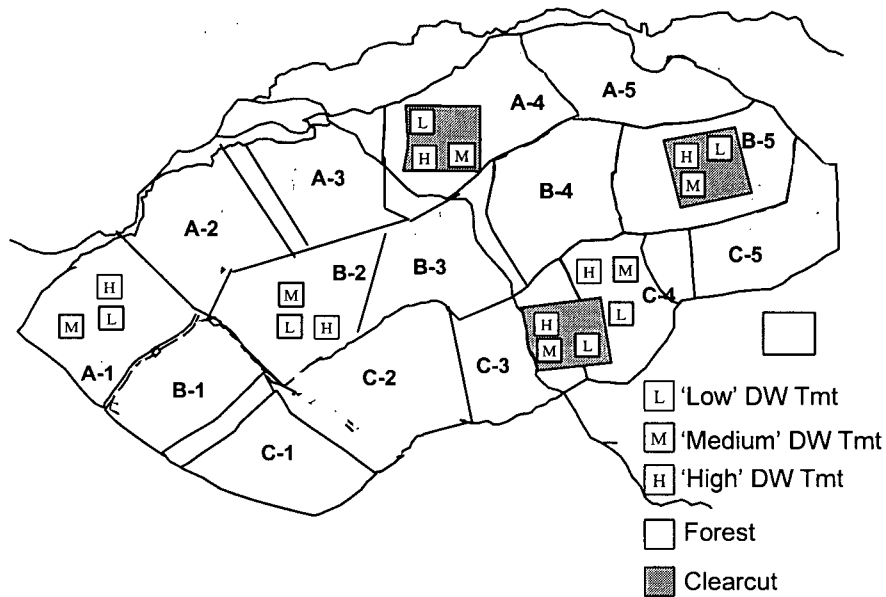


Figure 4. Map showing the placement of the downed wood treatment areas in the Sicamous Creek Silvicultural Systems project study area. Detail for other silvicultural treatments illustrated in Fig. 2b was removed for clarity. Downed wood treatment areas were placed in the 10-ha cut-blocks in harvest treatment units A4, B5, and C3, and in the forested control units (A1, B2, and C4).

what occurred during harvesting. On *high* treatment areas, downed wood pieces that normally would be removed from the site (*e.g.*, snags) were retained and distributed across the treatment area. A few large logs on clear-cut *high* treatments at the Opax study area that could potentially provide habitat for the Douglas-fir beetle (*Dendroctonus pseudotsugae*) that was present on the study area (Miller and MacLauchlan 1998), had their bark scraped off by the excavator before they were left on the area. Logs were de-barked on site and the branches, bark, and associated lichens were left on the treatment area. Downed wood on all clear-cuts was distributed evenly across the site.

Downed wood treatments (*low*, *medium*, and *high*) on forested blocks were randomly assigned to each of three, 1.7-ha treatment areas within each forested block. On forested areas at Opax and Sicamous, intact pieces of downed wood >6 cm in diameter were removed from *low* treatment areas and all wood of decay class 4 or 5 was crushed and scattered over the ground.

Methods for achieving *medium* and *high* treatments on forested sites varied between Opax and Sicamous because the high levels of downed wood at the Sicamous study area made it more difficult and time-consuming to move wood by hand. At Opax, *medium* treatments had approximately half of the downed wood removed in proportion to the naturally occurring variability in diameter, length and decay class. Downed wood volumes on *high* treatment areas at Opax were not manipulated and represented the natural forest condition. On Sicamous forested blocks, *medium* treatment areas were not manipulated, and approximately 12 snags were felled on to each *high* treatment area.

2.2.1.2 Measurement of Downed Wood

Downed wood was sampled in three plots on each small-mammal sampling grid pre- and post-downed wood manipulation (M. Feller, unpubl. data). Each plot was an equilateral triangle 30 m long on each side. The initial plot point was randomly chosen on the grid, and the initial compass bearing was randomly chosen. Data on the diameter, species and decay class (four decay classes, Feller 1997) of all downed wood ≥ 1 cm in diameter that crossed the lines were recorded. The length of every fifth piece of wood ≥ 1 cm in diameter that crossed each transect was also measured. Data collected on diameter of pieces were used to calculate the volume of downed wood present before and after treatment. The formula to calculate volume is as follows (Van Wagner 1968):

$$V (m^3 / ha) = ([\pi^2 \times \sum(D^2) \times 10^2 \text{ cm} / m] / [8 \times L]) \times 10^4 m^2 / ha$$

where D = diameter of the piece of wood (in centimetres)

L = length of the transect (in metres)

2.2.1.3 Downed Wood, Vegetation, and Litter and Moss Sampling

Data on vegetation, trees and downed wood were collected on each small mammal sampling grid. Data were collected in 1996 in 5.65-m radius vegetation plots centred on every other trap

station (25 plots per sampling grid). Plots were divided into four sections and the following data collected for each section (visual estimation to the closest percent): 1) canopy cover, 2) percent ground cover by mineral soil, 3) percent ground cover by moss, 4) mean moss depth (three estimates per section), 5) percent ground cover of fine litter, 6) mean depth of the litter layer (three estimates per section), 7) mean cover of herbs (including grasses), 8) mean cover by short shrubs (<2 m tall), 9) mean cover by tall shrubs (≥ 2 m tall), 10) estimate of ground cover from all sources (including downed wood). This was a visual estimate of the potential amount of security/thermal cover for small mammals, estimated by the ground covered by all vegetation (including canopy) and downed wood within the entire plot. This variable will be referred to hereafter as an estimate of protective cover on the area, 11) within each section a list of all trees ≥ 7.5 cm DBH were recorded, along with their diameter, species, and an estimated height. As well, a triangular transect was superimposed with the main axis along the centre of each habitat plot and data on downed wood ≥ 7.5 cm in diameter were collected. For each piece of downed wood ≥ 7.5 cm in diameter that crossed the transect, data on its attributes such as diameter, species, and decay class (following Maser *et al.* 1979) were recorded. Mean values for each habitat component for each sampling grid are provided in Appendix 1.

2.2.2 Data Analyses

2.2.2.1 Downed Wood Treatments

To determine whether the amount of downed wood changed with harvesting, volumes on clear-cut *medium* grids (unmanipulated) were compared with volumes present on forested unmanipulated treatment areas with one-way analysis of variance (ANOVA). Volume data were square-root transformed to normalize the data prior to analysis. Significant results were investigated with pairwise contrasts (two-sample t-tests). Pairs were first tested for homogeneity of variance with a pairwise F-test. Based on the result of the F-test, the appropriate t-test was

used to compare the grids (1-tailed t-test assuming equal or unequal variances). In all tests where there were multiple comparisons, I adjusted alpha by the number of comparisons ($0.05 / \text{number of comparisons}$) to compensate for experiment-wise error.

Downed wood volumes across treatments (*low to high*) within harvest treatments (clear-cut, forest) were compared with a one-way ANOVA to determine whether downed wood volume on treatment areas differed from each other. Significant results were investigated using pairwise contrasts, after testing for homogeneity of variance, as above.

To describe the composition of downed wood on each area (diameter and decay class), I constructed histograms using post-treatment downed wood data collected on each sampling grid. I counted number of pieces within eight diameter classes (1-5 cm, 5-10, 10-20, 20-30, 30-40, 40-50, and >50 cm) and 5 decay classes (following Maser *et al.* 1979). I graphed means, where means were calculated as the total number of pieces tallied within each class across all plots within sampling grids, divided by the number of sampling grids (3) within each downed wood treatment.

2.2.2.2 Downed Wood, Vegetation, and Litter and Moss Sampling

I compared differences in percent ground cover by vegetation across downed wood treatments and blocks by constructing graphs of means ± 2 SE to provide an indication of the variability around the mean to compare to other values. This was a more appropriate method than using statistical tests to compare a large number of variables over relatively few sampling grids (nine per seral stage). However, SE varies asymmetrically around a proportional variable and confidence intervals should be interpreted as an exploratory indicator only.

2.3 Results

2.3.1 Downed Wood

At both the Opax ($F_{1,16} = 0.00$, $P > 0.5$) and Sicamous Creek ($F_{1,16} = 0.05$, $P > 0.5$) study areas, the volume of wood on unmanipulated clear-cuts was similar to the volumes found on untreated forested areas (Figs. 5 and 8).

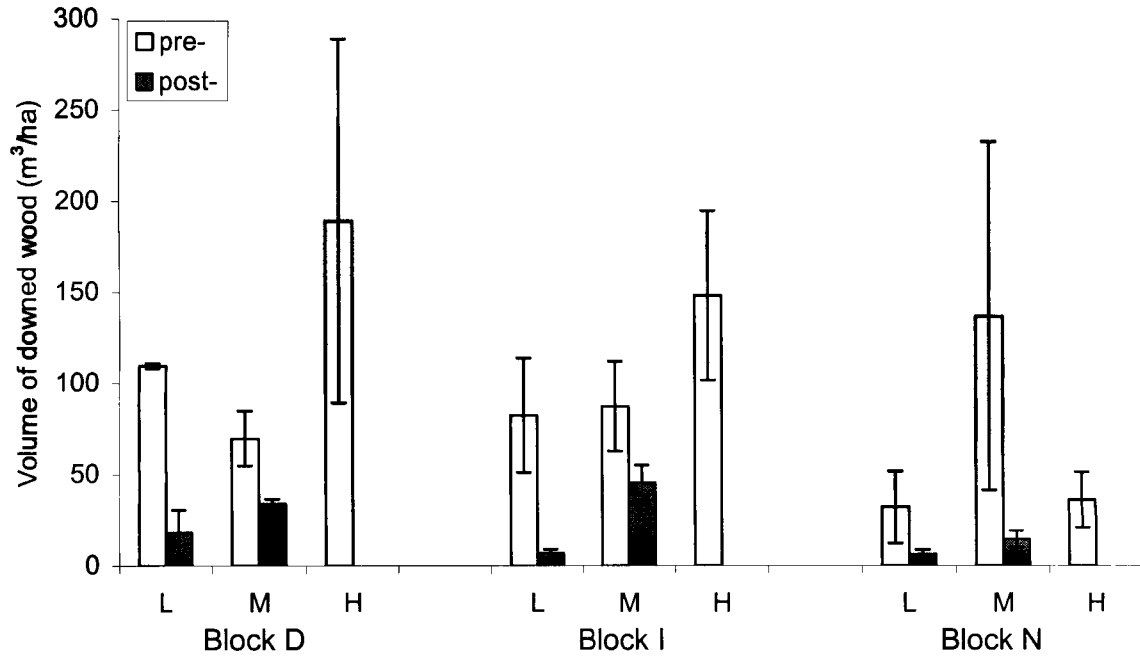
2.3.1.1 Opax Mountain: Forest

On Opax forested grids, pre-treatment levels of downed wood were similar across all (future) downed wood treatment classes ($F_{2,24} = 0.30$, $P > 0.05$). I removed 83%, 92% and 81% of downed wood volume from *low* treatment replicates on D, I, and N, respectively (Fig. 5a). On *medium* treatments 52%, 48%, and 81% of the downed wood volume was removed. Downed wood manipulations created a significant range in the amount of downed wood ($F_{2,24} = 7.80$, $P < 0.005$). Post-treatment *low* areas had lower downed wood volumes than either *medium* ($t_{16} = 3.5$, $P_{1\text{-tail}} < 0.002$, $\alpha = 0.017$) or *high* areas ($t_9 = 3.29$, $P_{1\text{-tail}} < 0.005$, $\alpha = 0.017$). *Medium* treatment areas tended to have lower downed wood volumes than *high* areas (Fig. 5a); however the difference was not statistically significant ($t_9 = 2.07$, $P_{1\text{-tail}} = 0.03$, $\alpha = 0.017$).

Low downed wood treatments had no pieces >15 cm in diameter left on the grids after treatment (Fig. 6a). Therefore, the volume of downed wood on *low* treatment areas was mostly composed of moderately sized (5-15 cm) pieces of downed wood (Fig. 7a). Small pieces (<5 cm) contributed a greater proportion of overall volume on *low* treatment areas than on *medium* or *high* areas (Fig. 7a).

Volumes on *medium* treatment areas appeared to have a slightly greater proportion composed of small pieces than *high* areas (Fig. 7a), but recalculating downed wood volumes without small pieces (<5 cm in diameter) indicated the same pattern as described above.

a) Forest



b) Clear-cut

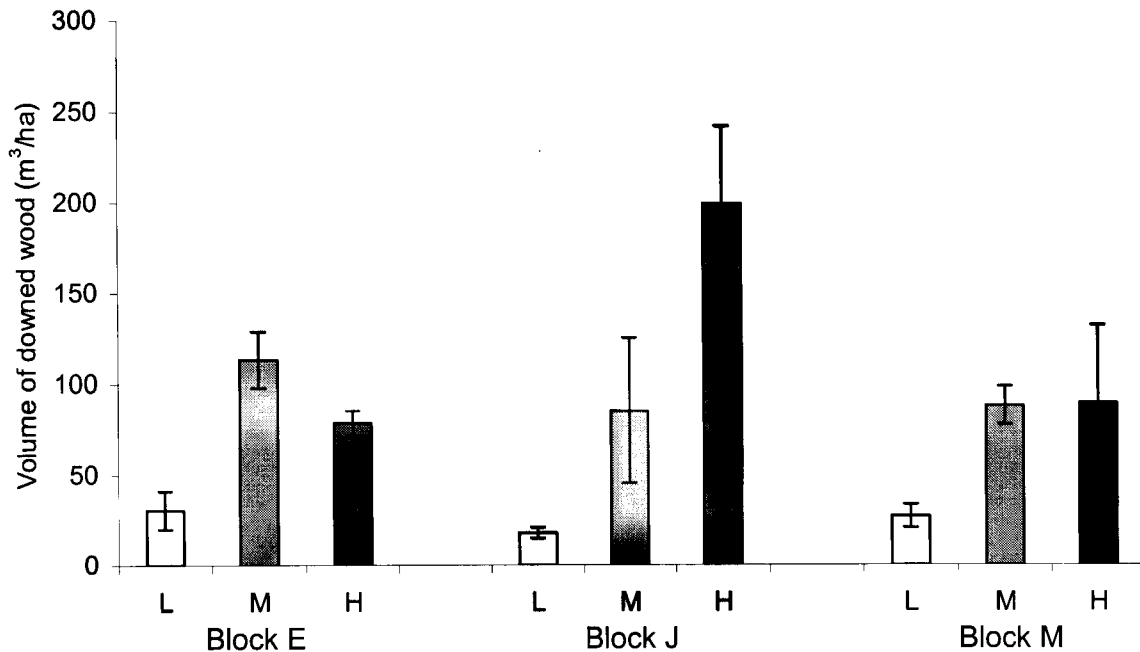
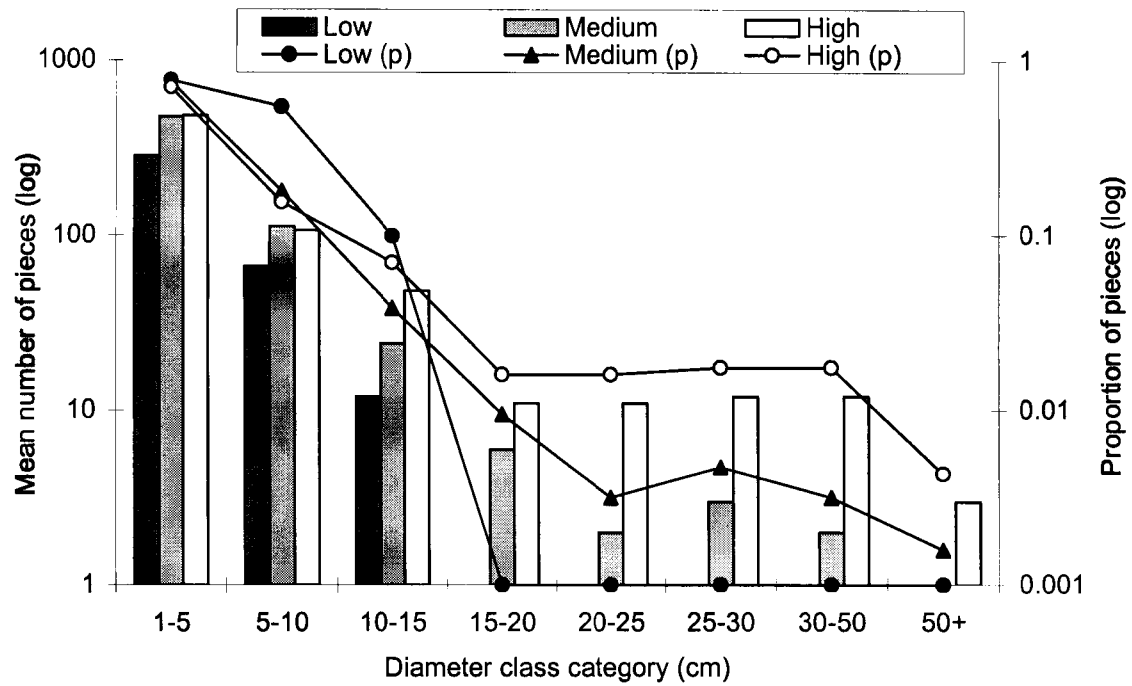


Figure 5. Downed wood volume on treatment areas at the Opax study area. a) Pre- and post-treatment mean downed wood volumes (m³/ha) on each of the forested treatment areas, where downed wood on *high* treatment areas was not manipulated (therefore only pre- data are shown), and b) mean downed wood volumes (m³/ha, post-treatment) on clear-cut downed wood treatment areas. L = *low*, M = *medium*, and H = *high* treatments. Note that the scale of the Y axis is smaller than in Figure 8. Means are shown $\pm$ 2 SE.

a)



b)

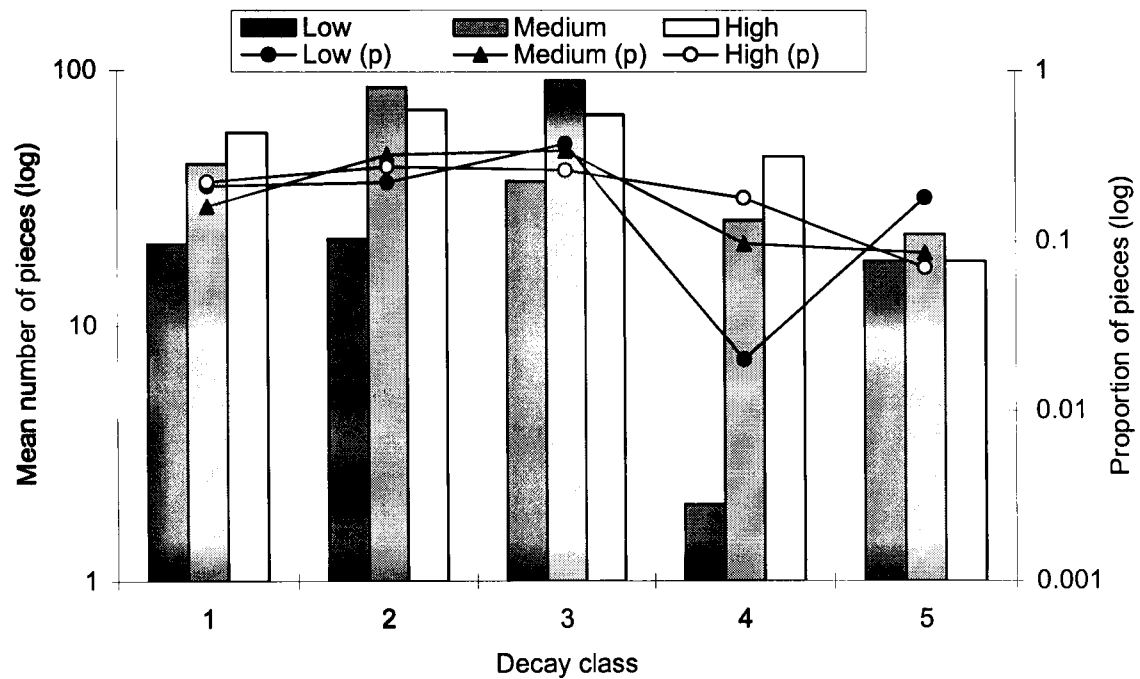
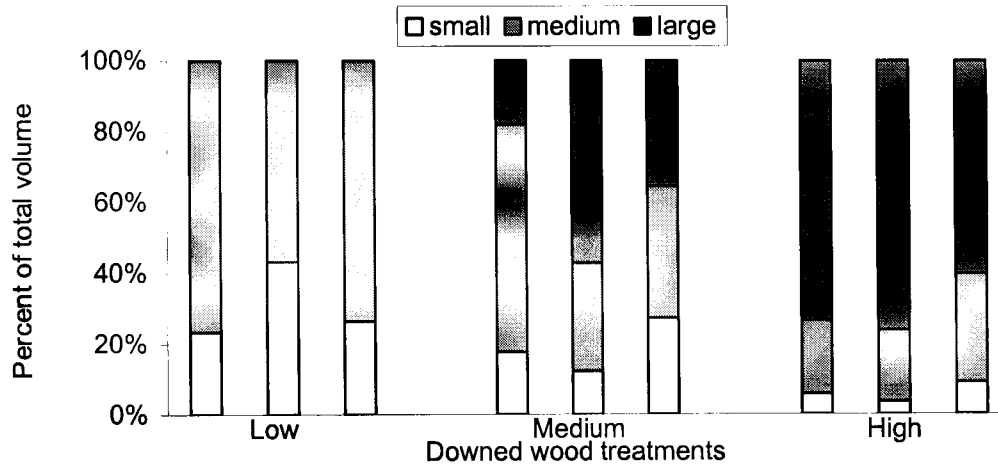


Figure 6. Mean number of pieces (bars, logarithmic scale) and the proportion of pieces (lines; logarithmic scale) within a) diameter class categories, and b) each of 5 decay classes for pieces ≥ 7.5 cm in diameter, for *low*, *medium*, and *high* treatment areas on Opax forested sampling grids.

a) Forest



b) Clear-cut

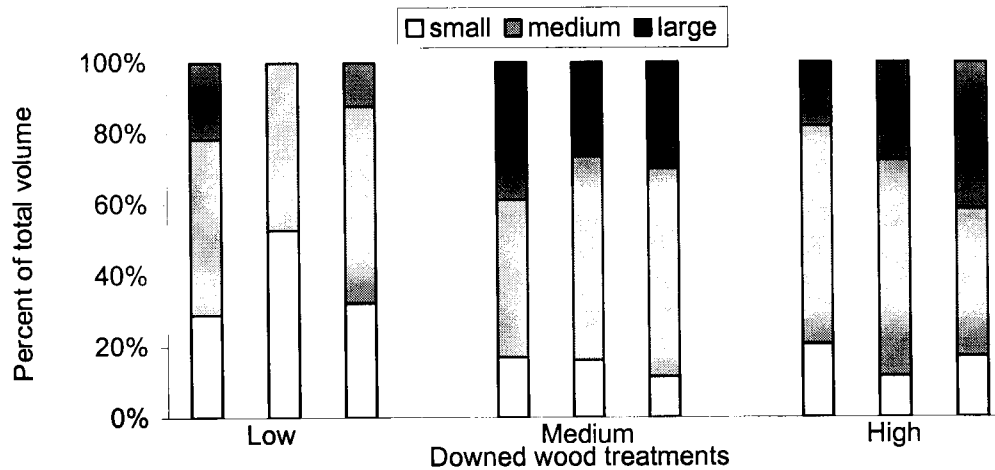


Figure 7. Percent of post-treatment downed wood volume on each treatment area comprised of small (<5 cm in diameter), medium (5-15 cm) or large (>15 cm in diameter) pieces on a) forested and b) clear-cut areas at Opax. Forest data are presented within downed wood treatment class for blocks D, I, and N, and clear-cut data are presented for blocks E, J, and M.

Downed wood treatments created a range in the volume of downed wood across treatment classes ($F_{2,24} = 10.80$, $P < 0.001$). Although volumes on *medium* treatments tended to be lower, treatments did not reduce downed wood volume below that on *high* treatment areas ($t_{10} = 2.3$, $P_{1\text{-tail}} = 0.02$ $\alpha = 0.017$). The proportion of pieces on *low* areas in decay class 4 was lower than on *medium* or *high* treatment areas (Fig. 6b). Although the number of decay class 5 pieces appeared to be similar on *low*, *medium* and *high* treatment areas, the majority of pieces recorded on *low* areas were chunks of downed wood that were spread across the area (small pieces).

2.2.1.2 Opax Mountain: Clear-cut

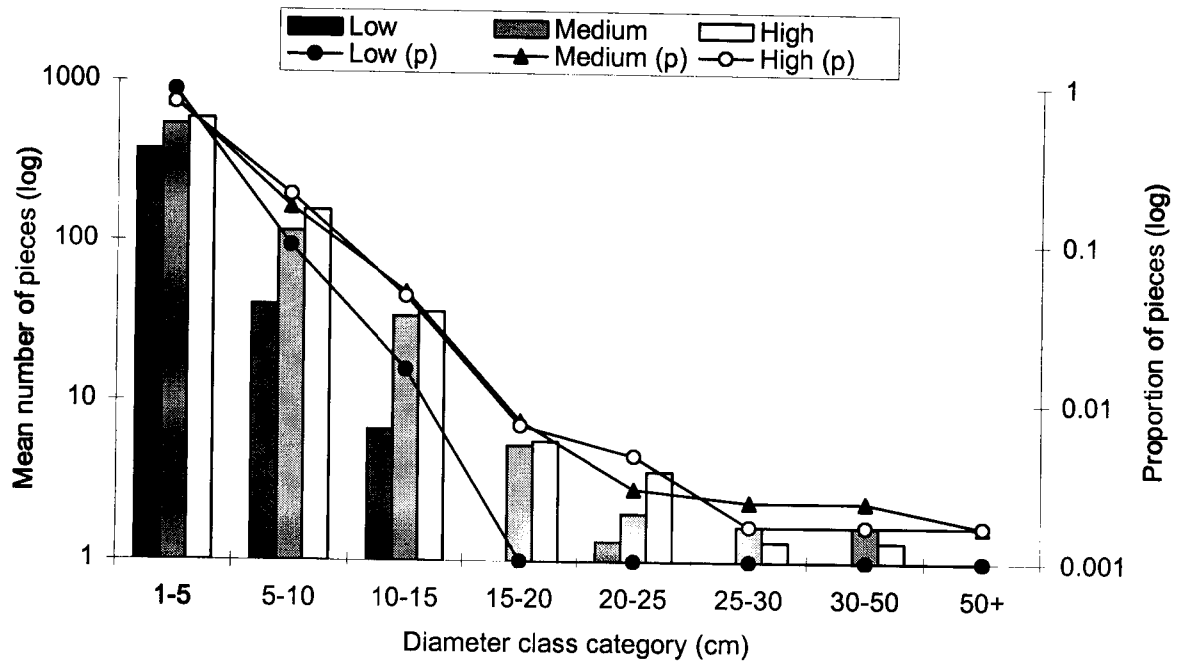
Downed wood treatments on Opax clear-cuts created a range in the amount of downed wood on treatment areas ($F_{2,24} = 31.98$, $P < 0.001$). *Low* treatment areas had lower downed wood volumes than *medium* ($t_{16} = 9.92$, $P_{1\text{-tail}} < 0.001$, $\alpha = 0.017$) or *high* ($t_{10} = 6.68$, $P_{1\text{-tail}} < 0.001$, $\alpha = 0.017$) areas (Fig. 5b). *Medium* and *high* treatment areas had similar volumes of downed wood ($t_{12} = 0.78$, $P_{1\text{-tail}} > 0.20$, $\alpha = 0.017$), primarily because of high variability among *high* treatment grids. *Low* treatments had a greater proportion of the downed wood volume composed of smaller pieces (<5 cm in diameter) than *medium* or *high* areas (Fig. 7b). The proportion of volume contributed by medium-sized (5-15 cm diameter) and large (>15 cm diameter) pieces was similar on *medium* and *high* treatments (Fig. 7b).

The majority of the downed wood on all treatments was small (<5 cm) debris left after harvesting (Fig. 8a). Larger pieces remained on *medium* and *high* treatments post-harvest. The majority of downed wood on all of the clear-cut sampling grids was in relatively early stages of decay (decay classes 1-3, Fig. 8b).

2.3.1.3 Sicamous Creek: Forest

Downed wood manipulations on forested areas at Sicamous Creek were successful in creating a range in the amount of downed wood on the forested grids ($F_{2,24} = 78.0$, $P < 0.001$, Fig. 9a). Post-treatment volume of downed wood on *low* treatment areas was lower than on *medium* or *high* areas ($t_{10} = 11.43$, $t_{12} = 12.63$, $P_{1\text{-tail}} < 0.001$, $\alpha = 0.017$ for both comparisons); however, volumes on *medium* and *high* treatments did not differ ($t_{15} = 1.24$, $P_{1\text{-tail}} > 0.10$, $\alpha = 0.017$). Most of the larger pieces of downed wood were removed from *low* treatment areas, but the treatment was not 100% (Fig. 10a). Some pieces of larger logs remained on site, but the majority of these were small sections of larger logs that had been cut and removed from the site. The sections of log remaining composed a variable proportion of the downed wood volume on

a)



b)

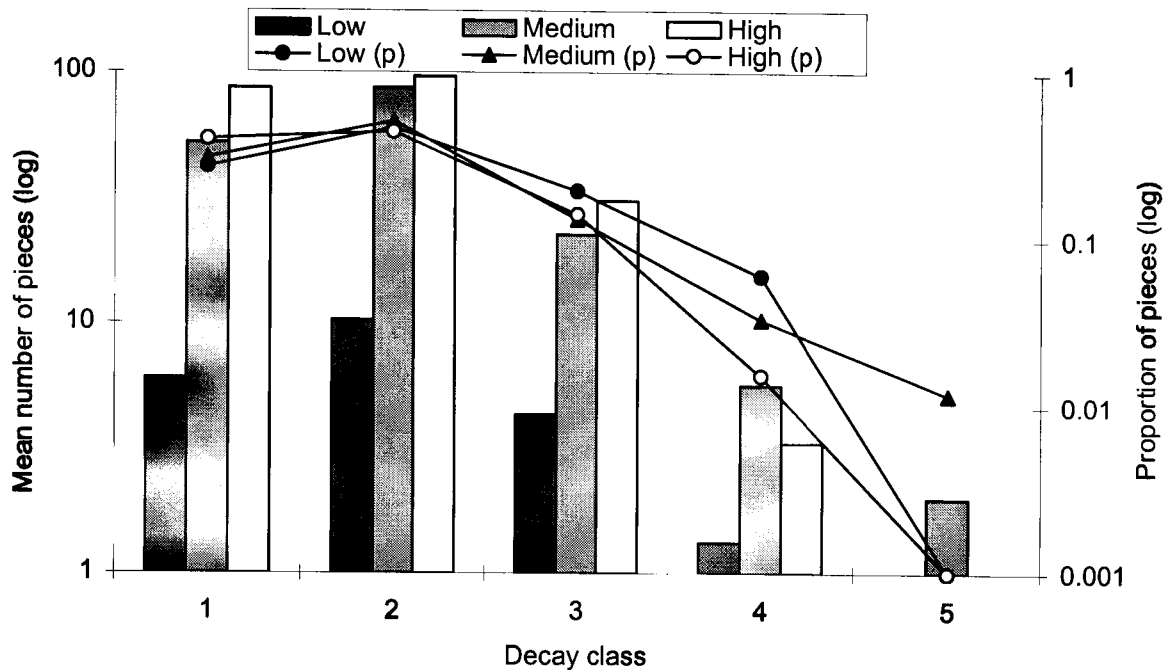
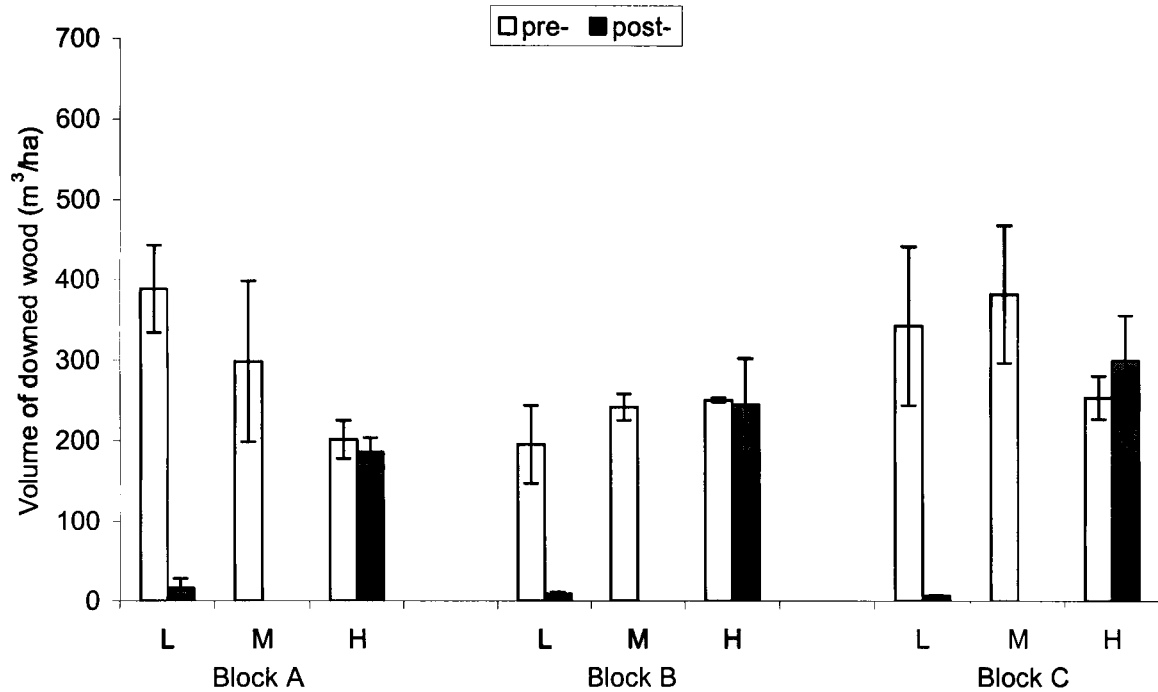


Figure 8. Mean number of pieces (bars, logarithmic scale) and the proportion of pieces (lines; logarithmic scale) within a) diameter class categories, and b) each of 5 decay classes for pieces ≥ 7.5 cm in diameter, for low, medium, and high treatment areas on Opax clear-cut sampling grids.

a) Forest



b) Clear-cut

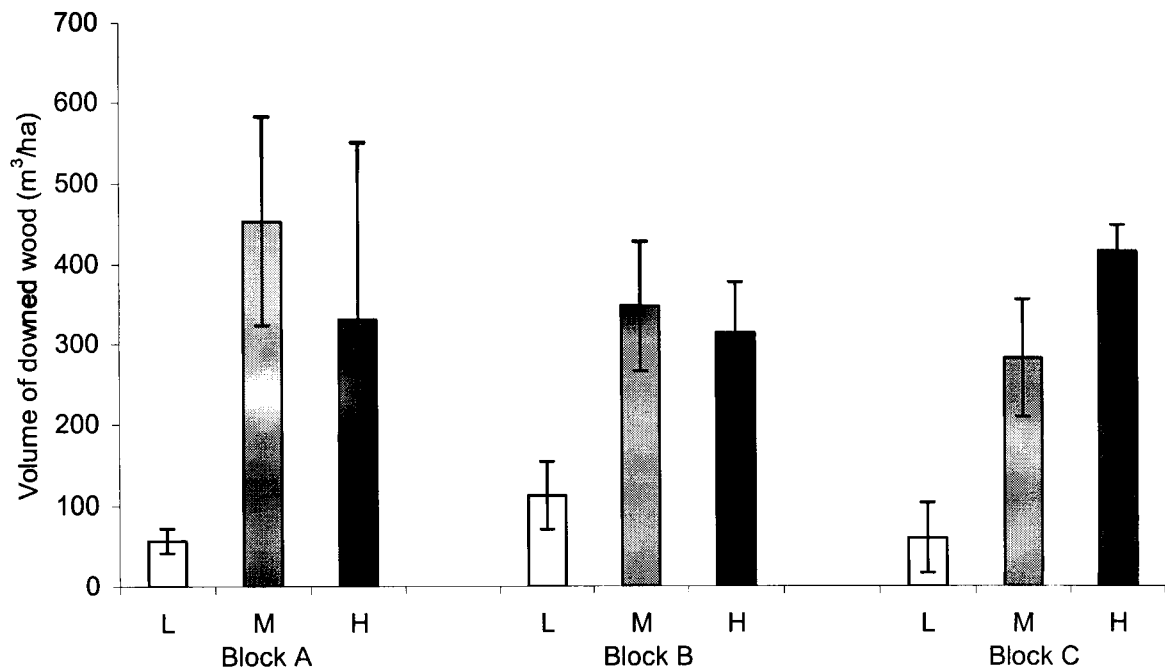


Figure 9. Downed wood volume on treatment areas at the Sicamous Creek study area. a) Pre- and post-treatment downed wood volume (m^3/ha) on forested treatment areas, where downed wood on *medium* treatments was not manipulated (therefore only pre- data are shown), and b) mean downed wood volumes (m^3/ha , post-treatment) on clear-cut treatment areas. L = *low*, M = *medium*, H = *high* downed wood treatments. Note that the scale of the Y axis is larger than that for Figure 5. Means are shown ± 2 SE.

low areas (Fig. 11a). The number of large pieces was similar on *medium* and *high* treatment areas, and they contributed most of the downed wood volume on both *medium* and *high* areas (Fig. 10a, Fig. 11a). As at Opax, the apparently large number of heavily decayed pieces (decay class 4 and 5, Fig. 10b) on *low* treatment areas was composed of small chunks (generally <50 cm long) of decayed logs that were scattered over the area. *Medium* and *high* treatment areas had similar amounts of downed wood in each decay category, but *high* treatments tended to have more pieces in decay classes 3-5.

2.3.1.4 Sicamous Creek: Clear-cut

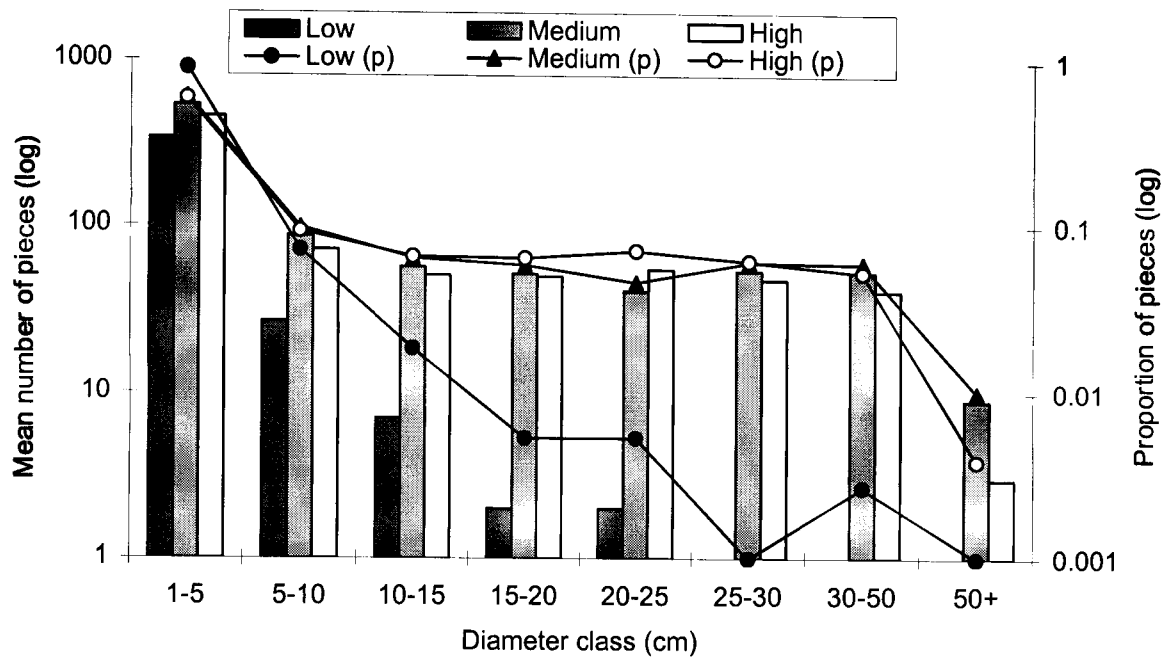
Downed wood volumes varied across downed wood treatments ($F_{2,24} = 38.09$, $P < 0.001$). *Low* treatment areas had lower wood volumes than on *medium* or *high* areas ($t_{16} = 8.2, 7.9$, $P_{1\text{-tail}} < 0.001$, $\alpha = 0.017$ for both comparisons, Fig. 9b). However, *medium* and *high* sites had similar volumes of downed wood ($t_{16} = 0.4$, $P_{1\text{-tail}} > 0.10$, $\alpha = 0.017$). The vast majority of downed wood pieces on clear-cuts were <5cm in diameter, but they generally contributed little to overall volume (Fig. 11b and Fig. 12a). Most of the larger pieces of downed wood were removed from *low* treatment areas, but the occasional large piece remained, which contributed heavily to overall volume (Fig. 11b and Fig. 12a). In general, *medium* and *high* treatments had 5-10x the number of large pieces that *low* treatments did. Few heavily decayed pieces of downed wood were present on any of the clear-cut treatment areas post-harvest (Fig. 12b), likely because they were broken apart during harvesting and site-preparation. Decay class 4 and 5 pieces on *low* treatment areas were generally chunks left after the logs were crushed and broken apart.

2.3.2 Downed Wood, Vegetation, and Litter and Moss Sampling

2.3.2.1 Opax

Forested areas at Opax had greater amounts of shrub, moss, and litter cover than on clear-cuts (Fig. 13a, Appendix 1). However, mean protective cover was similar on clear-cut and

a)



b)

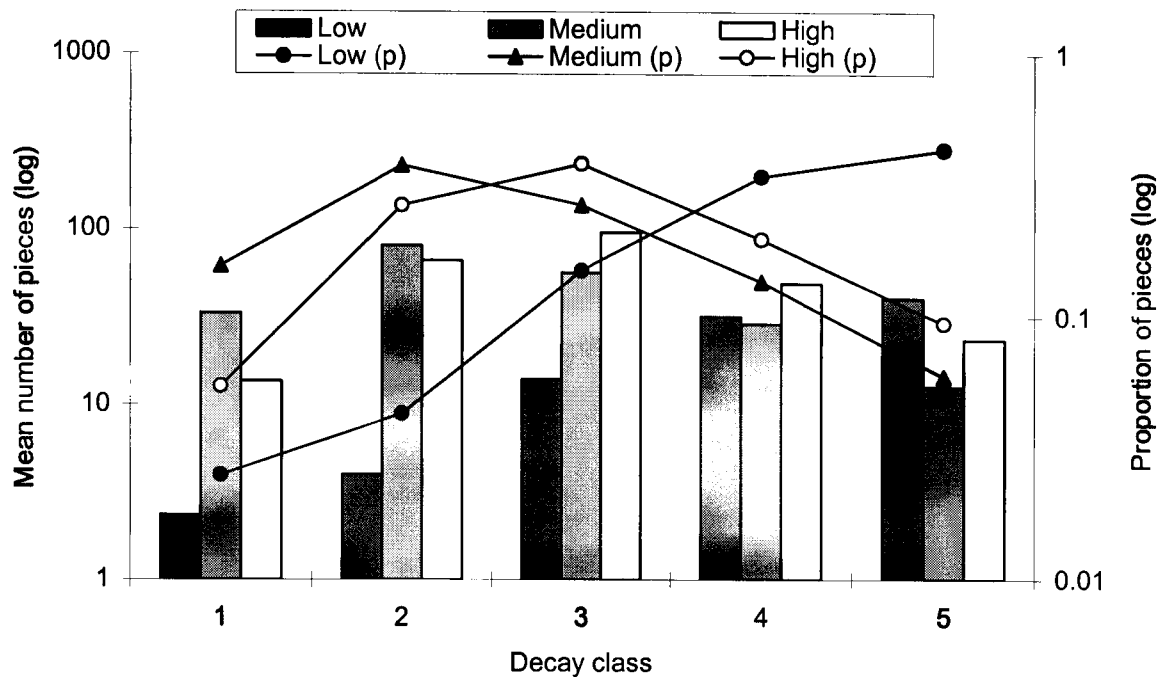
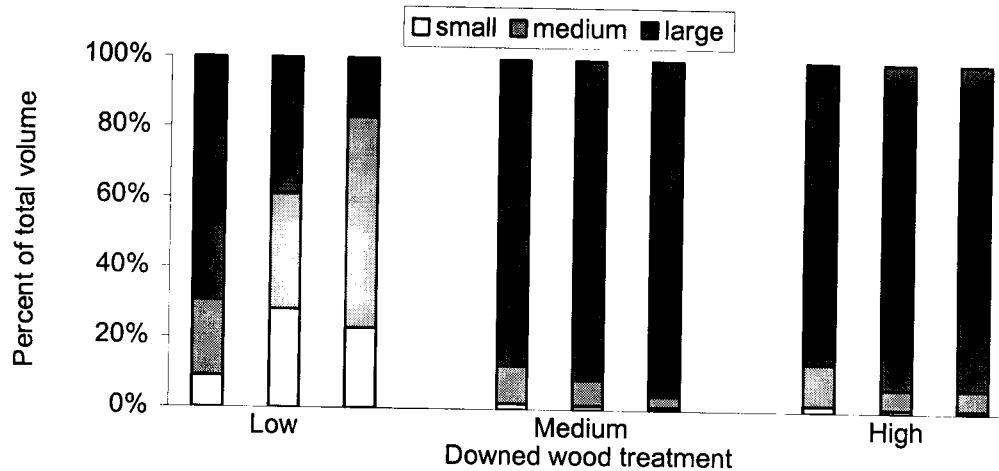


Figure 10. Mean number of pieces (bars, logarithmic scale) and the proportion of pieces (lines; logarithmic scale) within a) diameter class categories, and b) each of 5 decay classes for pieces ≥ 7.5 cm in diameter, for low, medium, and high treatment areas on Sicamous forested sampling grids.

a) Forest



b) Clear-cut

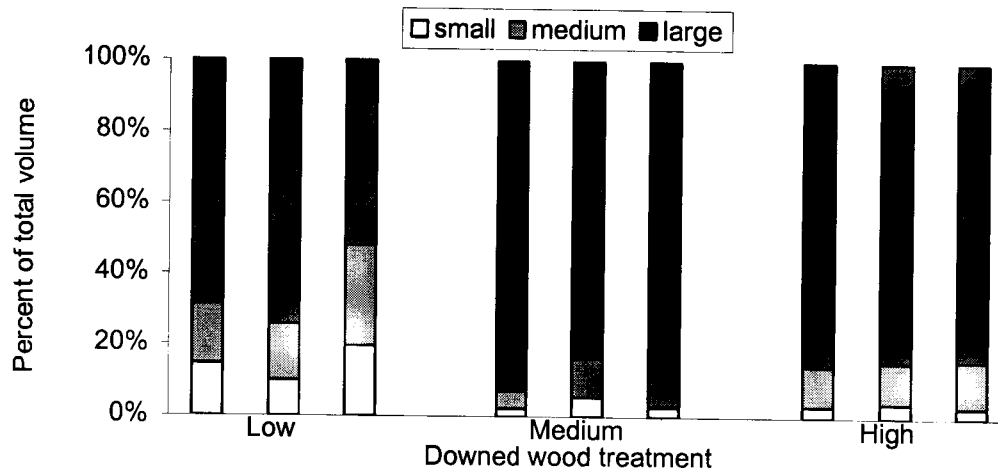
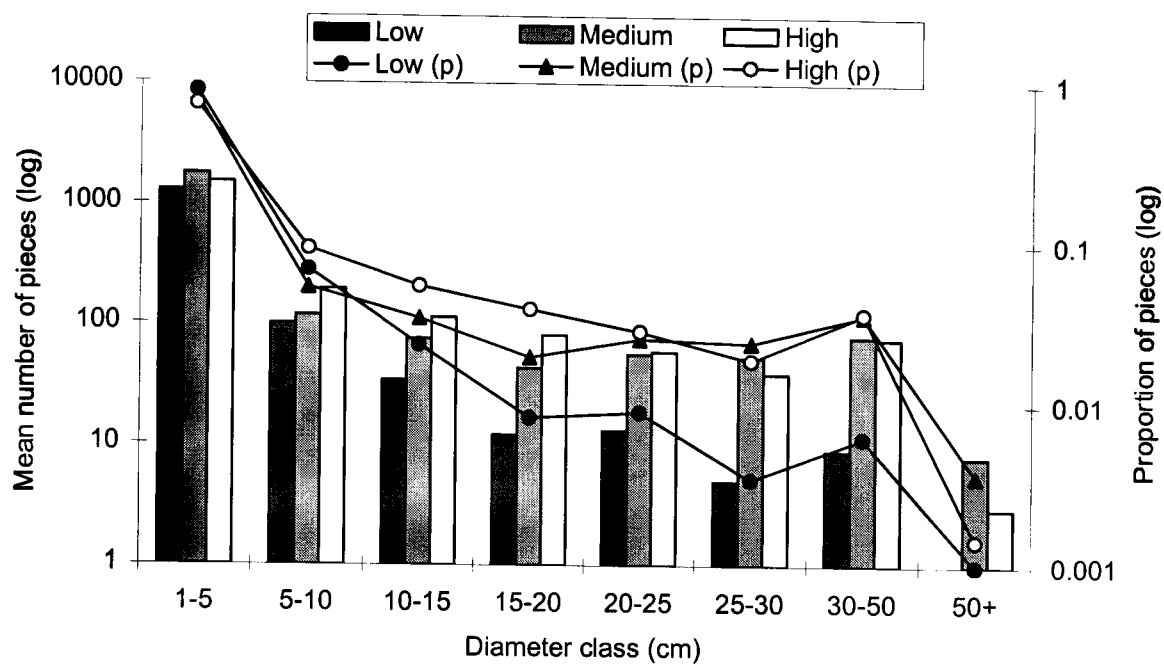


Figure 11. Percent of post-treatment downed wood volume on each downed wood treatment area comprised of small pieces <5 cm in diameter, medium-sized pieces (5-15 cm in diameter) or larger pieces (>15 cm in diameter) on a) forested and b) clear-cut areas at Sicamous. Forest and clear-cut data are presented within downed wood treatment for blocks A, B, and C.

forested areas because of the greater amount of herb cover on clear-cuts. Herbs (including grass) were the dominant form of vegetation on both forested and clear-cut areas. Clear-cuts had greater amounts of exposed mineral soil, which likely was exposed during harvesting and site preparation.

On forested areas, percent ground cover in the herb and grass, and tall shrub layer (≥ 2 m in height) was greater on *high* than on *medium* or *low* areas (Fig. 13b). The herb and perhaps shrub layer was likely disturbed by crews that conducted downed wood removals on *low* and *medium*

a)



b)

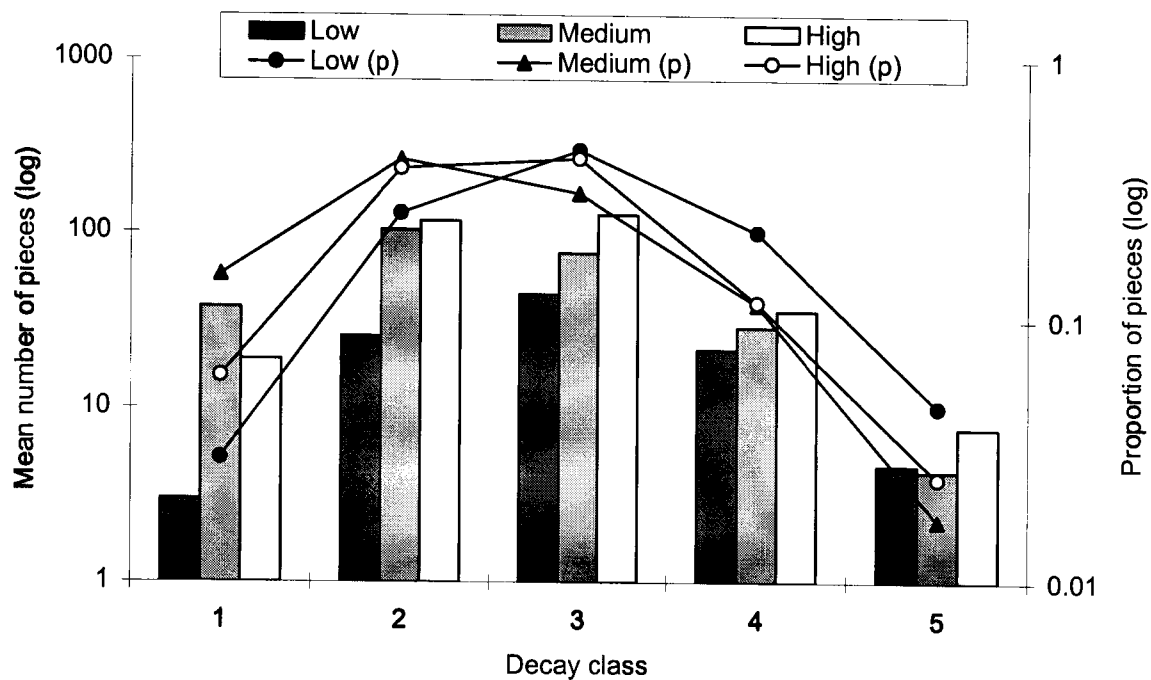


Figure 12. Mean number of pieces (bar, logarithmic scale) and the proportion of pieces (line; logarithmic scale) within a) diameter class categories, and b) each of 5 decay classes for pieces ≥ 7.5 cm in diameter, for low, medium, and high treatment areas on Sicamous clear-cut sampling grids.

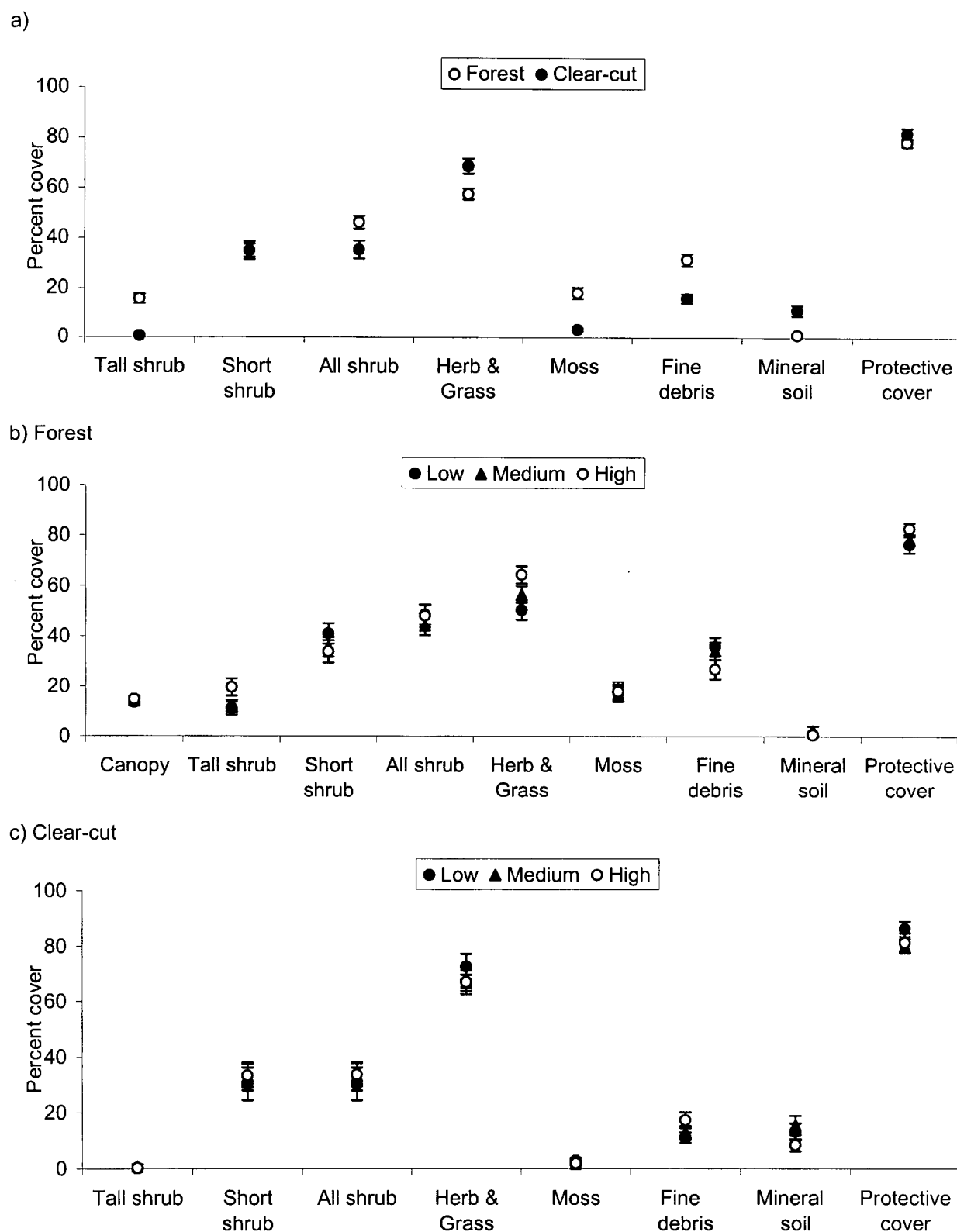


Figure 13. Mean (± 2 SE) percent ground cover by vegetation on a) forested and clear-cut areas, and on *low*, *medium*, and *high* downed wood treatment areas on b) forested treatment areas and c) clear-cut treatment areas at the Opax study area.

treatment areas. Although *high* sites tended to have more ground cover from herbs and shrubs, mean protective cover was similar among downed wood treatments.

Mean herb cover and mean protective cover from all sources tended to be higher on *low* clear-cut treatment areas, and litter cover higher on *high* treatment areas, but mean values for all habitat components were <2 SE of other downed wood treatment areas (Fig. 13c). There were no substantive differences in percent ground cover by vegetation between downed wood treatments.

2.3.2.2 Sicamous Creek

Vegetation was affected differently by clear-cutting at Sicamous than at Opax. Percent ground cover by shrubs, herb and grass, and moss was higher on forested than clear-cut areas at Sicamous (Fig. 14a, Appendix 1). Clear-cut areas had more exposed mineral soil, and lower amounts of protective cover than forested areas.

Percent ground cover by vegetation on forested areas varied strongly across blocks. Percent ground cover by herb and grass was higher on the lowest elevation A block, and mean protective cover was lower on the highest-elevation C block (Fig. 14b). Vegetation on clear-cuts also varied across blocks (Fig. 14c). Although no one component obviously differed across blocks, mean protective cover was highest on the two lower elevation blocks, and lower on the highest elevation block.

On forested areas, percent ground cover in the shrub, and herb and grass layer was much lower on *low* than on *medium* or *high* downed wood treatment areas (Fig. 15a). Herb cover was also lower on *high* treatment areas than *medium* areas. This pattern likely reflected the relative disturbance to areas during the downed wood manipulations. Mean protective cover was lower on *low* treatment areas, and similar on *medium* and *high* treatments. Percent ground cover by

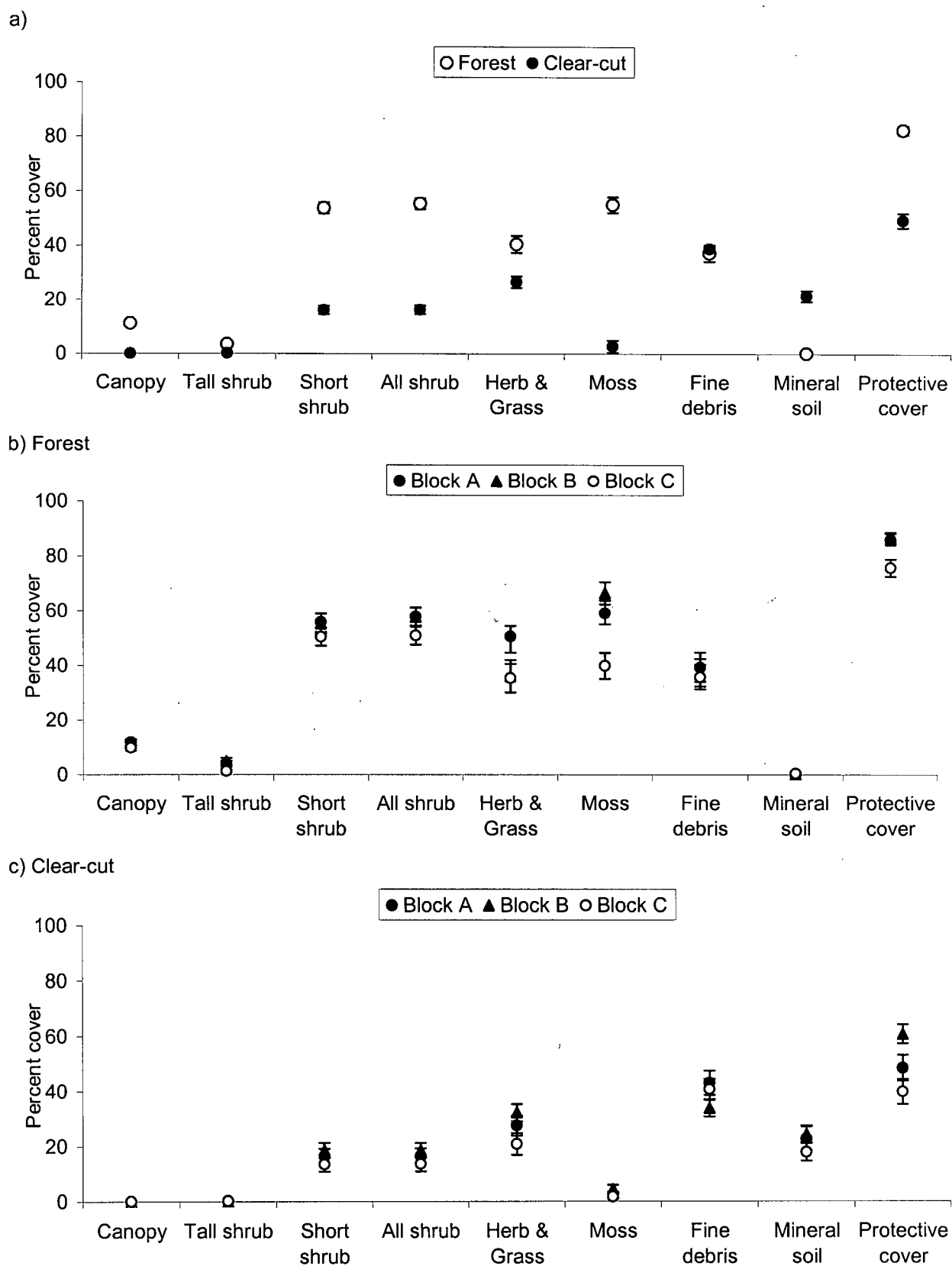


Figure 14. a) Mean percent ground cover (± 2 SE) on forested and clear-cut areas at Sicamous, and mean percent ground cover on A, B, and C blocks on b) forested treatment areas and c) clear-cut areas at Sicamous.

vegetation was similar across clear-cut downed wood treatments (Fig. 15b). *Medium* sampling grids tended to have more protective cover, but the means were within 2 SE of *low* and *high* treatments.

2.4 Discussion

The downed wood treatments resulted in a wide range in the availability of downed wood

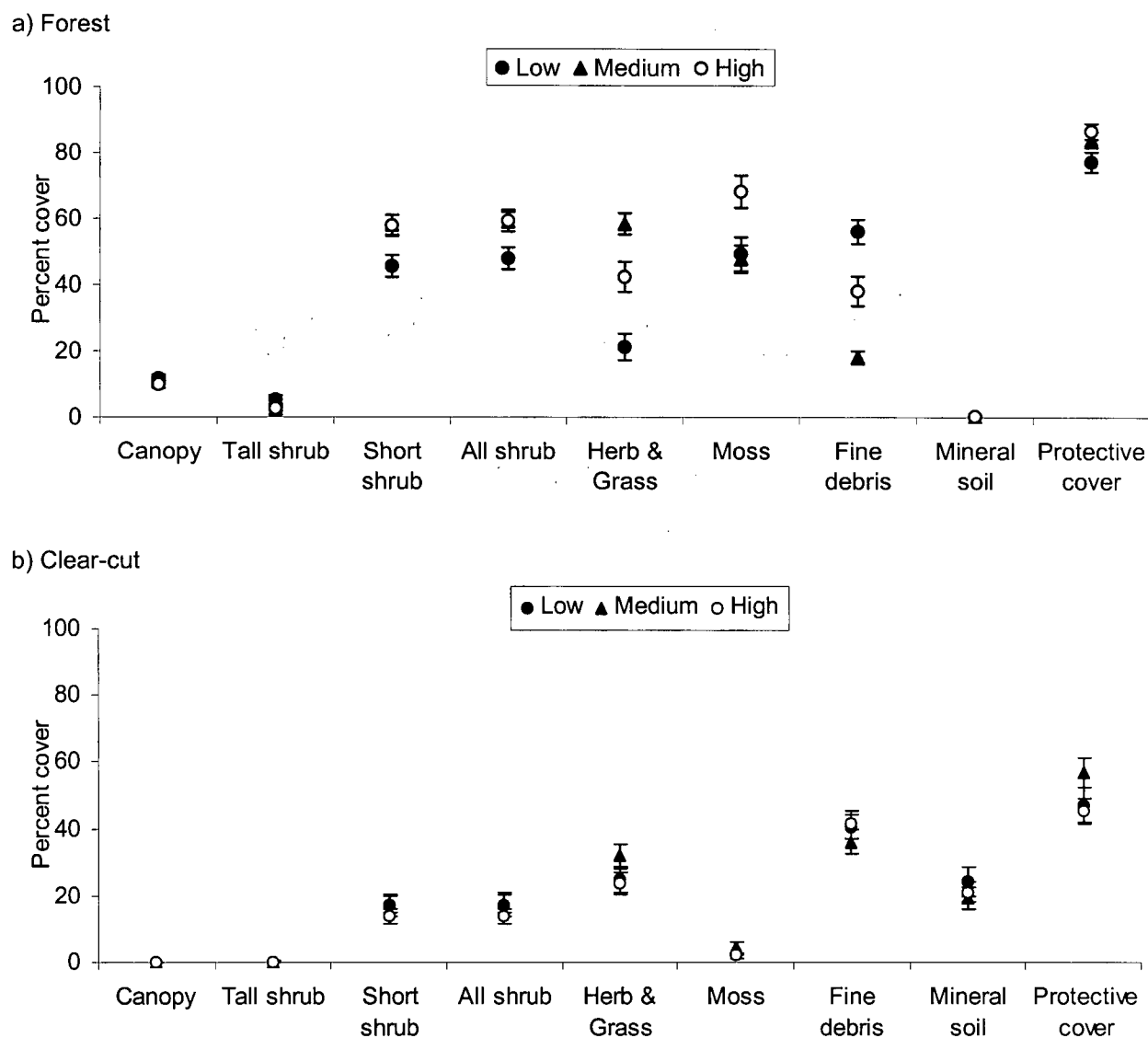


Figure 15. Mean percent ground cover (± 2 SE) for *low*, *medium*, and *high* downed wood treatment areas on a) forested, and b) clear-cut areas at Sicamous.

across the treatment areas. *Low* treatments reduced the levels of downed wood below the amounts normally found on the study area, and in all cases *low* areas had less downed wood after treatment than on *medium* and *high* treatment areas. The patchy nature of downed wood made it difficult to distinguish differences between *medium* and *high* downed wood treatments. Although additional downed wood was added to *high* treatments in some cases (clear-cuts at both study areas and forested treatment areas at Sicamous), and removed in others (*medium* forested treatment areas at Opax), the resulting levels of downed wood were not outside the normal range for the area. Thus in my study, I was able to examine the response of small mammals to a range of downed wood availability (including areas with very low levels of downed wood), but I was not able to address the potential response by small mammals to much greater volumes of downed wood.

The study areas represented climatic extremes. The Opax study area was in a warm, dry open forest, with grasses and herbs dominating the understorey. At Sicamous, the site was cool and wet, and the dominant understorey vegetation was shrubs. The amounts of downed wood were much greater at Sicamous than Opax. A greater proportion of trees were >30 cm at the Sicamous Creek site than at Opax (Parish 1997, Klenner and Huggard 1998), creating large volume logs when they fell. As well, the slower decay rate of downed wood at the Sicamous site (Feller 1997) means that the logs will be available on the area for longer periods.

Vegetation was affected differently by harvesting at the two study areas. On the warm, dry study area (Opax Mountain), clear-cuts were heavily vegetated within two years post-harvest. All of the sampling grids had $\geq 75\%$ ground cover from vegetation and downed wood within two years post-harvest. The shorter growing season at the Sicamous Creek study area slowed

vegetative growth after harvesting. Even two years post-harvest, mean protective cover on clear-cuts was low, averaging $<50\%$ across the sampling grids.

Chapter 3. Population Dynamics of Deer Mice in Relation to Downed Wood

3.1 Introduction

Recent research on maintaining biodiversity across the managed forest landscape has emphasized the importance of mimicking natural patterns, and maintaining important stand- and landscape-level attributes over space and time (Carey and Johnson 1995, Bunnell *et al.* 1999). Downed wood has long been reported as an important habitat component for many vertebrate species, including small mammals (Elton 1966, Harmon *et al.* 1986, Bunnell *et al.* 1999, Butts and McComb 2000). However, critical issues for management, such as the existence of minimum requirements or substitutable resources, remain unresolved. Intensive forest management practices, if continued over the long term, could cause the widespread loss of downed wood from managed forests (Angelstam 1997); therefore, it is important to quantify the role of downed wood in forest environments.

In this chapter, I report the results of a study on the response of deer mouse (*Peromyscus maniculatus*) populations to experimental manipulations of downed wood on clear-cut and forested areas. The deer mouse is considered to be flexible in its habitat requirements (Thomas 1979); however, previous research has established relationships between this species and downed wood (Carey and Johnson 1995). Most research to date has investigated the relationship between deer mice and downed wood at the microhabitat scale. *Peromyscus* construct nests in downed wood (McCay 2000) and also use downed wood for travelling (Graves *et al.* 1988, Barnum *et al.* 1992, Planz and Kirkland 1992, McMillan and Kaufman 1995). Deer mice are omnivorous and will forage on insects and mycorrhizal fungi, which are associated with downed wood (Harmon *et al.* 1986, Clarkson and Mills 1994, Waters *et al.* 1997, Carey *et al.* 1999, Gagné *et al.* 1999, Pyare and Longland 2001).

Two recent studies (Loeb 1999, Moses and Boutin 2001) investigated the relationship between downed wood and *Peromyscus* population dynamics with equivocal results. Loeb (1999) found that cotton mice (*P. gossypinus*) in forested stands responded positively to increased abundance of downed wood in a 45-year-old forest with sparse vegetation cover. Moses and Boutin (2001) did not find a relationship between the amount of downed wood and deer mouse abundance in clear-cut areas in a young boreal mixedwood forest, where ground cover grew rapidly after harvesting. I extended these studies by studying the response of deer mouse populations to the removal of downed wood on both forested and clear-cut areas, replicated at two different study areas with very different forest types. The study was designed to test the hypotheses that: 1. deer mouse population dynamics are related to the amount of downed wood on site; specifically that deer mouse population density, survival rates and indices of reproductive success will be higher on forested areas with more downed wood, 2. deer mouse populations will be a) larger on clear-cuts than on forested areas, and b) population density, survival rates, and reproductive rates will be higher on clear-cut areas with more downed wood, and 3) the relationship between deer mice and downed wood will not change across ecosystems.

3.2 Methods

3.2.1 Field Methods

I conducted this study of deer mouse population dynamics at both the Opax and the Sicamous Creek study areas (described in Chapter 1), on the downed wood treatment areas described in Chapter 2. The research was conducted in unharvested treatment areas (blocks D, I, and N at Opax, Fig. 3, Chapter 2; and A1, B2, and C4 at Sicamous Creek, Fig. 4, Chapter 2) and in clear-cut treatment areas on the two study areas (1.7-ha patch-cuts within the 50% patch-

removal harvest treatment areas [E, J, and M at Opax, Fig. 3, Chapter 2] and the 10-ha cut-blocks on A4, B5, and C3 at Sicamous Creek, Fig. 4, Chapter 2).

3.2.1.1 Small Mammal Sampling

Deer mouse populations on downed wood treatment areas were studied using a mark-recapture program. A 1.1-ha small mammal sampling grid was established in the centre of each 1.7-ha treatment area. Each sampling grid consisted of a 7 x 7 trap array with stations 15 m apart. A Longworth-style live-trap was placed at each station and filled with coarse brown cotton, oats, and apple. A board was placed over each trap to protect traps from sun and rain. Traps were pre-baited a minimum of one week before trapping commenced each season. Grids were not sampled during winter because of logistical difficulties of trapping in snow. During a trapping season, grids were trapped for two consecutive days approximately every three weeks. Traps were set on the evening of days 0 and 1, and checked soon after dawn on days 1 and 2. Traps were locked open in between trapping session to allow animals to move in and out of the traps freely. Animals captured were identified to species, and their sex, weight, and reproductive condition recorded. Males were classified as having scrotal or abdominal testes, and females were classified as F1 (immature, no sign of breeding), F2 (nipples evident, perforate vagina), or F3 (nipples swollen, pregnant, and/or sign of lactation, Krebs *et al.* 1969). Each newly captured animal was tagged with a small, individually numbered ear tag, and released at its point of capture.

I conducted 26 small mammal trapping sessions from 1994-1997 at Opax. No pre-harvest/downed wood treatment data were collected on clear-cuts. The 1994 trapping season represented pre-treatment data for forested downed wood treatments. Trapping seasons at Opax were June-October 1994, May-October 1995 and 1996, and May-July 1997 (two sessions only). I sampled the Sicamous populations 21 times from 1994-1998. All sampling grids at Sicamous

were trapped July-October 1994, 1995, 1996, June-September 1997, and June-August 1998 (three sessions only). Data collected in 1994 were pre-harvest/downed wood treatment data for clear-cut treatment areas; 1994 and 1995 were pre-treatment years for forested treatment areas.

3.2.2 Data Analysis

3.2.2.1 Deer Mouse Population Dynamics

I generated Jolly-Seber (Seber 1982) estimates of population size using Small Mammal Programs for Mark-Recapture Data Analysis (C.J. Krebs, Department of Zoology, University of British Columbia). I calculated the effective trapped area (ETA) for each grid for each year based on mean maximum distance moved (MMDM) by deer mice between trapping sessions. Half the value of the MMDM was added to the grid size, and used to calculate the total area within which populations were sampled (Wilson and Anderson 1985). Population estimates were converted to a density estimate (number of deer mice/ha) by dividing population estimates for each trapping session by the ETA calculated for that year. All analyses of population size used these ETA-adjusted data.

I analyzed density estimates with a split-plot design in time, where time (split-plot) and block were considered random factors, and downed wood treatment was considered a fixed effect. For this analysis the interaction term between downed wood treatment and block is assumed to be nonsignificant. To compensate for the dependence between repeated samples of the same sampling grids, I adjusted degrees of freedom (df) of the split-plot effect and split-plot error term by dividing the df of the numerator (time or interactions between treatment and time) and the denominator (error term B) by the df of the split-plot effect (time). Thus, the df of the split-plot effect (time) becomes one. This adjustment is conservative, and most appropriate when split-plot measures are totally dependent. Therefore for tests of the split-plot effect and

interactions, I used $\alpha = 0.1$ to assess statistical significance. To test main effects, I used the main plot error (Error term A), unless an F-test indicated that Error Terms A and B were not significantly different at $P > 0.1$. In this case, I used Error Term B (with adjusted df) as the main plot error term to benefit from the increased df (A. Kozak, *pers. comm.*). I used $\alpha = 0.05$ when testing main effects. To investigate significant main plot effects, I graphed means ± 2 SE to identify patterns in the data.

I estimated weekly survival and recapture rates with the Cormack-Jolly-Seber (CJS) analysis in program MARK (White and Burnham 1999). I used a "step-down" approach to model selection (Lebreton *et al.* 1992) in which modelling began with a fully parameterized (global) model followed by simpler, more parsimonious models. This procedure allowed systematic testing for potential sources of variation in parameters. Model selection in MARK uses the Akaike Information Criterion corrected for small sample sizes (AICc; Akaike 1985), which, unlike likelihood ratio testing, allows comparison between non-nested models (Lebreton *et al.* 1992). The CJS modelling option in MARK allows estimation of the following population parameters:

ϕ_t = survival; the probability that a member of the population at time t survives and remains in the population at $t+1$.

p_t = recapture probability; the probability that a marked animal known to be in the population is captured.

I used model $\phi_{\text{grid*time}} p_{\text{grid*time}}$ as the global model (parameters were permitted to vary for each grid and each period). I did not include covariates such as sex or age classes in the global model because my data were too sparse to support these categories. I calculated TEST 2 and TEST 3 in Program RELEASE (Burnham *et al.* 1987) to detect evidence of lack-of-fit to the

data (Cooch and White 2000). As well, I used TEST 2 and TEST 3 results to calculate $\hat{c}$, and used it in Program MARK to correct for overdispersion of data (Anderson *et al.* 1994). If $\hat{c}$ is greater than 1, then variability in the data set is underestimated, which can be compensated for (up to $\hat{c}$ of approximately 10, Anderson *et al.* 1994) by adjusting the AIC and variance estimates in MARK.

Biologically plausible reduced models, in which some parameters were constrained to be equal (thereby reducing the number of parameters to arrive at a more parsimonious model), were created and compared using AICc to identify sources of parameter variation. Models within $\Delta\text{AIC} < 2$ of the most parsimonious model were considered to have support (Anderson *et al.* 1994). Following the suggestion by Lebreton *et al.* (1992), I first modelled capture (p) probabilities. This method reserves the greatest power for modelling survival estimates, which are normally of more biological interest than capture rates. I modelled capture and weekly survival rates with respect to variation in grid grouping and time grouping (Table 1). I constructed models where recapture and weekly survival rates varied by block, downed wood treatment, or capture effort to determine whether the treatments or underlying experimental design influenced these rates. I also tested seasonal and year effects to look for underlying patterns in how rates changed over time. On the Opax site in 1996, red foxes (*Vulpes vulpes*) occasionally broke open traps on every sampling grid. To test whether foxes had an effect on recapture or weekly survival rates, I used *fox* as a covariate and compared sessions where there was fox activity on the grid with those where fox activity was absent.

I investigated deer mouse reproduction on the study areas by comparing the proportion of deer mice captured that were females in reproductive condition (reproductive females), or juveniles, across downed wood treatment types and years with a split-plot in time ANOVA.

Table 1. Variables used in Program Mark to model variation in survival (ϕ) and recapture (p) rates with grid and time.

Variability across	Modelled by	Test to determine if survival and/or recapture rates
Grids	Constant	Do not differ across grids
	Grid	Vary differently across grids
	Block	Are more similar within blocks than across blocks
	Downed wood treatment level	Vary similarly within treatments, grouped by the final downed wood volume
Time	Constant	Do not vary across time
	Time	Are different at each sampling period
	Year	Are similar across years
	Season	Are similar across seasons
	Pre/post treatment	Differ pre- and post- treatment
	Temporal trend (T)	Increase or decrease with time
	Number of traps available (num trap)	Varies with capture effort (recapture only)
	Fox effect (Opax only)	Are different during time periods when a fox disturbed traps on the grid

Years of partial data collection (1997 at Opax and 1998 at Sicamous) were not included in analyses. A female was considered to be in reproductive condition if there was evidence of pregnancy or parturition (large weight decrease, lactation, or signs of maturity such as a high weight combined with swollen nipples). Juveniles were defined as those individuals weighing ≤ 14 g at first capture. This likely generated a reasonable estimate of the number of young born on each sampling grid because it was less than the weight of deer mice known to immigrate from other sampling grids (16 g), and was less than the weight of over-wintered deer mice (over-winter weight: Opax, $\bar{x} = 21.8 \pm 0.6$ g, range 16-36 g; Sicamous, $\bar{x} = 23.5 \pm 1.0$ g, range 18-33 g).

Weights of over-wintered males were compared with 1-way ANOVAs to identify differences in post-winter condition by forest type or treatment. Significant effects were investigated with t-tests.

3.2.2.2 Downed Wood, Vegetation, and Litter and Moss Sampling

To explore how population density of deer mice varied with percent ground cover by vegetation, I constructed scatterplots of mean post-treatment population density on each sampling grid with mean cover values for habitat components. This was a more appropriate method of looking at general differences among grids than using statistical tests because of the large number of variables I measured, over relatively few sampling grids (nine per seral stage). If deer mouse population density appeared to vary across sampling grids in a manner similar to a habitat component, I ran a simple regression analysis to identify the proportion of the variability in deer mouse density that was related to the habitat component.

3.2.2.3 Downed Wood

3.2.2.3.1 Opax Mountain Study Area

Only the *high* clear-cut treatment on block J had relatively large volumes of downed wood. Therefore, for survival and recapture analyses, data from E and M *high* treatment areas were grouped with *medium* areas. Data for *low* grids were also compared with data combined for all *medium* and *high* grids. Because of the difficulty of analysing an unbalanced split-plot design, I analysed population density using *low*, *medium*, and *high* groupings, and identified significant downed wood effects by examining graphs of population means.

Based on downed wood volume data, I considered the *medium* treatment site on N forested block to be *low*, and the *high* site on N block to be *medium* for analyses of survival and captures rates. Split-plot analyses for density require a balanced design, so I could not reclassify sampling grids across downed wood treatment classes. Therefore, for analysis of population density, I analysed data for D and I blocks only.

3.2.2.3.2 *Sicamous Creek Study Area*

On both forests and clear-cuts, *low* treatments significantly reduced the volume of downed wood on site, but the downed wood added to *high* areas did not increase volumes above the level found on the *medium* treatment areas. Based on trends in downed wood volume across sampling grids, I compared population parameters for deer mice among *low*, *medium* and *high* treatments for survival, recapture and density estimates, as well as *low* versus *medium/high* data combined (survival and recapture estimates only).

Unless otherwise stated, all means are presented ± 2 standard errors of the mean. On some occasions I present percent variables (such as survival rate) ± 2 standard errors of the mean to provide an indication of the variability around the mean to compare to other values. SE varies asymmetrically around a proportional variable and confidence intervals presented are approximate only.

3.3 Results

3.3.1 Deer Mouse Populations at Opax

I captured 1377 different deer mice 5762 times during the study; trap mortalities comprised less than 1% of captures. Species captured in addition to deer mice included southern red-backed voles (*Clethrionomys gapperi*), meadow voles (*Microtus pennsylvanicus*), montane voles (*M. montanus*), jumping mice (*Zapus* spp.), northwestern chipmunks (*Eutamias amoenus*), red squirrels (*Tamiasciurus hudsonicus*), flying squirrels (*Glaucomys sabrinus*), shrews (*Sorex* spp.), and weasels (*Mustela* spp.).

ETA was similar among all sampling grids and years ($F_{8,27} = 0.8$, $P > 0.5$). Mean ETA overall was 1.36 ± 0.02 ha (range: 1.10-1.65 ha); however, there was substantial movement of deer mice among sampling grids within harvest treatment blocks. I captured 105 deer mice

(7.6% of 1377 mice) that emigrated from an original capture grid to a different grid, and 64 deer mice (4.6% of 1377 mice) that were captured primarily on one grid, but were captured at least once on another grid before returning to the original grid. I investigated patterns of movement to determine whether they varied with downed wood treatments. On clear-cuts, the proportion of deer mice that were captured on >1 sampling grid appeared to be similar among downed wood treatments ($\bar{x} = 0.09 \pm 0.08$, $\bar{x} = 0.03 \pm 0.02$, and $\bar{x} = 0.07 \pm 0.05$ for *low*, *medium*, and *high* treatments respectively; 1-way ANOVA on arcsine squareroot transformed proportion data, $F_{2,6} = 1.47$, $P > 0.1$). However, patterns in immigration and emigration appeared to differ across downed wood treatments. A count of deer mice known to immigrate to a sampling grid suggested that more deer mice emigrated from, than immigrated to, *low* clear-cut treatment areas (emigrate $\bar{x} = 12.3 \pm 1.3$, immigrate $\bar{x} = 4.3 \pm 2.7$), whereas similar numbers of deer mice immigrated to and emigrated from *medium* (immigrate $\bar{x} = 6.7 \pm 4.7$, emigrate $\bar{x} = 4.0 \pm 3.1$) and *high* (immigrate $\bar{x} = 7.7 \pm 1.8$, emigrate $\bar{x} = 5.3 \pm 1.8$) treatment areas. The proportion of deer mice moving among forested treatment areas appeared to be similar across downed wood treatments ($\bar{x} = 0.13 \pm 0.13$, $\bar{x} = 0.15 \pm 0.14$, $\bar{x} = 0.14 \pm 0.05$ for *low*, *medium*, and *high* treatments respectively; 1-way ANOVA on arcsine squareroot transformed proportion data, $F_{2,6} = 0.17$, $P > 0.5$), and numbers of deer mice immigrating ($\bar{x} = 3.0 \pm 1.2$, $\bar{x} = 2.0 \pm 1.2$, $\bar{x} = 2.0 \pm 1.2$ for *low*, *medium*, and *high* treatments respectively) and emigrating ($\bar{x} = 2.0 \pm 2.0$, $\bar{x} = 1.3 \pm 1.3$, $\bar{x} = 2.7 \pm 3.3$ for *low*, *medium*, and *high* treatments) were similar across downed wood treatments.

If deer mice on treatment areas accessed downed wood or other habitat features outside of the treatment areas, then treatment effects might not be detectable. I explored this issue by comparing the proportion of deer mice captured >once that were captured at least once in traps

at the edge of sampling grids. My prediction was that if deer mice on *low* sampling grids were more likely to access downed wood off the treatment area, then the proportion of mice on *low* areas captured at least once on edge traps should be greater than on *medium* or *high* treatment areas. On clear-cuts, a similar proportion of deer mice were captured in edge traps on *low* as on *medium* (2.5% more deer mice captured in edge traps on *medium* areas than *low*) or *high* areas (0.9% fewer deer mice captured in edge traps on *high* areas). On forested areas, a smaller proportion of deer mice were captured in edge traps on *low* areas than *medium* (2.8% more) or *high* (1.5% more) areas. Although this is not a rigorous statistical test, it does suggest that deer mice on *low* areas were not more likely to be captured in edge traps, and therefore might not have been more likely to access habitat features off the treatment area.

3.3.1.1 Population Density

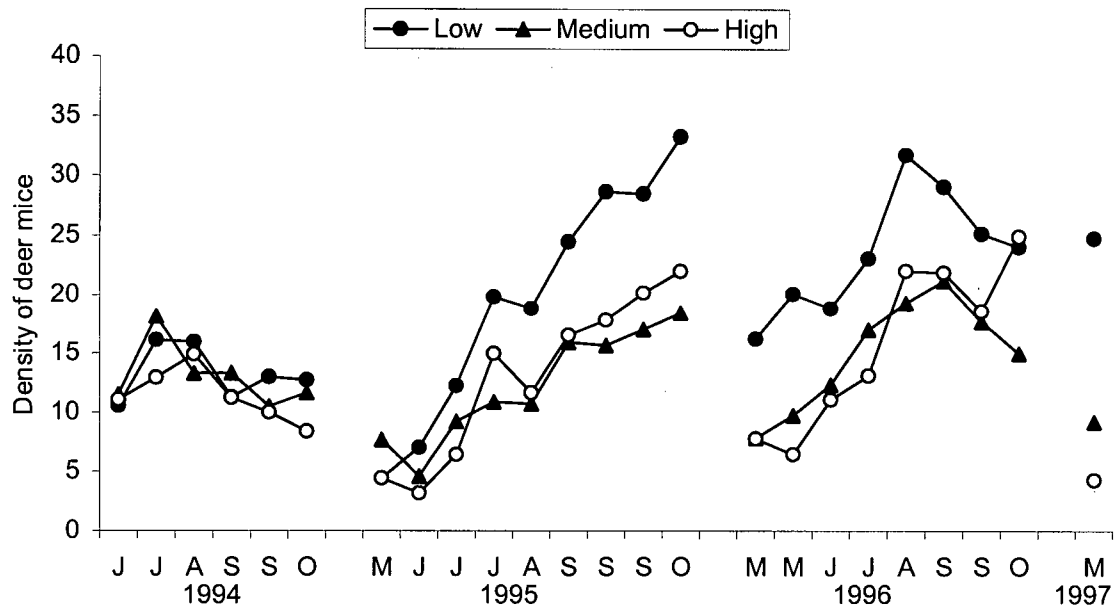
Densities of deer mice on forested areas tended to be lower than on clear-cuts in all years of the study (comparing mean density on unmanipulated forest *high* areas with unmanipulated clear-cut *medium* areas; forest $\bar{x} = 3.6 \pm 2.4$, clear-cut $\bar{x} = 13.3 \pm 7.7$, $F_{1,4} = 5.8$, $P = 0.07$, Fig. 16, Appendix 2).

3.3.1.1.1 Clear-cut

Deer mice were the most numerous small mammal species on clear-cuts at Opax during the study. Population densities varied within the trapping season, increasing from relatively low densities in the spring (generally <10) to higher densities in the fall (generally >20, Fig. 16a, Appendix 2a).

Population density on clear-cut treatment areas varied with downed wood treatment and block (Table 2a). Mean deer mouse density was higher on *low* treatment areas than *medium* or *high* areas within each block in 1995 and 1996 (Fig16a). Comparing overall means among years did not indicate the same trend, likely because of the large variability in population density

a) Clear-cut



b) Forest

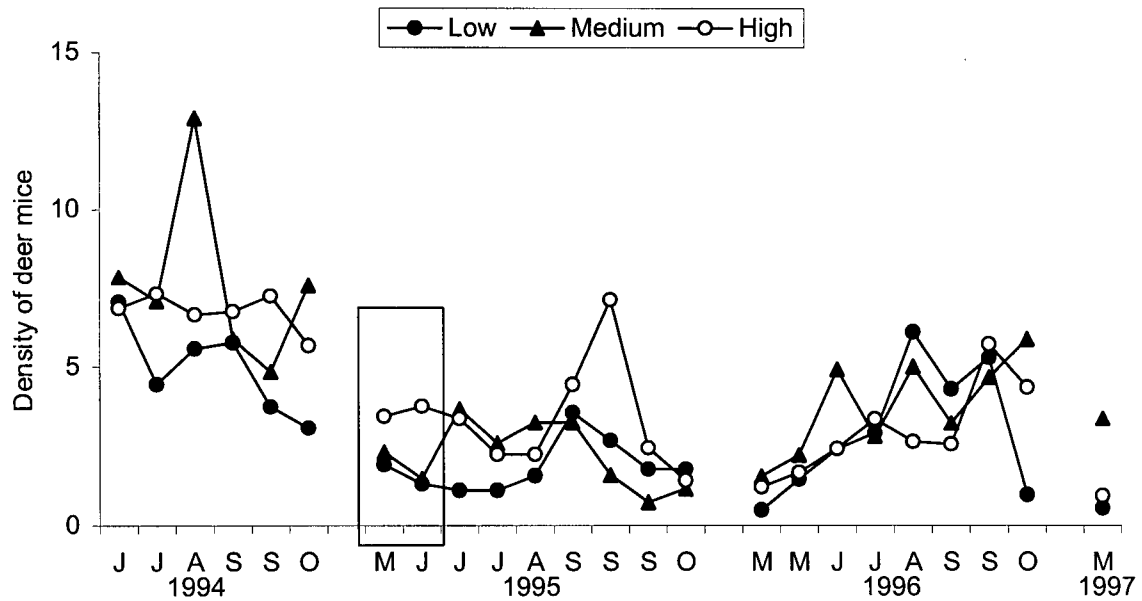


Figure 16. a) Mean density of deer mice on *low*, *medium*, *high* treatment areas on a) clear-cut grids, and b) D and I forested grids at Opax. Harvest and downed wood manipulations occurred in winter 1993-1994 to spring 1994 on clear-cut areas, and in summer 1995 on forested areas (indicated by outlined area). Error bars were omitted for readability; graphs of population estimates for each sampling grid separately are presented in Appendix 2. Note the different Y axis scales on a) and b).

Table 2. Results of split-plot analysis of deer mouse density at the Opax study area on a) clear-cuts and, b) forested areas. Split-plot data are presented for i) split-plot in time (time), and ii) split-plots across years (year). An * indicates effects that are statistically significant.

a i) Clear-cut

Effect	Error term	Test
Downed wood*	B ($F_{4,6} = 2.48, P > 0.1$)	$F_{2,6} = 15.31, P < 0.005$
Block*	B	$F_{2,6} = 76.96, P < 0.001$
Time*	B	$F_{1,6} = 4.63, P < 0.1$
Downed wood x time interaction	B	$F_{2,6} = 0.52, P > 0.5$

ii) Clear-cut (year)

Effect	Error term	Test
Downed wood	B ($F_{4,6} = 1.25, P > 0.1$)	$F_{2,6} = 3.02, P > 0.1$
Block*	B	$F_{2,6} = 11.12, P < 0.05$
Year	B	$F_{1,6} = 0.62, P > 0.1$
Downed wood x year interaction	B	$F_{2,6} = 0.55, P > 0.5$

b i) Forest

Effect	Error term	Test
Pre-harvest/treatment		
Downed wood	A ($F_{2,3} = 36.02, P < 0.05$)	$F_{2,2} = 0.17, P > 0.5$
Block	A	$F_{1,2} = 0.40, P > 0.5$
Time*	B	$F_{1,3} = 7.28, P < 0.1$
Downed wood x time interaction	B	$F_{2,3} = 1.19, P > 0.1$
Post-treatment		
Downed wood	A ($F_{2,3} = 15.48, P < 0.05$)	$F_{2,2} = 0.05, P > 0.5$
Block	A	$F_{1,2} = 0.03, P > 0.5$
Time	B	$F_{1,3} = 2.27, P > 0.1$
Downed wood x time interaction	B	$F_{2,3} = 0.86, P > 0.1$

ii) Forest (year)

Effect	Error term	Test
Downed wood	A ($F_{2,3} = 7.39, P < 0.1$)	$F_{2,2} = 0.23, P > 0.5$
Block	A	$F_{1,2} = 0.15, P > 0.5$
Year*	B	$F_{1,3} = 7.88, P < 0.1$
Downed wood x year interaction	B	$F_{2,3} = 0.46, P > 0.1$

within year. The high density of deer mice on the low elevation E block (*low* $\bar{x} = 32.1 \pm 7.4$, *medium* $\bar{x} = 20.7 \pm 3.9$, *high* $\bar{x} = 20.9 \pm 4.3$) heavily influenced the overall relationship between density and downed wood treatment; however, the same trend in population density across downed wood treatments occurred on J (*low* $\bar{x} = 16.3 \pm 3.1$, *medium* $\bar{x} = 11.3 \pm 2.3$, *high* $\bar{x} = 11.2 \pm 3.0$), and to a lesser extent on M (*low* $\bar{x} = 10.5 \pm 2.0$, *medium* $\bar{x} = 7.9 \pm 2.0$, *high* $\bar{x} = 7.6 \pm 1.7$, Appendix 2a). Densities on *medium* and *high* treatment areas were similar.

3.3.1.1.2 Forest

Deer mouse population density did not differ significantly with downed wood treatment (*low* $\bar{x} = 4.4 \pm 1.0$, *medium* $\bar{x} = 4.6 \pm 1.0$, *high* $\bar{x} = 3.6 \pm 0.7$, Table 2b, Fig. 16b). Unlike population density on clear-cuts, deer mouse population density was not higher on the lower elevation replicate (D block $\bar{x} = 2.7 \pm 0.6$) than on the higher elevation replicates (I block $\bar{x} = 3.0 \pm 0.8$, N block $\bar{x} = 3.8 \pm 1.0$, Appendix 2b).

3.3.1.2 Downed Wood, Vegetation, and Litter and Moss Sampling

Scatterplots of mean deer mouse density on clear-cuts with habitat components suggested that deer mouse population density tended to be higher on areas with more exposed mineral soil (Fig. 17a); however, linear regression analysis indicated that the relationship was not significant ($F_{1,7} = 1.33$, adjusted $r^2 = 0.04$, $P > 0.1$). No habitat component was strongly correlated with deer mouse population density.

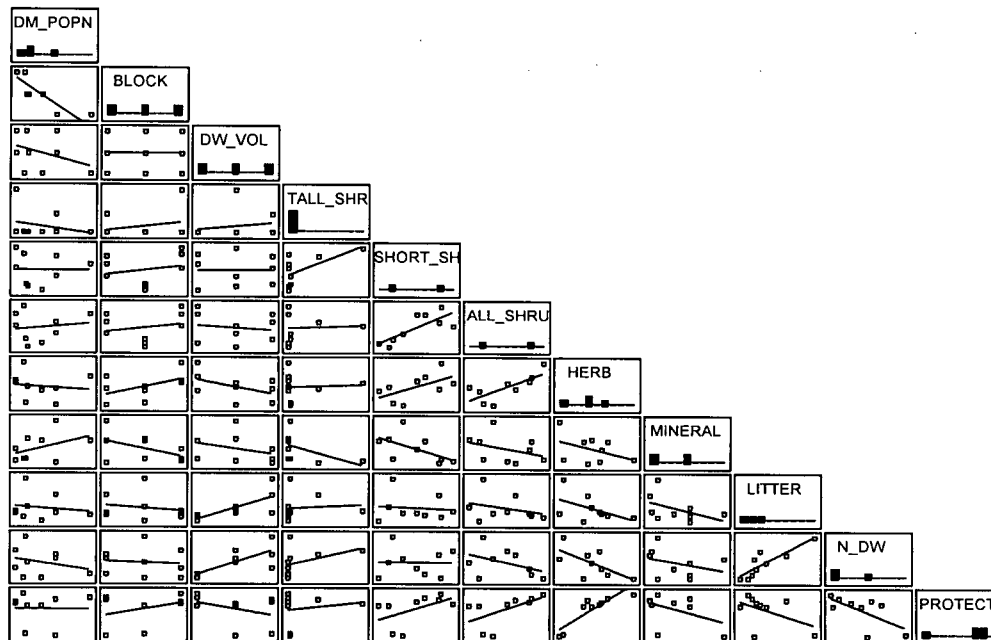
Although overall population density was low on forested areas, mean deer mouse density varied with patterns in percent ground cover by vegetation independently of downed wood treatment or block (Fig. 17b). In particular, deer mouse density appeared to be higher on sampling grids with less canopy and tall shrub cover (≥ 2 m in height), which were correlated with each other. Cover by tall shrubs explained approximately 41% of variability in deer mouse population density across sampling grids ($F_{1,7} = 6.51$, $P < 0.05$).

3.3.1.3 Survival and Recapture Rates

3.3.1.3.1 Clear-cut

There were too few data in most cells to calculate goodness-of-fit statistics with Program RELEASE. However, cells with sufficient data did not show a systematic lack of fit. As well, analyses did not identify overdispersion in the data. Accordingly, $\phi_{\text{grid*time}} p_{\text{grid*time}}$ was used as the global model, and $\hat{c}$ was not adjusted.

a) Clear-cut



b) Forest

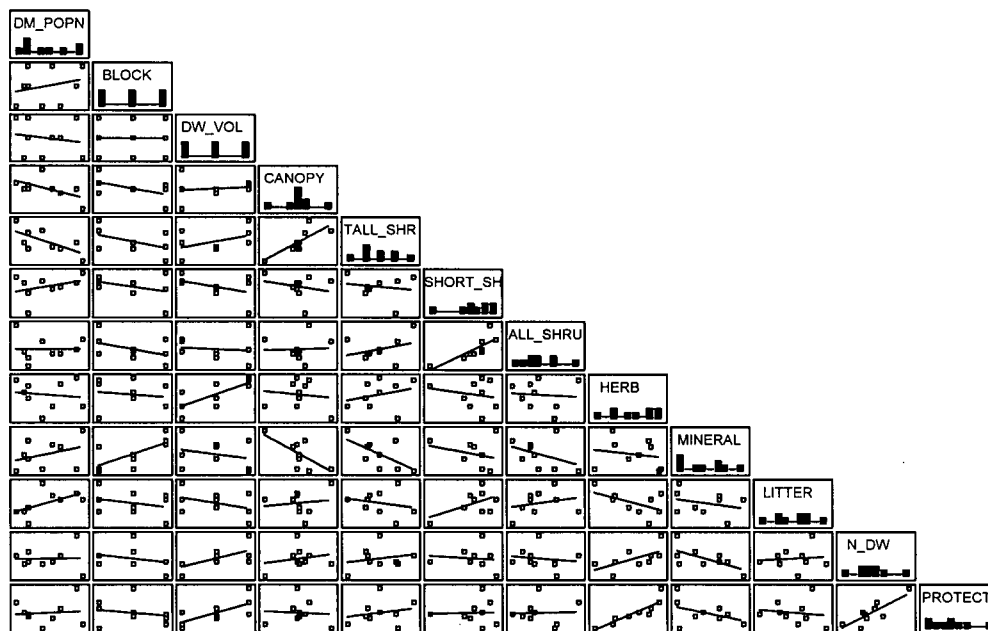


Figure 17. Scatterplots (with trend line) of mean Opax deer mouse population density, block, and downed wood volume treatment class (9 grids) with habitat components on a) clear-cuts and b) forest, including: tall, short, and overall shrub cover, herb and grass cover, mineral soil, litter layer, mean number of pieces of downed wood (N_DW), and mean protective cover. The trend line in each section is meant as a guide only; it does not signify a statistically significant relationship. The scatterplots are for exploratory purposes only, and the scale of each correlation is different, depending on the habitat variable involved. Density of deer mice is on the X axis, habitat component is on the Y axis.

Recapture rates of deer mice on Opax clear-cut grids were first modelled with the most general models to identify overall variation among grids and periods. Both grid and time were identified as important sources of variation. All models where time varied by year, season, or linear time trend (T) were more parsimonious than time alone, but were rejected in favour of the additive model where capture rates were parallel across grids with time (on a logit scale). Models where grids were grouped by block, downed wood treatment, or *fox* effect were also rejected in favour of this model. Recapture rates were >70% for most time periods; mean recapture rate was $76.6\% \pm 1.9$.

General survival models indicated that grid and time variability were important. The model with the lowest AIC of the general models was $\phi_{\text{grid+time}} p_{\text{grid+time}}$. Models constraining time with respect to year and season were rejected in favour of this model. As well, models where grids were grouped by block or downed wood treatment also were rejected in favour of the additive model. Thus, survival varied in a parallel manner across grids over time; there were no discernable trends with downed wood treatments, blocks, seasons, or years. Survival rates were quite high, and were generally >80%. Mean overall survival rate was $90.2\% \pm 1.2$.

3.3.1.3.2 Forest

General models indicated that both grid and time were important sources of variability in recapture rates. The additive model, where recapture rates are parallel (on a logit scale) across grids, had the lowest AIC. Modelling time variation with respect to year and season did not improve the parsimony of the model; nor did grouping grids by block, downed wood treatment or *fox* effect. Mean recapture rate was $69.6\% \pm 2.9$.

The general survival models identified time as an important factor; variability across grids was less important. Grouping grids by downed wood treatment did have some support (the

model grouping grids by downed wood treatment received more support than assuming grids varied independently). Models grouping grids by block also received more support than the constant-survival model, but less than the downed wood model. However, both these models had much less support than those modelling time alone. Modelling time as a function of year, season, or a combination of both indicated that survival varied both across season and year. Subsequent models indicated that survival rates tended to decline over the length of the study, and that survival rates were higher over-winter than during the rest of the year. Re-introducing downed wood or block with the more parsimonious time model was not supported by the data. One other model within $2\Delta\text{AIC}$ of the top model identified the same temporal pattern in the data; survival rates tended to be lower post-treatment ($\bar{x} = 85.9\% \pm 2.7$) and higher over-winter ($\bar{x} = 95.3\% \pm 0.9$) than during the rest of the year.

3.3.1.4 Reproduction

The length of the breeding season of female deer mice was longer on clear-cuts (18-20 weeks/year) than on forested areas (12-18 weeks/year). Over-wintered males were similar in weight on unmanipulated forest ($\bar{x} = 21.0 \pm 0.7$) and clear-cut areas ($\bar{x} = 20.0 \pm 3.5$; $t_3 = 4.30$, $P > 0.5$).

3.3.1.4.1 Clear-cut

The proportion of the population composed of reproductive females (*low* $\bar{x} = 10.4\% \pm 3.1$, *medium* $\bar{x} = 12.6\% \pm 1.9$, *high* $\bar{x} = 12.4\% \pm 3.7$) and the proportion of juveniles in the population (*low* $\bar{x} = 41.5\% \pm 6.6$, *medium* $\bar{x} = 40.6\% \pm 12.1$, *high* $\bar{x} = 39.0\% \pm 7.6$) were similar among downed wood treatments (Table 3). Proportion of juveniles increased after the first year post-harvest (1994 $\bar{x} = 29.7\% \pm 8.0$, 1995 $\bar{x} = 47.7\% \pm 5.1$, 1996 $\bar{x} = 43.7\% \pm 8.4$). Over-winter weight of male deer mice was similar across downed wood treatments ($\bar{x} = 22.1 \pm$

0.6 g, $\bar{x} = 22.2 \pm 1.7$ g, $\bar{x} = 21.7 \pm 0.6$ g for *low*, *medium*, and *high* treatments respectively; $F_{2,6} = 0.25$, $P > 0.5$).

3.3.1.4.2. Forest

Neither the proportion of reproductive females (*low* $\bar{x} = 14.4\% \pm 8.2$, *medium* $\bar{x} = 36.9\% \pm 42.2$, *high* $\bar{x} = 6.7\% \pm 8.2$) nor proportion of juveniles (*low* $\bar{x} = 42.3\% \pm 17.5$, *medium* $\bar{x} = 27.7\% \pm 30.1$, *high* $\bar{x} = 32.5\% \pm 18.9$) in the population varied with downed wood treatment or harvest treatment block, or significantly across years (Table 3). Mean weight of overwintered males was similar across downed wood treatments (*low* $\bar{x} = 21.1 \pm 1.7$ g, *medium* $\bar{x} = 21.8 \pm 1.8$ g, *high* $\bar{x} = 19.5 \pm 2.9$ g; $F_{2,6} = 1.14$, $P > 0.1$).

Table 3. Results of split-plot analysis of deer mouse reproductive parameters from the Opax study area. Proportion of population comprised of a) reproductive females, and b) juveniles. An * indicates a statistically significant result.

a) Reproductive females

Effect	Error term	Test
Clear-cut		
Downed wood	B ($F_{4,6} = 0.87$, $P > 0.1$)	$F_{2,6} = 0.62$, $P > 0.5$
Block	B	$F_{2,6} = 0.70$, $P > 0.1$
Year	B	$F_{1,6} = 0.43$, $P > 0.1$
Downed wood x year interaction	B	$F_{2,6} = 0.49$, $P > 0.5$
Forest		
Downed wood	B ($F_{2,3} = 0.51$, $P > 0.1$)	$F_{2,3} = 2.54$, $P > 0.1$
Block	B	$F_{1,3} = 4.57$, $P > 0.05$
Year	B	$F_{1,3} = 0.92$, $P > 0.1$
Downed wood x year interaction	B	$F_{2,3} = 0.91$, $P > 0.1$

b) Juveniles

Effect	Error term	Test
Clear-cut		
Downed wood	B ($F_{4,6} = 1.90$, $P > 0.1$)	$F_{2,6} = 0.14$, $P > 0.5$
Block	B	$F_{2,6} = 3.49$, $P > 0.05$
Year*	B	$F_{1,6} = 7.22$, $P < 0.1$
Downed wood x year interaction	B	$F_{2,6} = 0.16$, $P > 0.5$
Forest (post-treatment data)		
Downed wood	A ($F_{2,3} = 7.49$, $P < 0.05$)	$F_{2,2} = 0.22$, $P > 0.5$
Block	A	$F_{1,2} = 0.41$, $P > 0.5$
Year	B	$F_{1,3} = 0.00$, $P > 0.5$
Downed wood x year interaction	B	$F_{2,3} = 0.09$, $P > 0.5$

3.3.2 Deer Mouse Populations at Sicamous

Between 1994 and 1998 I captured 906 individual deer mice a total of 2604 times; trap mortalities comprised less than 1% of captures. Species captured in addition to deer mice included southern red-backed voles, long-tailed voles (*Microtus longicaudus*), heather voles (*Phenacomys intermedius*), jumping mice (*Zapus* spp.), bog lemmings (*Synaptomys borealis*), northwestern chipmunks, red squirrels, shrews, and weasels.

Mean ETA across all grids and years was 1.53 ± 0.01 ha (range: 1.10 to 2.3 ha); however, as on the Opax study area there was substantial movement of deer mice among sampling grids. I captured 96 deer mice (10.6% of 906) that emigrated from their original capture location to another grid. Sixty-nine (7.6%) deer mice were primarily captured on one sampling grid, but on at least one occasion were captured on a different sampling grid. On both clear-cuts ($F_{2,6} = 0.17$, $P > 0.5$) and forested areas ($F_{2,6} = 0.10$, $P > 0.5$), the proportion of deer mice that were captured on a different grid was similar among downed wood treatment areas. To investigate the possibility that deer mice on *low* treatment areas might access downed wood off the treatment areas, I compared the proportion of deer mice captured >once, that were captured at least once in a trap at the edge of the sampling grid. On clear-cuts, deer mice on *low* areas appeared to be captured more frequently in edge traps than on *high* areas. Although the means were within 2 SE of each other, 3.5% more mice on average were captured in edge traps on *low* grids than *high* grids. Although the proportion of mice captured in edge traps was similar among downed wood treatments on A and B blocks, approximately 1.5 x as many mice were captured in edge traps on *low* than *high* areas on C block. *Medium* grids had the lowest proportion of mice captured in edge traps. On forested areas, a smaller proportion of mice were captured in edge traps on *low* areas than *medium* (5% less) or *high* (2% less) areas.

Although data were too sparse in many cells for goodness of fit tests in Program RELEASE, those that did have sufficient data (frequencies > 2) did not identify lack-of-fit in the global model for clear-cut or forest data; therefore, $\phi_{\text{grid} \times \text{time}} p_{\text{grid} \times \text{time}}$ was used as the global model. There was evidence of overdispersion in the deer mouse forest data; therefore, $\hat{c}$ was adjusted to 2.82 (within acceptable limits; Anderson *et al.* 1994). It was not necessary to adjust $\hat{c}$ for clear-cut data.

3.3.2.1 Population Density

Population densities on unmanipulated *medium* clear-cut and forested treatment areas were similar post-harvest (clear-cut $\bar{x} = 1.9 \pm 6.6$, forest $\bar{x} = 2.4 \pm 2.6$; $F_{1,4} = 0.14$, $P > 0.5$, Fig. 18, Appendix 2).

3.3.2.1.1 Clear-cut

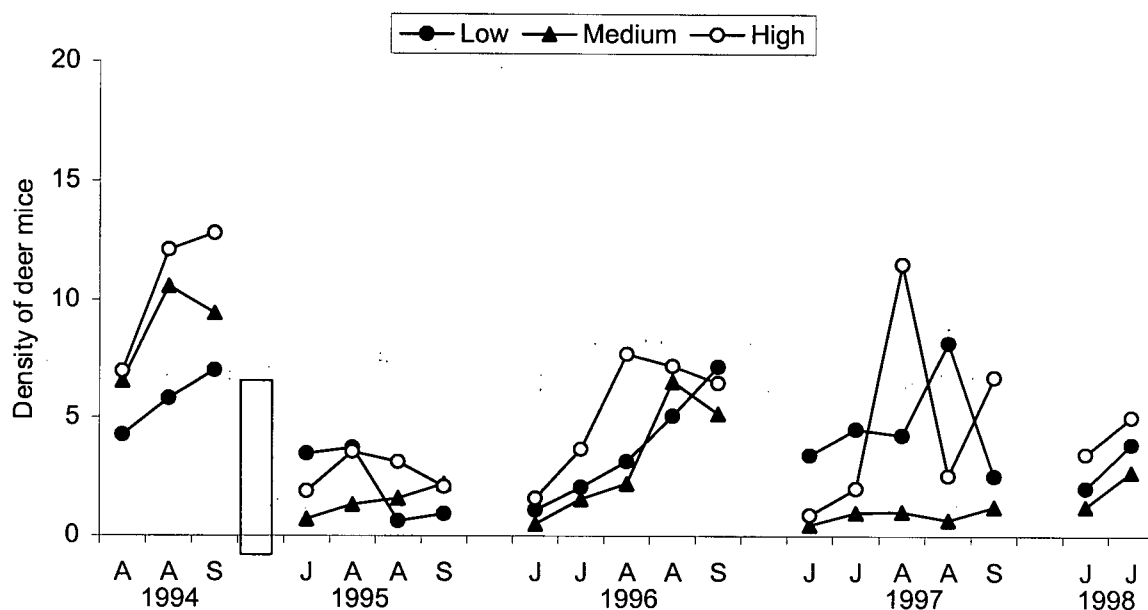
Deer mouse population density declined after 1994 and remained low (generally <10 deer mice/ha) throughout the rest of the study, although there were signs of recovery in 1998 (Fig. 18a, Appendix 2c). Deer mouse population density varied significantly with downed wood treatment (*low* $\bar{x} = 3.5 \pm 1.0$, *medium* $\bar{x} = 1.9 \pm 0.9$, *high* $\bar{x} = 4.3 \pm 1.3$, Table 4). On two blocks, mean density on *medium* treatments was lower than on either *low* or *high* areas (Appendix 2c). Population density did not vary overall among blocks (Table 4). There was no pre-harvest/treatment effect (Table 4), so the results of the analysis suggest that deer mouse populations tended to be lower on *medium* treatment areas than on *low* or *high* areas.

3.3.2.1.2 Forest

Mean deer mouse density declined on all forested grids after 1994 (1994 $\bar{x} = 12.7 \pm 1.5$ to 1997 $\bar{x} = 2.3 \pm 1.7$; Table 4, Fig. 18b, Appendix 2d). Pre-treatment densities (1994-1995) did not differ significantly among (future) downed wood treatment areas or across blocks (Table 4).

Mean deer mouse density from 1996-1998 (post-treatment) did not differ significantly

a) Clear-cut



b) Forest

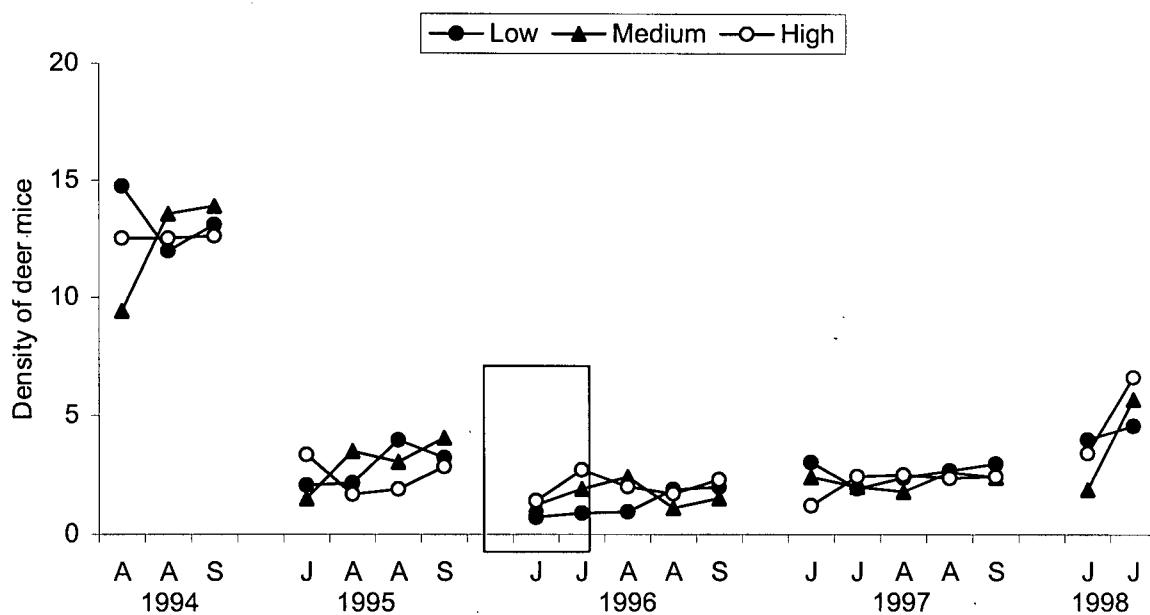


Figure 18. Mean estimated density of deer mice at Sicamous on *low*, *medium* (control), and *high* downed wood treatment areas on a) clear-cuts, and b) forests. Downed wood was manipulated on clear-cuts during harvesting in winter 1994-1995 and spring 1995, and summer of 1996 on forested areas (indicated by outlined area). Error bars were omitted for readability; population estimates are presented separately for each sampling grid in Appendix 2.

Table 4. Results of split-plot analysis of deer mouse density from the Sicamous study area a) Clear-cut and b) Forest. Data are presented for i) split-plot in time, and ii) split-plot across years. An * indicates effects that are statistically significant.

a i) Clear-cut

Effect	Error term	Test
Pre-harvest/treatment		
Downed wood	A ($F_{4,6} = 9.89, P < 0.05$)	$F_{2,4} = 0.75, P > 0.5$
Block	A	$F_{2,4} = 1.16, P > 0.1$
Time*	B	$F_{1,6} = 5.44, P < 0.1$
Downed wood x time interaction	B	$F_{2,6} = 0.53, P > 0.1$
Post-treatment		
Downed wood*	B ($F_{4,6} = 2.73, P > 0.1$)	$F_{2,6} = 6.33, P < 0.05$
Block	B	$F_{2,6} = 0.84, P > 0.5$
Time	B	$F_{1,6} = 2.16, P > 0.1$
Downed wood x time interaction	B	$F_{2,6} = 0.84, P > 0.1$

a ii) Clear-cut (year)

Effect	Error term	Test
Downed wood	B ($F_{4,6} = 1.67, P > 0.1$)	$F_{2,6} = 2.19, P > 0.1$
Block	B	$F_{2,6} = 0.25, P > 0.5$
Year*	B	$F_{1,6} = 5.72, P < 0.1$
Downed wood x time interaction	B	$F_{2,6} = 0.57, P > 0.5$

b i) Forest

Effect	Error term	Test
Pre-treatment		
Downed wood	B ($F_{4,6} = 1.91, P > 0.1$)	$F_{2,6} = 0.02, P > 0.5$
Block	B	$F_{2,6} = 4.09, P > 0.05$
Time*	B	$F_{1,6} = 36.65, P < 0.05$
Downed wood x time interaction	B	$F_{2,6} = 0.69, P > 0.1$
Post-treatment		
Downed wood	B ($F_{4,6} = 1.31, P > 0.1$)	$F_{2,6} = 0.33, P > 0.5$
Block*	B	$F_{2,6} = 32.18, P < 0.001$
Time*	B	$F_{1,6} = 4.80, P < 0.1$
Downed wood x time interaction	B	$F_{2,6} = 0.53, P > 0.1$

b ii) Forest (year)

Effect	Error term	Test
Downed wood	B ($F_{4,6} = 0.99, P > 0.1$)	$F_{2,6} = 0.10, P > 0.5$
Block*	B	$F_{2,6} = 7.91, P < 0.05$
Year*	B	$F_{1,6} = 59.04, P < 0.001$
Downed wood x time interaction	B	$F_{2,6} = 0.19, P > 0.5$

among downed wood treatments, but was highly variable across blocks (Table 4). Population densities, although low overall, were highest on the lowest elevation forested block ($A \bar{x} = 4.8 \pm 0.8$, $B \bar{x} = 1.3 \pm 0.6$, $C \bar{x} = 1.6 \pm 0.5$, Appendix 2d).

3.3.2.2 Downed Wood, Vegetation, and Litter and Moss Sampling

Scatterplots of mean deer mouse density with habitat components did not suggest the presence of any significant correlations between deer mouse density and habitat components on clear-cuts (Fig. 19a) or forested sampling grids (Fig. 19b).

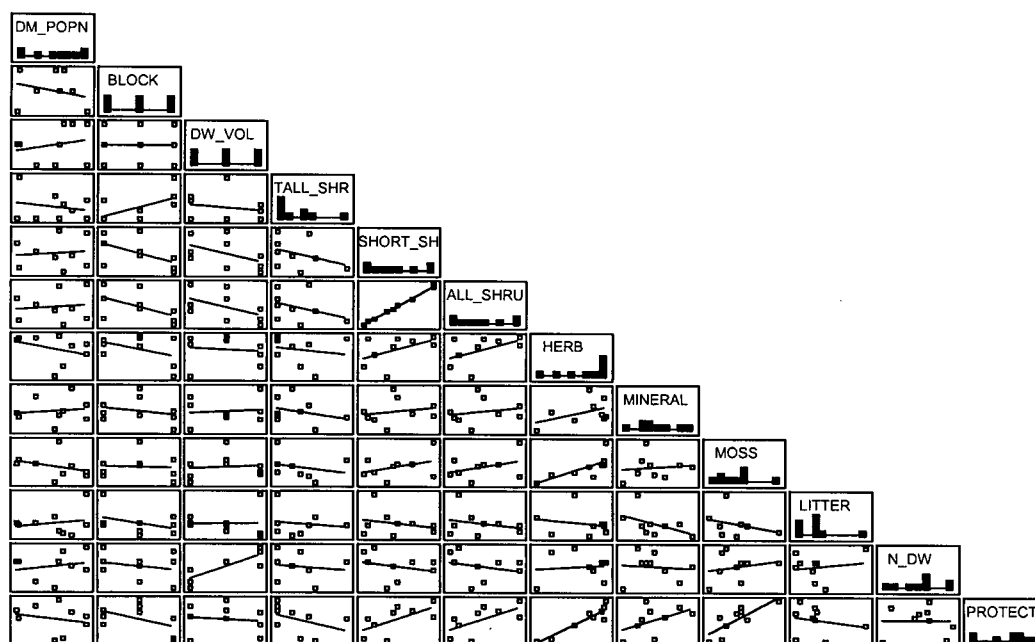
3.3.2.3 Survival and Recapture Rates

3.3.2.3.1 Clear-cut

General models supported including variability by grid and over time. Models that included variation in time by season or year had less support than modelling recapture rates pre-harvest (1994) versus post-harvest (1995-8); recapture rates were lower once sites had been harvested (pre, $\bar{x} = 91.0\% \pm 7.7$; post, $\bar{x} = 69.3\% \pm 24.4$). Grouping grids by downed wood treatment was rejected in favour of grouping by block. Block B ($96.1\% \pm 5.1$) had higher overall recapture rates than A ($73.9\% \pm 28.8$) or C blocks ($70.6\% \pm 31.3$).

Based on initial models of survival rate, both grid and time were important sources of variability. Modelling time variation by year and season identified season as an important variable. Using block to model variability across grids was also supported by the data. The final model included effects of seasonal survival and variability in survival across blocks. Survival rates (wk^{-1}) were high during the study, but tended to be lower on the mid-elevation block (B block, $\bar{x} = 82.2\% \pm 5.0$; A block, $\bar{x} = 89.0\% \pm 3.4$; C block, $\bar{x} = 90.8\% \pm 2.9$) and higher overall in winter ($\bar{x} = 89.7\% \pm 4.4$) and fall ($\bar{x} = 88.7\% \pm 4.8$) than spring/summer ($\bar{x} = 83.6\% \pm 6.5$). Adding downed wood treatment (*low* versus *medium/high* combined) also had support ($\Delta\text{AIC} = 0.08$). Survival rates on *low* areas were $2\% \text{ wk}^{-1}$ lower than on *medium/high* areas.

a) Clear-cut



b) Forest

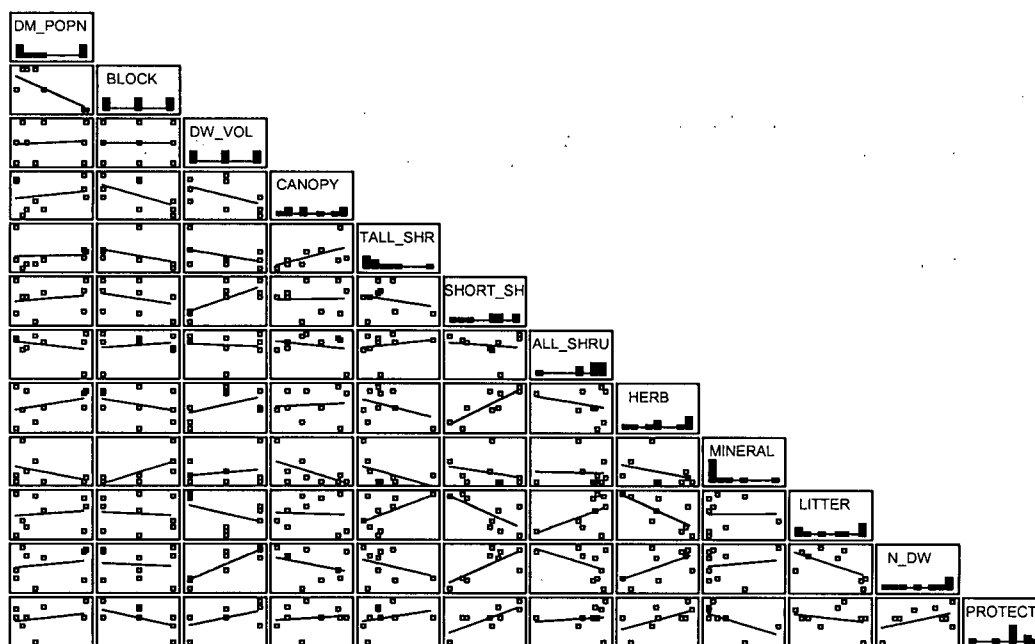


Figure 19. Scatterplot and frequency distribution histogram (and trend line) of mean Sicamous deer mouse population density, block, and downed wood volume treatment class (9 grids), with habitat components on a) clear-cut and b) forested sampling grids including: tall, short, and overall shrub cover, herb and grass cover, moss, mineral soil, mean number of pieces of downed wood, and mean protective cover. The trend line in each section is meant as a guide only; it does not signify a statistically significant relationship. The scatterplots are for exploratory purposes only, and the scale of each correlation is different, depending on the habitat variable involved. Density of deer mice is on the X axis, habitat component is on the Y axis.

3.3.2.3.2 Forest

Recapture rates of deer mice on Sicamous forested grids varied strongly with time and there was some support for overall variability amongst grids. Models that grouped time by year and year+season were better supported than the additive general model, $p_{\text{grid}+\text{time}}$. Recapture rates declined across time over the study; fitting a linear time trend (logit) model to the data was better supported than modelling variability with random time intervals or grouping by year and season. Grouping grids by block or downed wood treatment did not improve the parsimony of the model. A model using capture effort as a covariate was also supported ($\Delta\text{AIC} \leq 2$); however, survival rates were modelled with the most parsimonious model $p_{\text{linear trend time}}$. Recapture rates declined slightly over the course of the study from a mean of 77% to 68%.

Variability in survival rates over time was best explained by the additive effect of year and season. Modelling grid variability by grouping by block and downed wood treatment indicated that survival rates varied by block. The most parsimonious model was $\phi_{\text{block}+\text{year}+\text{season}} p_{\text{linear trend time}}$. Weekly survival rates were lower during summer ($\bar{x} = 83.7\% \pm 3.9$) than in fall ($\bar{x} = 93.9\% \pm 1.9$) and winter ($\bar{x} = 95.0\% \pm 1.2$). Survival rates (wk^{-1}) tended to be lower on the two higher-elevation blocks (B block, $\bar{x} = 88.1\% \pm 4.6$; C block, $\bar{x} = 89.2\% \pm 4.3$) than A block ($\bar{x} = 93.8\% \pm 2.6$).

3.3.2.4 Reproduction

Female deer mice in reproductive condition were consistently captured during the first trapping session each year. There was no evidence of juvenile female deer mice breeding. Male deer mice generally did not breed in their first year either; only six of 129 males tagged as juveniles were known to reach reproductive status during their first summer. Over-wintered male deer mice at Sicamous Creek were similar in weight on clear-cut and forested grids (clear-cut $\bar{x} = 22.3 \pm 2.5$, forest $\bar{x} = 26.3 \pm 6.8$, $t_5 = 2.6$, $P > 0.1$).

3.3.2.4.1 Clear-cut

Proportion of reproductive females in the population did not differ significantly by downed wood treatment ($low \bar{x} = 17.4\% \pm 10.0$, $medium \bar{x} = 15.3\% \pm 11.9$, $high \bar{x} = 18.1\% \pm 10.4$), block, or year (Table 5). Proportion of juveniles in the population also did not differ significantly ($low \bar{x} = 27.8\% \pm 24.9$, $medium \bar{x} = 33.3\% \pm 34.1$, $high \bar{x} = 38.4\% \pm 31.7$; Table 5).

3.3.2.4.2 Forest

The proportion of reproductive females in the population on forested treatment areas post-treatment did not differ significantly with downed wood treatment ($low \bar{x} = 15.3\% \pm 13.9$, $medium \bar{x} = 6.1\% \pm 7.8$, $high \bar{x} = 23.6\% \pm 3.2$), block or year (Table 5). The proportion of

Table 5. Results of split-plot analysis of the deer mouse reproductive parameters from the Sicamous study area. Proportion of population comprised of a) reproductive females, and b) juvenile deer mice.

a) Reproductive females

Effect	Error term	Test
Clear-cut		
Downed wood	B ($F_{4,6} = 0.53$, $P > 0.1$)	$F_{2,6} = 0.43$, $P > 0.5$
Block	B	$F_{2,6} = 3.55$, $P > 0.05$
Year	B	$F_{1,6} = 2.10$, $P > 0.1$
Downed wood x year interaction	B	$F_{2,6} = 0.19$, $P > 0.5$
Forest		
Downed wood	B ($F_{4,6} = 3.01$, $P > 0.1$)	$F_{2,6} = 0.99$, $P > 0.1$
Block	B	$F_{2,6} = 0.46$, $P > 0.1$
Year	B	$F_{1,6} = 2.29$, $P > 0.1$
Downed wood x year interaction	B	$F_{2,6} = 1.13$, $P > 0.1$

b) Juveniles

Effect	Error term	Test
Clear-cut		
Downed wood	B ($F_{4,6} = 0.09$, $P > 0.1$)	$F_{2,6} = 0.21$, $P > 0.5$
Block	B	$F_{2,6} = 2.74$, $P > 0.1$
Year	B	$F_{1,6} = 1.42$, $P > 0.1$
Downed wood x year interaction	B	$F_{2,6} = 0.34$, $P > 0.5$
Forest		
Downed wood	B ($F_{4,6} = 0.41$, $P > 0.1$)	$F_{2,6} = 0.94$, $P > 0.1$
Block*	B	$F_{2,6} = 7.69$, $P < 0.05$
Year	B	$F_{1,6} = 0.09$, $P > 0.5$
Downed wood x year interaction	B	$F_{2,6} = 0.14$, $P > 0.5$

juveniles post-treatment was higher on A block ($\bar{x} = 31.7\% \pm 8.1$) than either B (0%) or C ($\bar{x} = 6.7\% \pm 6.7$) blocks. After 1995, no juvenile deer mice were captured on the B sampling grids.

3.4 Discussion

3.4.1 Experimental Design

Movements of deer mice between grids indicated that downed wood treatment areas within blocks were not completely distinct sampling units. Ideally, sampling grids should have been more widely spaced on the landscape. The placement of sampling grids in my study was influenced by the operationally sized harvest treatment blocks established as part of two large silvicultural systems projects. As well, the size of the manipulations, particularly on forested areas, was constrained by the labour-intensive nature of removing downed wood by hand. More than 90% of the deer mice I captured during the study were captured on only one sampling grid, and the proportion of deer mice moving among grids appeared to be similar across downed wood treatments. As well, patterns in emigration and immigration followed patterns in population density across downed wood treatments. In only one case (Sicamous clear-cuts) was there evidence that deer mice on *low* treatment areas were more likely to be captured on the edge of sampling grids than on *medium* or *high* areas. The likely effect of the movement of some proportion of the population outside treatment areas would be to reduce variation in deer mouse densities among treatment areas within blocks, making it more difficult to detect differences associated with treatments. Especially where population densities were low, movements of mice might have obscured relationships with downed wood that would have been apparent if population sizes, or treatment areas, were larger.

3.4.2 Deer Mouse Population Dynamics

3.4.2.1 Clear-cut

My study suggests that deer mouse populations at Opax were not negatively affected by the removal of downed wood, contrary to my first and second hypotheses. I did not detect higher population densities, survival, or reproductive rates associated with higher levels of downed wood on clear-cut or forested sites.

Deer mice responded positively to harvesting at Opax. Densities increased to relatively high levels on all clear-cut study grids while densities on the adjoining forested areas remained low throughout the study. On Opax clear-cuts, population density was higher on *low* treatment areas than on *medium* or *high* areas, which was opposite to the result predicted in hypothesis 2b. The positive response by deer mice to the *low* treatments was significant; in fact, the presence of higher population densities, relatively high survival and reproductive rates, and higher emigration rates than the *medium* and *high* areas suggests that *low* clear-cut treatment areas might have been “source” populations for the surrounding area (Van Horne 1983). This is a surprising result, based on previous research which reported that downed wood was an important habitat component for *Peromyscus* at the microhabitat scale (Goodwin and Hungerford 1979, Barry and Francq 1980, Kaufman *et al.* 1983, Harmon *et al.* 1986, Graves *et al.* 1988, Barnum *et al.* 1992, Planz and Kirkland 1992, Carter 1993, Carey and Johnson 1995, McMillan and Kaufman 1995, Roche *et al.* 1999, McCay 2000). The Opax clear-cuts were heavily vegetated within two years post-harvest, and *low* treatment areas tended to have more herb cover and protective cover than *medium* or *high* areas. Downed wood and vegetation can be complementary habitat components for mice (Carey and Johnson 1995), so the apparent positive response to the removal of downed wood might not have occurred if there had been little vegetation cover. It is also possible that deer mice were not responding to the lack of wood

per se, but to some other beneficial attribute (likely vegetation or ground disturbance) that also varied with downed wood treatment. These data suggest that downed wood was not a necessary habitat component for deer mice on Opax clear-cuts within three years post-harvest.

Unlike at Opax, I did not detect a positive response by deer mice to harvesting or to the downed wood treatments on Sicamous clear-cuts. Deer mouse populations remained small on both clear-cut and forested areas at the high elevation site, which might have limited my ability to detect treatment effects. There was evidence that deer mice were negatively affected by the removal of downed wood on clear-cuts at Sicamous, in agreement with hypothesis 2b. Survival rates were on average 2% lower on *low* areas than *medium/high* areas post-treatment, and mouse capture rates in edge traps tended to be slightly higher on *low* areas than on *medium* or *high* areas. The difference in survival rates could be important when considered over the long-term, but did not result in lower population densities on *low* treatment areas during the study period; in fact, mean population density was higher on *low* than *medium* areas during the study. Sicamous clear-cuts remained sparsely vegetated during the study, and downed wood provided the majority of protective cover for mice. Although these results suggest that retention of downed wood is not sufficient to provide suitable habitat for deer mice on Sicamous clear-cuts, it is unclear whether downed wood might be a necessary component when deer mice are more abundant.

Deer mouse abundance is usually higher on clear-cuts than forested areas in coniferous habitat (Kirkland 1990). The positive response by deer mice to clear-cutting is generally considered to be a response to an increase in vegetation cover (Potvin *et al.* 1999, Moses and Boutin 2001), or to the disturbance of the forest floor which would expose food such as seeds or mycorrhizal fungi (Gagné *et al.* 1999). Other researchers have reported increases in deer mouse

abundance with increased disturbance of the forest floor. Deer mice have been reported to be more abundant on burned clear-cuts than on unburned sites, even though the treatment removed most downed wood and other types of ground cover (Gunther *et al.* 1983, Martell 1984, Sullivan *et al.* 1999a). Similarly, deer mice were reported to be more abundant on a scarified clear-cut than an unscarified clear-cut (Martell and Radvanyi 1977, Martell 1983). The lack of a positive response at Sicamous could indicate that clear-cutting at the site did not generate changes in habitat that are favourable for deer mice. Harvesting, site preparation, and downed wood treatments all disturbed the ground and would have exposed previously buried food resources, so the most likely explanation for the lack of response by deer mice to clear-cutting at Sicamous was the low amount of vegetation on harvested areas. The cold, short growing season limited vegetation growth, and vegetation was not as abundant on clear-cuts as on forested areas during the study. Previous research on the effects of clear-cutting in colder climates has found no response by deer mice (Sullivan and Boateng 1996); however, most of these studies were conducted on older clear-cuts (Walters 1991, Sullivan *et al.* 1999a) or on areas with greater amounts of vegetation than on the Sicamous clear-cuts (Walters 1991, Gagné *et al.* 1999). Others did not report levels of vegetation on their study area (Martell and Radvanyi 1977). Thus, at Sicamous, deer mice may require some threshold level of vegetation to become abundant on clear-cuts.

3.4.2.2 Forest

I did not detect a difference in deer mouse population density, survival rates or reproductive indices with downed wood treatments on forested sites at either study area. On Opax forested areas, population density tended to be higher on more open areas (less tall shrub and canopy cover). The volume of downed wood, which ranged by a factor of four across the forested sampling grids, did not appear to influence population dynamics in forests. At Sicamous, deer

mouse density, survival and reproductive indices varied strongly across blocks. All of the measured population parameters were highest on the lowest elevation block. Downed wood volume, which ranged by a factor of 10 across treatments, did not result in detectable differences in parameters. On both study areas, high levels of protective cover by vegetation and low population densities combined with potential edge effects might have limited either the importance of downed wood for mice and/or my ability to detect a treatment effect.

Elevation and, potentially, vegetation at the Sicamous study area appeared to be the primary factor affecting deer mouse density and survival rates on forested areas. Density, survival rates, and reproductive indices were highest on the lowest elevation block, which had the most herb, moss, and protective cover. Although mean vegetation cover was not directly correlated with mean deer mouse density, vegetation was likely an important component at the Sicamous study area. Vegetation would provide protection from the many predators on the site, including raptors, owls, weasels (rare), and marten (Kotler *et al.* 1988, Longland and Price 1991, Korpimäki *et al.* 1996, Rohner and Krebs 1996). Vegetation would also likely be important in creating suitable winter microhabitats. The study area was covered with 1-2 m of snow for 7-9 months of the year. Blocks at lower elevations had less snow than those higher upslope, and tended to be snow-free earlier in the year. The longer growing season likely contributed to the greater amounts of vegetation on the lower blocks. Vegetation creates subnivean spaces for small mammals to move about (Spencer 1984, Taylor and Buskirk 1996). Access to these spaces, where temperatures remain relatively warm and stable (Pruitt 1978, Anderson 1986), is critical to overwinter survival of small mammals (Schlegl-Bechtold 1980, West *et al.* 1980, Pruitt 1984). Thus, the apparent negative trend in measures of population dynamics with elevation at Sicamous was likely related to the abundance of vegetation.

3.4.2.3 Cover

It is not clear whether deer mice, like other small mammals, require a minimum amount of cover before they become abundant on an area. Both the meadow vole (Adler and Wilson 1989), and the montane vole (*Microtus montanus*; Gashwiler 1970) appear to require $\geq 30\%$ cover in the grass and herb layer. Previous work suggested that downed wood and vegetation were complementary habitat components for deer mice in managed forests (Carey and Johnson 1995, Loeb 1999, Moses and Boutin 2001). Higher densities of vegetation have been associated with higher densities (M'Closkey and Lajoie 1975), and higher capture rates (Myton 1974) of deer mice. Carey and Johnson (1995) reported that 83% of variability in deer mouse abundance in managed stands could be explained by a combination of downed wood and shrub cover.

Previous research suggested that deer mice are relatively insensitive to moderate changes in the understorey. Research on the response of deer mice to herbicide applications, which reduces cover in shrub and herb layers (Santillo *et al.* 1989, Freedman *et al.* 1993), has generally reported either no response, or a positive response (Borrecco *et al.* 1979, D'Anieri *et al.* 1987, Santillo *et al.* 1989, Sullivan 1990, Lautenschlager 1993, Cole *et al.* 1998, Sullivan *et al.* 1998a, but see Gagné *et al.* 1999, Sullivan 1990). Research on the effect of other silvicultural treatments that modify vegetation and/or downed wood also report no response by deer mice (Von Treba *et al.* 1998, Waters and Zabel 1998, Sullivan *et al.* 2000). As well, the reduction of cover to very low levels generally does not have a negative impact on deer mouse population dynamics (Martell and Radvanyi 1977, Gunther *et al.* 1983, Martell 1983, Martell 1984, Sullivan and Boateng 1996, Sullivan *et al.* 1998a, 1998b). In contrast to these studies, Loeb's (1999) study documented a positive response by cotton mice at the population scale to the addition of downed wood above low, naturally occurring levels, which suggests that the naturally occurring levels of downed wood provided suboptimal habitat.

The amount of vegetation cover on my sampling grids was highly variable, but all grids had $\geq 30\%$ protective cover. Deer mouse densities were highest on Opax clear-cuts, which had higher levels of herb and grass cover ($>60\%$) and lower amounts of shrub cover ($<40\%$) than forested areas (generally $<60\%$ herb and $>40\%$ shrub). Population densities were low across the entire Sicamous study area where forested areas were dominated by shrub cover ($>50\%$ shrub and $<40\%$ herb), and clear-cuts were sparsely vegetated ($<30\%$ herb and $<20\%$ shrub). The differing response by deer mice to downed wood treatments and harvesting at the two study areas might be more closely related to patterns in vegetation rather than to the abundance of downed wood.

Although downed wood appears to be an important habitat component for deer mice at the microhabitat scale, my study supports the suggestion that this relationship might not extend to the population level (Wiens *et al.* 1993, Bunnell *et al.* 1999). At a microhabitat scale, deer mice use downed wood for nest sites (Harmon *et al.* 1986) and as travel corridors (Graves *et al.* 1988, Barnum *et al.* 1992, Planz and Kirkland 1992, Carter 1993, McMillan and Kaufman 1995, Roche *et al.* 1999). Deer mice also appear to use downed wood as a navigational aid (Barry and Francq 1980, 1982, Planz and Kirkland 1992, McMillan and Kaufman 1995). They preferentially travel in areas with downed wood, and avoid areas without downed wood (Planz and Kirkland 1992). Deer mice are insectivorous, and also eat mycorrhizal fungi, both of which are often associated with downed wood (Harmon *et al.* 1986, Amaranthus *et al.* 1994, Clarkson and Mills 1994, Waters *et al.* 1997, Carey *et al.* 1999, Gagné *et al.* 1999, Pyare and Longland 2001).

Most previous work on the relationship between downed wood and deer mouse populations has been based on correlative studies. Researchers have reported that deer mouse abundance

(Goodwin and Hungerford 1979, Kaufman *et al.* 1983, Carter 1993, Lee 1993, Carey and Johnson 1995), or capture rates (Barry and Francq 1980, *P. leucopus*) were positively associated with downed wood, but others reported a negative relationship (Meierotto 1967), or did not find a relationship (Bowman *et al.* 2000). Manipulative studies have shown contradictory results, which appears to be related to the abundance of other sources of security or thermal cover. Loeb (1999) reported that abundance of the cotton mouse was higher on forested areas where downed wood was added by a tornado, compared to other areas where the additional wood was removed. Loeb (1999) described the vegetation on the study area as sparse, so downed wood likely provided the majority of security and thermal cover for mice (McCay 2000). Moses and Boutin (2001) reported that deer mouse abundance, survival, and reproduction parameters were similar between clear-cuts with downed wood distributed in swaths and those where downed wood had been piled and burned on site. Moses and Boutin (2001) did not report the amount of vegetation on clear-cuts, but mentioned that there was rapid growth of ground cover. They suggested that deer mice might not have responded differently to the availability of downed wood because wood was not evenly distributed throughout the area, which was not a factor in my study.

3.5 Conclusions, Management Implications, and Suggestions for Future Research

The results of this study suggest that, although *Peromyscus* seem to associate with downed wood at a microhabitat scale (Barry and Francq 1980, 1982, Harmon *et al.* 1986, Graves *et al.* 1988, Barnum *et al.* 1992, Planz and Kirkland 1992, Carter 1993, McMillan and Kaufman 1995, Roche *et al.* 1999, McCay 2000), it may not be a necessary habitat component for deer mice in areas with sufficient amounts of vegetation cover, at least in the short term.

Additionally, in areas with low amounts of vegetation cover, downed wood might not be sufficient to provide suitable habitat for deer mice.

Although deer mice might not require downed wood in the short term, the temporal and spatial requirement of deer mice for downed wood is unknown. Both my and Moses and Boutin's (2001) studies, which detected no relationship between deer mice and downed wood at the population level, were short-term, and longer-term responses to the removal of downed wood might be different. As well, in my study, the response of deer mice, and my ability to detect treatment effects, might have been influenced by edge effects (deer mice accessing downed wood off treatment areas). It is still not clear how deer mice would respond to the large-scale loss of downed wood that could occur over time with intensive forest management (Angelstam 1997). The loss of downed wood at a large scale and over a long period would likely affect deer mice indirectly, by negatively affecting many other attributes of the ecosystem on which they rely, such as fungal and insect communities, and understorey vegetation. I was unable to address these issues within the context of my study.

Based on the high population densities of deer mice on Opax *low* clear-cut treatment areas, it appears that deer mice can exploit even small patches (*i.e.*, 1.7 ha) of suitable habitat, which would likely prevent them from disappearing entirely from a landscape with some habitat heterogeneity. Therefore, by including a variety of harvest techniques and rotation lengths across managed forest landscapes, components such as vegetation and downed wood, which appear to be important for deer mice, could be maintained (Hunter 1990, Bunnell *et al.* 1999, Sullivan *et al.* 1999b, Wilson and Carey 2000).

Providing adequate vegetation and downed wood cover for deer mice might be especially important in cold environments with short growing seasons where these components would

provide important structure under snow. Deer mice did not increase after clear-cutting at the Sicamous area with <30% cover by herbs and shrubs, but did at the Opax area with >60% cover by herbs and >35% cover by shrubs. Maintaining clumps of vegetation, especially herbs and grasses, during harvesting and site-preparation might mitigate some of the initial effects of harvesting in these high-elevation ecosystems. Where populations are larger, downed wood might be an important structural component in high-elevation ecosystems, but this question needs further research.

Suggested future research on the relationship between deer mice and downed wood:

1. Continued sampling of deer mouse populations on treatment areas at Opax and

Sicamous. This will provide:

- a) Longer-term data on the response of deer mice to the removal of downed wood;
- b) Opportunities to study populations during higher densities; and,
- c) An opportunity to study the response of deer mice to treatments on Sicamous clear-cuts when the openings become more heavily vegetated.

2. Vegetation control (treatments) on downed wood treatment areas at Opax and Sicamous.

This will provide:

- a) The opportunity to study the response of deer mouse populations to downed wood treatments on areas with little vegetation cover (particularly at Opax);
- b) The opportunity to test the response of deer mice to varying combinations of vegetation and downed wood cover to investigate the substitutability of these resources, and investigate whether minimum requirements exist; and,
- c) The opportunity to determine whether issues of substitutability or minimum requirements are different in the two ecosystems.

3. Trapping in the surrounding habitat matrix outside treatment areas, or radio-telemetry to identify whether deer mice are accessing downed wood outside of treatment areas.
4. In future studies:
 - a) Establish larger-scale treatments of at least 5 ha, and preferably larger (>10 ha) to minimize potential edge effects and more effectively address spatial issues of habitat use;
 - b) Conduct perturbation experiments to determine the response of deer mice to lower or higher levels of downed wood than normally available in the surrounding area; and,
 - c) Control vegetation from the beginning of the experiment to determine baseline levels of response to the removal (or varying levels) of downed wood, or remove downed wood and control the levels of vegetation to collect data on substitutability of habitat resources as well as minimum requirements of deer mice.

Chapter 4. Population Dynamics of Meadow Voles and Long-tailed Voles in Relation to Downed Wood

4.1 Introduction

Downed wood is considered to be important for a host of animals, plants and ecological processes (Harmon *et al.* 1986, Bunnell *et al.* 1999, Butts and McComb 2000). However, its role is poorly understood, and its importance may vary depending on the availability of other habitat features (Gunther *et al.* 1983, Walters 1991, Barnum *et al.* 1992, Carey and Johnson 1995). I investigated whether downed wood was an important habitat component for meadow and long-tailed voles on recent clear-cuts or on forested areas. The study was one portion of a larger project designed to investigate the relationship between small mammals and downed wood in different seral stages and ecosystems.

Meadow voles show a preference for habitats with dense vegetation (Wirtz and Pearson 1960, Bowker and Pearson 1975, Getz 1985). When long-tailed voles are found in forested habitats, they tend to be more common in open areas with grasses and sedges (Getz 1985); they are also common in shrubby habitats (Van Horne 1982, Spencer 1984). Both species are often captured on clear-cuts (Van Horne 1982, Kirkland 1990, Krupa and Haskins 1996).

Microtus respond positively to experimental increases in the amount of thermal/security cover (Birney *et al.* 1976, Taitt *et al.* 1981, Taitt and Krebs 1983), even in areas of low availability or quality of food (Monthey and Soutiere 1985, Getz *et al.* 2001). Downed wood and vegetation appears to fulfill some of the same habitat requirements for other species of small mammals (Barnum *et al.* 1992). Therefore, downed wood could be a useful habitat component for grassland voles, especially in marginal habitats. Research on the role of downed wood as an important habitat component for *Microtus* has been contradictory. Van Horne

(1982) reported that long-tailed vole abundance was correlated with the abundance of downed wood. However, Bowman *et al.* (2000) and Moses and Boutin (2001) did not find a relationship between meadow voles and downed wood in openings in deciduous forest.

In this chapter I report the results of a multi-year intensive mark-recapture project of meadow voles (at Opax) and long-tailed voles (at Sicamous). This study was designed to test the hypotheses that: 1) in areas with sparse vegetation, meadow vole populations will respond positively to the presence of downed wood; specifically that meadow vole population density, survival rates and reproductive rates will be lower on areas without downed wood (when other forms of cover are absent), 2) long-tailed vole population density, survival rates, and reproductive rates will be higher on areas with more downed wood regardless of the amount of vegetation present.

4.2 Methods

This study was conducted at the Opax Mountain and Sicamous Creek Silvicultural Systems project study areas described in Chapter 1. Populations were monitored from 1994-1997 at Opax and 1994-1998 at Sicamous on downed wood treatment areas described in Chapter 2. Downed wood was removed from and added to areas on clear-cuts and forested grids to create a range in the amount of downed wood. I studied meadow vole and long-tailed vole population dynamics on the downed wood treatment areas using an intensive mark-recapture study. I followed the same small mammal population sampling protocol, on the same sampling grids as described for deer mice in Chapter 3.

4.2.1 Data Analyses

4.2.1.1 Population Dynamics

I analysed the mark-recapture data of meadow voles and long-tailed voles using the same methods described for deer mice in Chapter 3. I compared Jolly-Seber population estimates, and survival and recapture rates generated in Program MARK across downed wood treatment areas to identify changes in population dynamics across downed wood treatments. I compared indices of reproduction (proportion of reproductive females and juveniles in the population) across downed wood treatments using the same methods described in Chapter 3. Voles were identified as juveniles if, at first capture, they weighed less than the minimum weight of male voles known to have over-wintered. At Opax, juveniles were defined as those voles weighing < 25 g, and at Sicamous < 24 g at first capture. It is not likely that immigrants were accidentally classified as juveniles using this method because the cutoffs were less than the smallest meadow vole (minimum weight 26 g, average weight of immigrant meadow voles was 35 g), and long-tailed vole (minimum 25 g, average weight of immigrants was 35 g) known to immigrate to a sampling grid. The cutoff was also lower than the weight of the smallest male vole known to over-winter at the site (meadow vole, minimum 25 g, $\bar{x}$ over-winter weight = 31.5 g; long-tailed vole, minimum 24 g, $\bar{x}$ over-winter weight = 40 g).

4.2.1.2 Downed Wood, Vegetation, and Litter and Moss Sampling

To investigate the relationship between mean population density with downed wood treatments, block, and patterns in vegetation, I constructed scatterplots of mean post-treatment population density on each sampling grid with various downed wood, vegetation, and forest floor characteristics, following the same procedure described in Chapter 3.

Unless otherwise stated, all means are presented ± 2 standard errors (SE) of the mean.

4.3 Results

Although I manipulated downed wood levels on forested areas as well as clear-cuts, *Microtus* were not captured frequently enough on forested areas to permit analysis. Therefore, I restrict my discussion to the results of the study on clear-cut areas at Opax Mountain and Sicamous Creek.

4.3.1 Meadow vole populations at Opax

Meadow voles were rare on the study area before harvesting and were captured almost exclusively on clear-cut areas in 1994-1997. Thus, their appearance marks a shift in the small mammal community from one dominated by red-backed voles and deer mice on forested areas to one dominated by meadow voles and deer mice on clear-cuts, similar to that reported elsewhere (Kirkland 1990). I had 1261 captures of 664 meadow voles on clear-cuts during the study, and only captured 21 voles on forested areas. Therefore, clear-cut treatment areas were placed in a matrix of inhospitable habitat for meadow voles (forest). Trap mortalities comprised approximately 1% of captures.

Two meadow voles (0.3% of 664 individuals) moved between sampling grids during the study; they were one-way movements (were not captured again on the original sampling grid). The low rate of movement among sampling grids suggests that treatment areas were distinct sampling units for meadow voles. To assess potential edge effects, I compared the proportion of resident meadow voles (captured >once) that were captured at least once in an edge trap, across downed wood treatments. In this case, the proportion of voles captured in edge traps was similar on *low* and *high* treatment areas, which suggests that downed wood treatment did not influence the frequency of vole movement at the edge of the sampling grid. Mean ETA over all sampling

grids was 1.11 ± 0.09 ha, and ranged from 1.1 ha to 1.8 ha. The estimated trapped area was always smaller than the 1.7 ha treatment site except on one grid in 1997.

4.3.1.1 Population density

Recapture rates were variable during the study, but were generally $< 70\%$. When trappability estimates are low, Jolly-Seber estimates provide the most accurate estimate of population density (Hilborn *et al.* 1976). Few meadow voles were present on the study area before harvesting in winter 1993-1994. After harvesting, meadow vole population density varied, but did not consistently increase or decrease over time (Fig. 20a, Appendix 2e, Table 6). Population density did not differ significantly across downed wood treatments (*low* $\bar{x} = 6.5 \pm 1.9$, *medium* $\bar{x} = 4.5 \pm 1.5$, *high* $\bar{x} = 7.9 \pm 2.1$, Table 6, Fig. 20a).

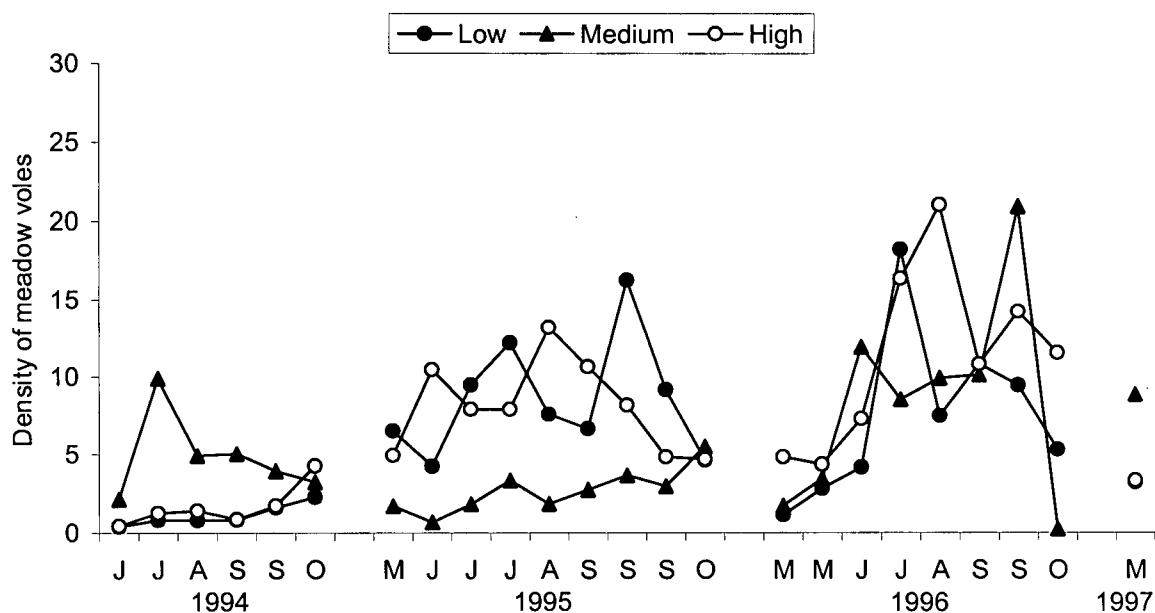
4.3.1.2 Stand Level Habitat Relationships

When investigating patterns in meadow vole population density across sampling grids, scatterplots suggested that variability in mean meadow vole density across sampling grids was correlated most strongly with the abundance of short shrubs (Fig. 21). A linear regression indicated that mean short shrub cover explained 35% of variability in meadow vole density across sampling grids (adjusted $r^2 = 0.35$, $F_{(1,7)} = 5.23$, $P = 0.05$, Fig. 22).

4.3.1.3 Survival and Recapture Rates

Recapture rates (the chance of capturing a vole known to be alive within a trapping session) of meadow voles varied across time and among sampling grids. Grouping sampling grids by downed wood treatment or block did not improve the model, nor did grouping time periods by year or season. Accordingly, recapture rates were modelled by the function $\phi_{\text{grid} \times \text{time}} p_{\text{grid} \times \text{time}}$. Recapture rates of meadow voles were variable, ranging from 17% to 77% across sampling sessions, with an average of 42.6%.

a) Opax



b) Sicamous

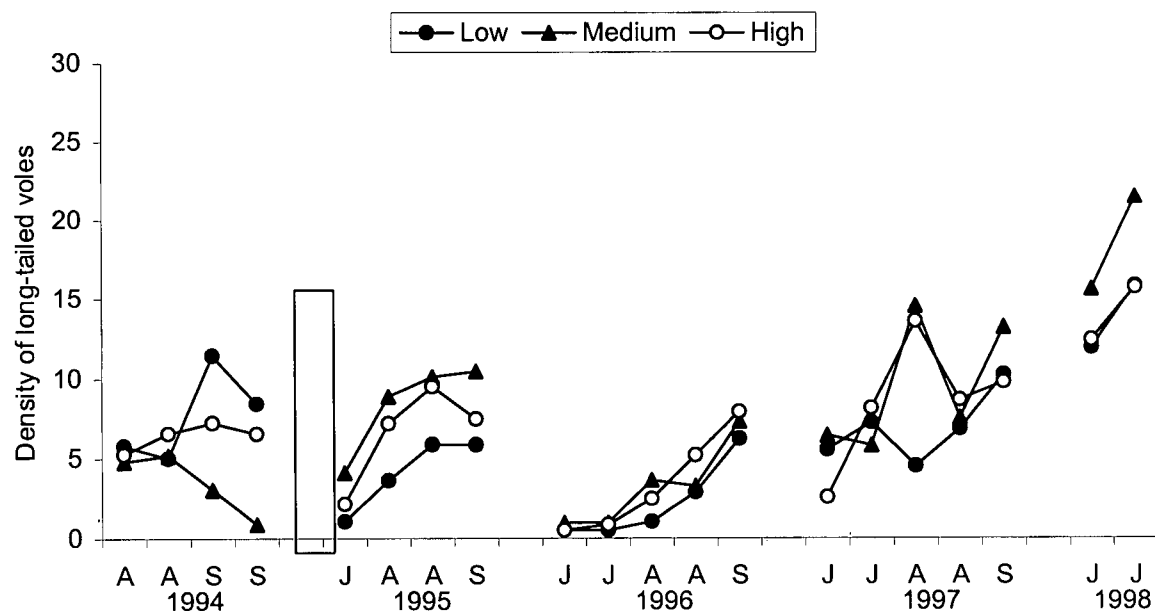


Figure 20. Estimated density of a) meadow voles on clear-cut sampling grids at Opax, and b) estimated density of long-tailed voles on clear-cut sampling grids at Sicamous. Downed wood was manipulated at Opax during harvesting in winter 1993-4, before trapping began on the site. Downed wood was manipulated at Sicamous during harvesting and site-preparation in winter 1994-1995 (indicated by outlined area). Error bars were omitted for readability; population estimates are presented separately for each sampling grid in Appendix 2.

Table 6. Results of split-plot analysis of meadow vole density at Opax. a) Split-plot where estimates for each sampling period were repeated measures, b) Split-plot where mean density estimates across years were repeated measures.

a)		
Effect	Error term	Test
Downed wood	A ($F_{4,6} = 3.86, P < 0.1$)	$F_{2,4} = 0.42, P > 0.5$
Block	A	$F_{2,4} = 3.66, P > 0.1$
Time	B	$F_{1,6} = 2.99, P > 0.1$
Downed wood x time interaction	B	$F_{2,6} = 1.05, P > 0.1$
b)		
Effect	Error term	Test
Downed wood	B ($F_{4,6} = 0.71, P > 0.1$)	$F_{2,6} = 0.15, P > 0.5$
Block	B	$F_{2,6} = 5.03, P > 0.05$
Year	B	$F_{1,6} = 1.96, P > 0.1$
Downed wood x time interaction	B	$F_{2,6} = 0.92, P > 0.1$

Modelling variability in survival rates over time by grouping sampling periods by season and year was better supported than using time alone. Introducing downed wood treatment (*low* versus *medium/high* combined) with season was also supported. Two models ($\phi_{\text{season+year}}$ $p_{\text{grid+time}}$, and $\phi_{\text{dw tmt+season}}$ $p_{\text{grid+time}}$) were within 2 ΔAICc of the top model (ϕ_{season} $p_{\text{grid+time}}$), and so were considered to have some support. Weekly survival rates were approximately 1% higher on *low* downed wood treatment sites than on *medium/high* treatment sites. Survival rates tended to decline during the study, but were high overall. Survival rates were approximately 5% lower in 1995 than 1994, and 2% lower in 1996 than 1995. Survival rates during summer (87% wk^{-1}) were slightly higher than in the fall (85% wk^{-1}); over-winter survival was highest (95% wk^{-1}).

4.3.1.4 Reproduction

The proportion of reproductive females in the population was similar across downed wood treatment areas (*low* $\bar{x} = 23.3\% \pm 5.3$, *medium* $\bar{x} = 29.4\% \pm 9.3$, *high* $\bar{x} = 27.2\% \pm 5.7$) and years (Table 7a). Proportion of juveniles in the population increased from 1994 (13%) to 1996 (29%), but did not differ significantly across downed wood treatments (*low* $\bar{x} = 24.9\% \pm 12.8$, *medium* $\bar{x} = 21.1\% \pm 7.5$, *high* $\bar{x} = 20.9\% \pm 7.8$; Table 7b).

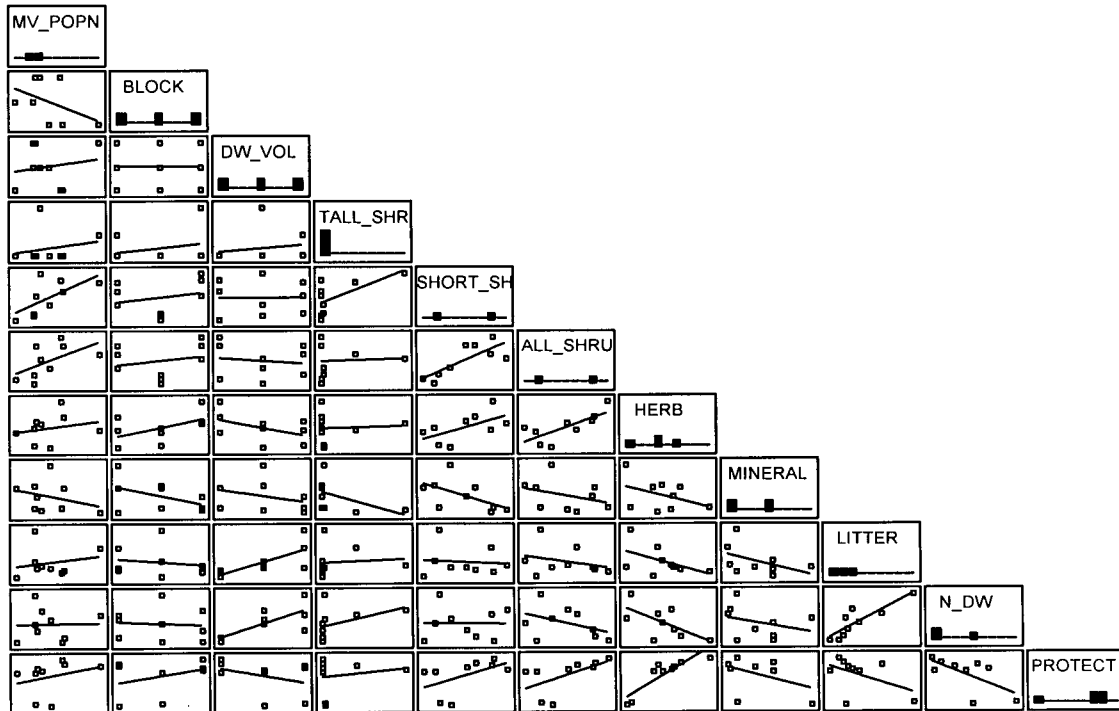


Figure 21. Scatterplot and frequency distribution histogram (and trend line) of mean meadow vole density with mean cover by tall and short shrubs, all shrubs, herbs and grasses (HERB), mineral soil, moss layer, and litter layer, as well as downed wood treatment volume class of downed wood (9 grids), number of pieces of downed wood (N_DW) and protective cover. The trend line in each section is meant as a guide only; it does not signify a statistically significant relationship. The scatterplots are for exploratory purposes only, and the scale of each correlation is different, depending on the habitat variable involved. Density of meadow voles is on the X axis, habitat component is on the Y axis.

4.3.2 Long-tailed Vole Populations at Sicamous

Long-tailed voles were frequently captured in 1994, but captures on forested areas declined during the rest of the study. There were 330 total captures on forested areas in 1995, and eight captures from 1996-1998. Because of the low number of captures, especially after 1996 when the downed wood manipulations on forested areas were completed, I did not include analyses of the long-tailed vole population response to downed wood treatments on forested areas.

During the study at the Sicamous study area (1994-1998), I had 2,164 total captures of 919 long-tailed voles on clear-cut treatment sites. Accidental trap mortalities comprised approximately 2.5% of captures.

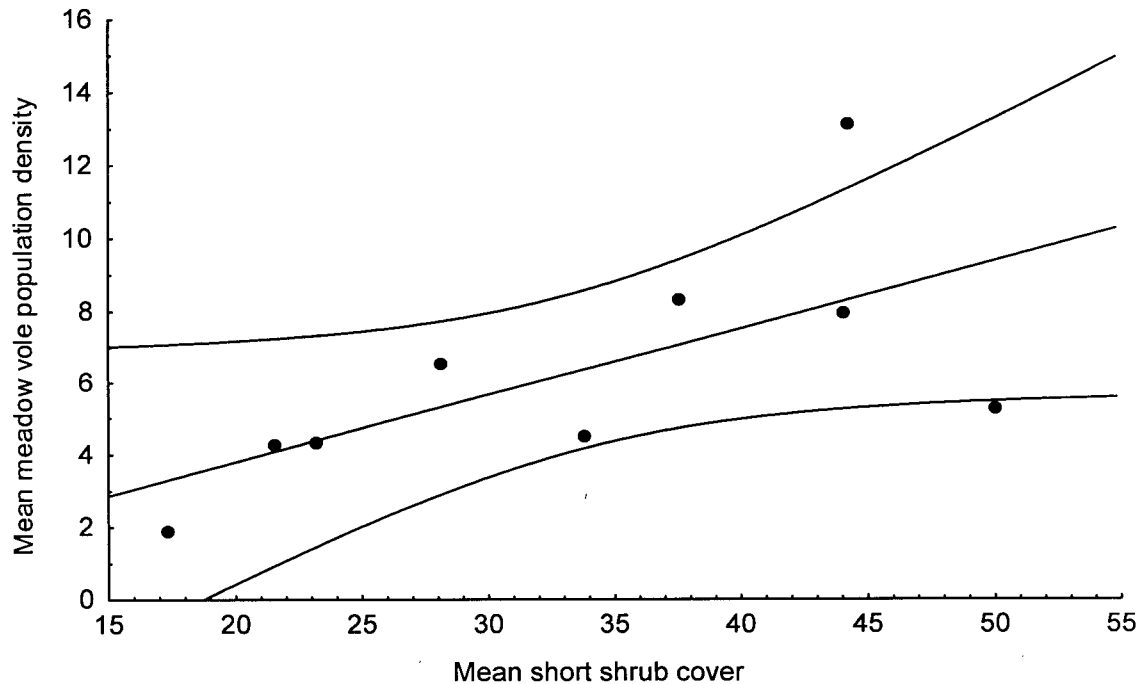


Figure 22. Relationship between mean post-treatment meadow vole population density and short shrub cover (<2 m tall) across sampling grids. Regression line and 95% Confidence Intervals are shown.

Thirty-three long-tailed voles (3.5% of 919) were captured on more than one grid. The majority of these captures (25/33 voles) were emigrants. Eight voles (0.9% of voles captured) were primarily captured on one sampling grid, but were captured at least once on another sampling grid before returning to the original grid. Any movement of long-tailed voles off treatment areas, particularly from *low* areas to the surrounding habitat where voles could access downed wood, would tend to make it more difficult to detect treatment effects. As with meadow voles, I explored potential edge effects by comparing the proportion of resident voles captured at least once in an edge trap. On average, a similar, and slightly smaller proportion of long-tailed voles were captured in *low* edge traps than on *high* treatment areas, which suggests that voles on *low* areas were not more likely to move to the edge of the sampling grid than voles on *high* areas. Mean ETA for long-tailed voles across all grids and years at Sicamous was $1.37 \pm$

Table 7. Results of split-plot analysis of meadow vole reproductive parameters from the Opax study area. a) Proportion of population comprised of reproductive females, and b) proportion of juveniles in the population. An * indicates statistically significant results.

a) Reproductive females

Effect	Error term	Test
Downed wood	B ($F_{4,6} = 0.52, P > 0.1$)	$F_{2,6} = 0.45, P > 0.5$
Block	B	$F_{2,6} = 1.16, P > 0.1$
Year	B	$F_{1,6} = 0.90, P > 0.1$
Downed wood x year interaction	B	$F_{2,6} = 0.11, P > 0.5$

b) Juveniles

Effect	Error term	Test
Downed wood	B ($F_{4,6} = 0.45, P > 0.1$)	$F_{2,6} = 0.23, P > 0.5$
Block	B	$F_{2,6} = 0.74, P > 0.1$
Year*	B	$F_{1,6} = 4.55, P < 0.1$
Downed wood x year interaction	B	$F_{2,6} = 0.25, P > 0.5$

0.01 ha. ETA varied between 1.30 and 1.49 ha, therefore it was always smaller than the 1.7 ha treatment site.

4.3.2.1 Population Density

Mean population density of long-tailed voles was relatively stable in 1994 (forested, pre-harvest) and 1995 (first year post-harvest), increasing through the summer and declining over-winter (Fig. 20b, Appendix 2f). Mean population density did not differ significantly across downed wood treatments (*low* $\bar{x} = 5.8 \pm 2.9$, *medium* $\bar{x} = 5.5 \pm 5.1$, *high* $\bar{x} = 6.8 \pm 3.0$, Table 8). Populations declined to very low levels (<5 voles/ha) during the first winter post-harvest. Population density then increased steadily across the study area from 1996-1998 at which point the study ended, with relatively high population densities (approximately 15 voles/ha, Fig. 20b). Populations appeared to be quickly increasing in size; mean density in spring 1998 was generally higher than the density the previous fall, thus the normal over-winter/spring mortality was lower.

4.3.2.2 Stand level habitat relationships

Scatterplots of mean post-treatment long-tailed vole density with habitat components suggested that density varied strongly with an index of the amount of downed wood on the

Table 8. Results of split-plot analysis of long-tailed vole density at Sicamous. a) Split-plot where estimates for each sampling period were repeated measures, b) Split-plot where mean density estimates across years were repeated measures. An * indicates effects that are statistically significant.

a)		
Effect	Error term	Test
Pre-harvest/treatment		
Downed wood	A ($F_{4,6} = 6.06, P < 0.05$)	$F_{2,4} = 0.01, P > 0.5$
Block	A	$F_{2,4} = 4.83, P > 0.05$
Time	B	$F_{1,6} = 0.85, P > 0.1$
Downed wood x time interaction	B	$F_{2,6} = 1.64, P > 0.1$
Post-treatment		
Downed wood	B ($F_{4,6} = 0.95, P > 0.1$)	$F_{2,6} = 2.48, P > 0.1$
Block	B	$F_{2,6} = 1.78, P > 0.1$
Time*	B	$F_{1,6} = 4.04, P < 0.1$
Downed wood x time interaction	B	$F_{2,6} = 0.67, P > 0.5$
b)		
Effect	Error term	Test
Downed wood	B ($F_{4,6} = 0.27, P > 0.1$)	$F_{2,6} = 1.63, P > 0.1$
Block	B	$F_{2,6} = 1.99, P > 0.1$
Year*	B	$F_{1,6} = 8.83, P < 0.05$
Downed wood x time interaction	B	$F_{2,6} = 0.29, P > 0.5$

sampling grid (Fig. 23). Variability in the number of pieces of downed wood could explain 62.5% of variability in mean long-tailed vole population density across sampling grids (Fig. 24, adjusted $r^2 = 0.625$, $F_{(1,7)} = 1.34$, $P < 0.01$). The relationship remained when data were analysed without data for the grid with the largest population size (outlier; adjusted $r^2 = 0.642$, $F_{(1,6)} = 13.55$, $P = 0.01$).

4.3.2.3 Survival and Recapture Rates

Modelling of recapture rates indicated that the assumption of a constant recapture rate across all sampling grids and time periods ($\phi_{\text{grid} \times \text{time}} p_{(.)}$) was best supported by the data (lowest AIC). The mean recapture rate was 75%.

Weekly survival rates varied with time and across grids. Downed wood treatments did not have an identifiable effect on survival rates. Survival rates were best modelled by including a season (spring/summer, fall and winter) and year effect ($\phi_{\text{season} + \text{year}} p_{(.)}$). Survival rates were temporarily reduced after harvesting. Survival rates over winter 1994-1995 when the site was

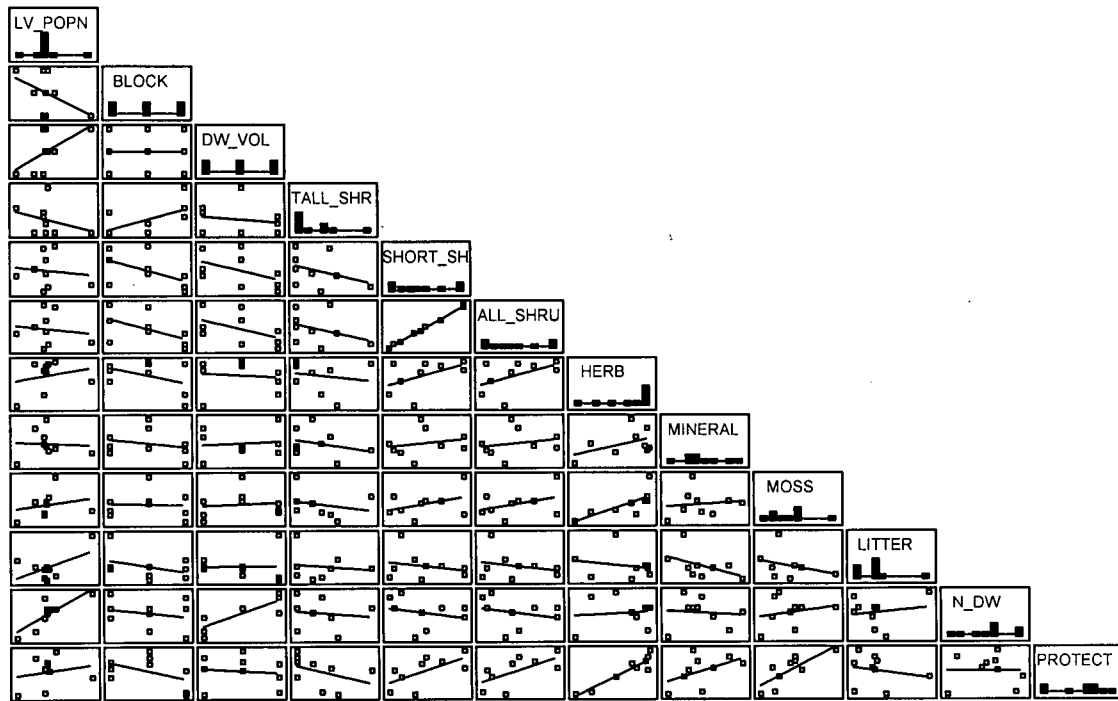


Figure 23. Scatterplot and frequency distribution histogram (and trend line) of mean long-tailed vole density with mean cover by tall and short shrubs, herb and grass (HERB), mineral soil, moss layer, litter layer, as well as volume of downed wood, number of pieces of downed wood (N_DW), and protective cover. The trend line in each section is meant as a guide only; it does not signify a statistically significant relationship. The scatterplots are for exploratory purposes only, and the scale of each correlation is different, depending on the habitat variable involved. Density of long-tailed voles is on the X axis, habitat component is on the Y axis.

harvested (50.4% wk⁻¹), and the following summer (72.1% wk⁻¹) were lower than during the rest of the study (summer: $\bar{x} = 88.2\%$, winter: $\bar{x} = 94.8\%$).

4.3.2.4 Reproduction

The proportion of reproductive females (*low* $\bar{x} = 15.3\% \pm 6.7$, *medium* $\bar{x} = 26.4\% \pm 5.0$, *high* $\bar{x} = 21.3\% \pm 3.3$) and proportion of juveniles (*low* $\bar{x} = 34.8\% \pm 8.9$, *medium* $\bar{x} = 36.3\% \pm 8.3$, *high* $\bar{x} = 37.2\% \pm 8.1$) in the population was similar across downed wood treatments and across years post-harvest/manipulation (Table 9).

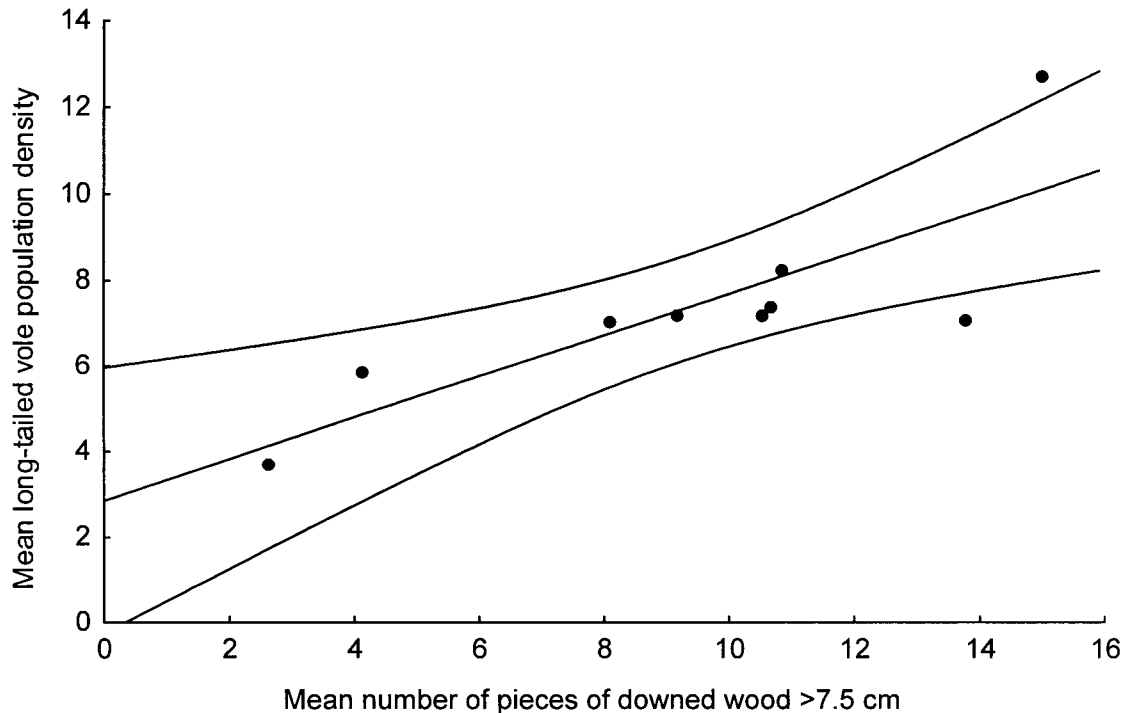


Figure 24. Relationship between mean long-tailed vole population density (post-treatment) and a relative index of the mean number of pieces of downed wood ≥ 7.5 cm in diameter (per 5.65-m radius sampling plot across sampling grids), with 95% confidence intervals. Variability in the number of downed wood pieces could explain 62.5% of the variability in long-tailed vole population density.

4.4 Discussion

4.4.1 Experimental Design

Downed wood volumes on *medium* and *high* treatments at both study areas were difficult to distinguish statistically because the volumes on manipulated areas fell within the natural range of variability in downed wood volume on unmanipulated treatment areas. However, the manipulations were effective in creating a range in the amount of downed wood among treatments within study area/seral stage combinations, which provided a base against which to compare vole abundance and demography.

Because this study focussed on downed wood, vegetation on the treatment sites was not manipulated during the study. This prevented me from studying the downed wood-vole

Table 9. Results of split-plot analysis of long-tailed vole reproductive parameters from the Sicamous study area. a) Proportion of population comprised of reproductive females, and b) proportion of juveniles in the population.

a) Reproductive females

Effect	Error term	Test
Downed wood	B ($F_{4,6} = 1.29, P > 0.1$)	$F_{2,6} = 2.25, P > 0.1$
Block	B	$F_{2,6} = 0.42, P > 0.5$
Year	B	$F_{1,6} = 0.37, P > 0.5$
Downed wood x year interaction	B	$F_{2,6} = 0.16, P > 0.5$

b) Juveniles

Effect	Error term	Test
Downed wood	B ($F_{4,6} = 1.54, P > 0.1$)	$F_{2,6} = 0.07, P > 0.5$
Block	B	$F_{2,6} = 0.26, P > 0.5$
Year	B	$F_{1,6} = 0.36, P > 0.1$
Downed wood x year interaction	B	$F_{2,6} = 0.72, P > 0.5$

relationship without the potential confounding effect of vegetation cover. Percent ground cover by vegetation was high on clear-cuts at the Opax study area within two years post-harvest. The shorter, colder growing seasons at the Sicamous study area slowed vegetation growth compared to Opax. The lower vegetation cover on clear-cuts at Sicamous potentially increased the relative value of downed wood as thermal and security cover at that site.

The fact that there was movement of voles between sampling grids within harvest treatment units indicated that the downed wood treatment sites might not have been distinct sampling units, particularly for long-tailed voles at Sicamous. The placement of sampling grids was influenced by the operationally-sized harvest treatment units. The patch-cuts at the Opax study area were placed in a forest matrix, which increased the separation between treatment sites (both visually, and because the voles would have to cross a different, inhospitable habitat type to reach another treatment area). However, at Sicamous, three treatment areas were placed in a 10-ha clear-cut. Downed wood treatments were randomly assigned to sampling grids within harvest treatment units, and downed wood treatments were replicated across blocks (not within), to improve the generality of the results. Movement of voles off the treatment area would tend to make it more difficult to detect differences in population density, survival or

reproductive rates across sampling grids. The mean estimated trapping area (ETA) for each grid, which was calculated from data on movements of voles, was in all but one case below the 1.7-ha treatment site size. As well, the proportion of voles captured in edge traps did not vary by downed wood treatment. The low rates of movement, the relatively small ETAs, and the lack of evidence of an edge effect suggests that the study design was adequate to test the relative importance of downed wood as a habitat component for voles, within the limitations discussed above.

Red foxes were present on the Opax study area, but did not cause a problem until 1996. Foxes in 1996 and 1997 cued in to live-trapping grids and broke open traps. Foxes disturbed traps on every sampling grid in my study, but were particularly active on clear-cut sampling grids. Traps were not disturbed every sampling session, and generally $\leq 10\%$ of traps were disturbed if the fox had visited the grid (the maximum level of disturbance was 30%). When I analysed survival and recapture data, I included a covariate to test whether survival rates or recapture rates were significantly lower during trapping sessions when the fox had disturbed traps on the grid. Fox disturbance did not appear to significantly affect recapture or survival rates across forested or clear-cut sampling grids. Survival rates dropped during the study (but still remained fairly high), but the largest decline was between 1994 and 1995, before foxes began disturbing traps. The combination of similar levels of fox disturbance across sampling grids within seral stages, and the lack of a significant fox effect on survival or recapture rates suggests that observed patterns in meadow vole population density across downed wood treatment areas was not influenced by trap disturbance by foxes.

4.4.2 Meadow voles

The retention of downed wood on clear-cut areas at Opax did not have a strong effect on meadow vole population dynamics within three years post-harvest. Meadow voles tended to remain on *low* treatment areas longer than on *medium* or *high* areas (survival rates were, on average, 1% higher on *low* areas). However, this difference was not sufficient to create detectable differences in population density more than three years post-treatment, and reproductive rates were similar among downed wood treatment areas. It is possible that edge effects hampered my ability to detect a treatment effect. This is unlikely because few meadow voles moved among grids and voles were not more likely to be captured in edge traps on *low* treatments. The result in this study is supported by a similar result reported by Moses and Boutin (2001), where meadow vole population density was similar on clear-cuts with and without downed wood in a boreal aspen mixedwood forest.

In the present study, clear-cuts were sparsely vegetated immediately post-harvest, but population densities were low until 1995 when percent ground cover by vegetation on the sampling grids was high. Thus, I could not directly address my first hypothesis, that meadow voles would be more abundant on areas with more downed wood in areas of sparse vegetation.

Downed wood is considered to be an important habitat component for many small mammal species, providing them with both cover and foraging opportunities (Dueser and Shugart 1978, Goodwin and Hungerford 1979, Maser *et al.* 1979, Kaufman *et al.* 1983, Maser and Trappe 1984, Harmon *et al.* 1986, Hayes and Cross 1987, Graham *et al.* 1994, Carey and Johnson 1995). Although wood will not provide foraging opportunities for *Microtus*, it could be an important security and/or thermal cover component, especially in areas with sparse vegetation. Downed wood is an important moisture reservoir, especially in dry ecosystems (Clarkson and

Mills 1994), and provides a sheltered, cooler microclimate that might be important for voles (Miller and Getz 1977, Getz 1985).

Previous research on *Microtus* demonstrated that they respond strongly to changes in the amount of cover. The experimental addition of cover to areas has resulted in an increase in numbers of females, a reduction in the spring decline of males, larger population sizes, and higher overall survival rates of voles (Birney *et al.* 1976, Taitt *et al.* 1981). Most of these effects were likely due to reduced predation pressure (Taitt *et al.* 1981). Vole populations decline on areas where all or most food and vegetation or downed wood is removed through burning, cattle grazing, mowing, or repeated applications of herbicides in orchards (Birney *et al.* 1976, Medin and Clary 1989, review in Fleischner 1994, Edge *et al.* 1995, Sullivan *et al.* 1998b, Getz *et al.* 2001, Lin and Batzli 2001).

Although the response of *Microtus* to significant modifications in the amount of cover is clear, the response to experimental changes in the relative proportion of cover types has been mixed. In a study on the effect of silvicultural treatments on small mammal populations, Sullivan *et al.* (2000) reported that meadow vole populations did not respond linearly to changes in the amount of vegetation, although they were generally more abundant above a threshold of shrub cover between 10-25%. In response to herbicide use, a common method of modifying vegetation cover in forestry (Sullivan 1990, Lautenschlager 1993, Gagné *et al.* 1999), *Microtus* has been reported to increase (Anthony and Morrison 1985), decrease (Santillo *et al.* 1989) or show no response (Sullivan 1990, Sullivan and Boateng 1996, Cole *et al.* 1998, Sullivan *et al.* 1998a). Herbicide temporarily reduces the amount of ground covered by the shrub and herb layers (Santillo *et al.* 1989, Freedman *et al.* 1993). The proportions of the herb and shrub layers left after spraying vary based on the efficiency of the application, as well as the

vegetation community present before spraying (Sullivan 1990, Freedman *et al.* 1993, Lautenschlager 1993, Cole *et al.* 1998). Although the differing responses of *Microtus* to conifer release is undoubtedly due in part to differing sampling techniques (Lautenschlager 1993), it is possible that the variability suggests that meadow voles may have separate thresholds of response to different types of cover.

Previous studies reported that meadow vole densities are related to percent ground covered by grass and herbs, and that voles require a minimum amount of ground cover by grass and/or herbs before they become abundant in an area (Getz 1985, Kirkland 1990, Getz *et al.* 2001). Adler and Wilson (1989) suggested that meadow vole density and survival rates increase linearly with the amount of grass until a critical level of ground cover is reached (30-40%), but they did not report the abundance of other vegetation. Getz *et al.* (2001) reported that meadow vole abundance was determined more by the presence of suitable cover, rather than quality of food. Montane voles are also reported to require at least 30% ground cover by vegetation (Gashwiler 1970). Voles associate at the microsite level with areas with greater vegetation cover (Eadie 1953, Wirtz and Pearson 1960, Bowker and Pearson 1975, Birney *et al.* 1976). Studies have reported that meadow vole abundance or capture rates seemed to be related to the presence of shrubby vegetation rather than herb or grass (Simon *et al.* 1998, Cadenasso and Pickett 2000); others have reported that meadow voles avoid shrub cover (Adler 1988).

In my study, the amount of ground covered by shrubs explained approximately one-third of the variability in meadow vole density across sampling grids. Although this leaves most of the variation in population density unexplained, it suggests that shrubs might be a useful habitat feature for meadow voles. Percent ground cover by herbs and grass on my sampling grids was always greater than the proposed threshold of 30%, which might explain why I did not detect a

relationship between meadow vole density and the amount of herb and grass cover. The relationship with shrubs did not appear to be a simple response to increasing cover, because percent ground cover by shrubs was not simply linearly related to mean protective cover, and mean protective cover was not as useful a predictor of density. The apparent relationship suggests that, once minimum requirements for herb and grass are met, shrub cover can be useful for meadow voles. Similarly, both Simon *et al.* (1998) and Cadenasso and Pickett (2000), who reported an association of meadow voles with shrub cover, conducted studies on areas that, although not explicitly stated, appeared to have herb and grass cover >30%.

It is unlikely that shrubs were a preferred food source for meadow voles on the study area. Although meadow voles are known to consume the bark of shrubs and trees over winter, in natural habitats this tends to happen when populations are large, and in times of nutritional stress (references in Bergeron and Jodoin 1989). Researchers studying vegetation growth and seedling survival on the study area did not report any incidences of feeding damage. There was >60% herb and grass cover on every sampling grid, so there probably was abundant food available. As well, population sizes were not exceptionally large during the study, compared to densities of *Microtus* cited in other studies (*e.g.*, Krebs *et al.* 1976, Galindo and Krebs 1985, Sullivan 1990, Sullivan and Boateng 1996, Getz *et al.* 2001).

Temperature regulation could be an important function of shrub cover at the Opax study area. Summers at the Opax Mountain study area are dry and hot, and winters are cold and snowy. Additional shrub cover could be important for mediating temperature extremes (Santillo *et al.* 1989). All of the study grids were quite well vegetated, so it is not clear whether temperature regulation would be sufficient to account for the distribution of meadow voles (Kirkland 1990). Subnivean spaces are important to winter survival of small mammals (Pruitt

1984). In addition to providing security and thermal cover during the snow-free months of the year, shrubs would create vertical structure under the snow, enabling voles to move about more easily (Spencer 1984, Taylor and Buskirk 1996). Greater amounts of vegetation in the subnivean layer can lead to increased winter survival (Schlegl-Bechtold 1980, West *et al.* 1980).

Shrub cover might also provide important protection from predators. Predation rates on meadow voles vary inversely with the amount of (vegetation) cover (Baker and Brooks 1982). The level of predation on *Microtus* by raptors (Korpimäki and Norrdahl 1989, 1991) and weasels (Pearson 1985) can be very high. Predators such as weasels and owls will specialize on meadow voles, and will cycle in synchrony with their prey (Boutin *et al.* 1995). Owls have greater difficulty identifying prey, and lower capture success, under heavy shrub cover (Kotler *et al.* 1988, Longland and Price 1991, Rohner and Krebs 1996); other raptors specifically hunt in areas with less cover (Sheffield *et al.* 2001). When under threat of predation by weasels, the field vole (*M. agrestis*) avoids shrubby habitat (Korpimäki *et al.* 1996). However, whenever they are under threat by raptors (even if weasels are in the area) they choose shrubby habitat (Korpimäki *et al.* 1996). Similarly, the kangaroo rat (*Dipodomys merriami*) under perceived risk of fox predation preferred feeding under shrub cover (Herman and Valone 2000). There were many predators at the Opax study area including weasels and red foxes, as well as many raptors, including owls. Both weasels and foxes appeared to be more active on clear-cuts than forested areas during the study. I had sixty-one captures of weasels (*Mustela* spp.) during the study, 44 of them being on clear-cuts. Weasel populations appeared to be highest in 1995, as 67% of captures occurred that year. Foxes were on the study area during the entire study, but actively targeted traps on clear-cuts in 1996 and 1997. This suggests that meadow voles on clear-cuts

were under substantial predation risk, which extra cover, in the form of shrubs, might have helped to mitigate.

There was no clear indication of whether meadow vole populations cycled on the study area, although my study, which covered three complete years, might have been too short to identify such a cycle. Meadow vole populations are reported to show annual as well as multiannual cycles, although multiannual cycles may not always be present (Tamarin 1977, Sullivan and Krebs 1981, Taitt and Krebs 1985, review in Krebs 1996). Getz *et al.* (2001) in a 25-year study of meadow voles on three types of grassland habitat found no evidence of regular multiannual fluctuations. Populations on my study area did show signs of increasing in size across years, and increasing amplitude in population density within years. However, in general, populations declined to low levels each year by spring. Maximum population estimates (for one sampling period) were less than 50, and mean estimates in 1996 (the year of largest population sizes) were less than 20/ha. Birney *et al.* (1976) suggested that meadow voles may require a specific threshold of cover by vegetation to reach large enough numbers to cycle, and that the threshold may be higher on drier sites with heavy predator pressure, both of which were factors on my study area.

The results of my study suggest that meadow vole population density is related to the availability of cover and vertical structure from shrubs. Although herb and grass cover was fairly high on all of the sampling grids, the additional structure created by shrubs resulted in higher densities of meadow voles, perhaps by increasing survival rates through reduced predation. Downed wood did not appear to influence meadow vole population dynamics. All of my sampling grids were well vegetated; therefore, I was not able to determine whether downed wood could be an important habitat component in sparsely vegetated areas.

4.4.3 Long-tailed Voles

Long-tailed vole population density was related to the number of pieces of downed wood (≥ 7.5 cm in diameter), but not volume of downed wood, on the Sicamous study area. These data support Van Horne's (1982) findings that long-tailed vole population density was related to the amount of downed wood, and support my second hypothesis, that long-tailed vole populations would be larger on areas with more downed wood.

Because downed wood volume did not appear important, the presence of large logs seems to be of less importance to long-tailed voles than increased ground cover by downed wood. Number of pieces of downed wood was highly correlated with downed wood volume, but some grids had fewer, albeit larger pieces, which increased volume disproportionately. Therefore, long-tailed voles might have been responding to a greater number of moderate-sized pieces rather than the presence of a few large pieces. Greater number of pieces would provide additional security and thermal cover for voles on the area.

Long-tailed voles appear to respond to cover similarly to other *Microtus* species. Previous research suggested that *Microtus* require approximately 30% cover before they will be present on a site (Gashwiler 1970). Although the clear-cuts in this study had low levels of vegetation, all the study areas had at least 30% protective cover, but not necessarily from herbs or shrubs. Few studies have included the long-tailed vole or had sufficient sample sizes to draw conclusions about habitat relationships. However, those that have all reported strong relationships with cover (Van Horne 1982, Sullivan and Boateng 1996, Sullivan *et al.* 1999a). Sullivan *et al.* (1999a) reported that long-tailed vole populations were much lower on some sites more than ten years after a prescribed burn; however, they did not report the abundance of vegetation on the area. Typically, herbaceous cover recovers quickly from a burn (within two years), but shrub cover takes longer (Peterson 1993). Approximately 50% of downed wood is

typically removed during a burn (Peterson 1993, Kranabetter and Macadam 1998). The long-term response of long-tailed voles to the burn suggests that a critical element, perhaps downed wood, was removed from the habitat.

Protection from predation would likely be an important function of downed wood on these sparsely-vegetated clear-cuts. The importance of downed wood for security cover while travelling has been well studied for other species of small mammals (Maser *et al.* 1979, Thomas 1979, Maser *et al.* 1981, Barry and Francq 1982, Maser and Trappe 1984, Hayes and Cross 1987, Barnum *et al.* 1992, Carter 1993, review by Loeb 1996, McMillan and Kaufman 1995). However, there has been little research on the minimum size of log that small mammals will use for travelling. Shrews appear to select logs at least 6 cm in diameter, and preferably 12 cm or larger (Craig 1995). White-footed mice (*P. leucopus*) select logs >5 cm in diameter (Barnum *et al.* 1992) for travelling. California red-backed voles also prefer larger logs (Hayes and Cross 1987). The response by long-tailed voles to larger numbers of moderate-sized (≥ 7.5 cm diameter) logs rather than the presence of a few large logs suggests that moderate-size logs ≥ 7.5 -cm-diameter provide adequate cover for long-tailed voles.

The threat of predation for long-tailed voles on clear-cuts was primarily from raptors. Weasels were rare on the Sicamous study area, and marten avoided the large 10-ha clear-cuts (Huggard 1999). Shrub cover, which reduces the efficiency of hunting by raptors (Kotler *et al.* 1988, Longland and Price 1991, Rohner and Krebs 1996), was sparse on the area, which might increase the relative importance of downed wood for protection from predators.

Logs provide access, and structure to, the subnivean space (Taylor and Buskirk 1996). The importance of the subnivean space is likely greater at Sicamous than Opax because the site is covered with snow one to two metres thick for six to eight months of the year. The temperature

at the soil-snow interface remains relatively warm and stable compared to that above the snow surface. This subnivean microclimate is critical to overwinter survival of small mammals (Pruitt 1978, Anderson 1986).

The lack of an identifiable relationship between herb or shrub cover and long-tailed vole density is surprising, especially based on the known biology of the species as a sedge or shrubby habitat dweller (Spencer 1984, Getz 1985). Herb and shrub cover was quite low on clear-cuts, and was likely <30% in some areas. Van Horne (1982) reported a strong influence of shrub and herb cover on population size, and in the present study meadow vole populations appeared strongly related to vegetation cover. The importance of downed wood to long-tailed voles does not appear to be solely due to the sparse vegetation on the Sicamous clear-cuts. The clear-cuts in Van Horne's (1982) study encompassed a wide range in the amount of vegetation (Van Horne 1981). Therefore, the relationship between long-tailed voles and downed wood appears to be important across a variety of conditions.

The long-tailed vole population at the Sicamous study area showed signs of cycling. When trapping began in 1993 and 1994 (pre-harvest), long-tailed voles were relatively common across the forested area, and may potentially have peaked in 1993. The survival rates of long-tailed voles were low in winter 1994-1995 and summer 1995 after the site was harvested. In 1995-1998 (post-harvest) long-tailed voles were captured almost exclusively on clear-cut areas, and rarely on forested sampling grids. Long-tailed vole populations were small even on clear-cuts during most of the study, but showed signs of starting to increase again in 1997-1998. Many species of *Microtus* are known to be cyclic (e.g., the meadow vole (*M. pennsylvanicus*, Tamarin 1977), prairie vole (*M. ochrogaster*, Tamarin 1977), and Townsend's vole (*M. townsendii*, Beacham 1980). *M. longicaudus* and *M. montanus* may also be cyclic (Taitt and Krebs 1985,

review in Krebs 1996). Long-tailed voles may only be numerous on forested areas in peak years, which is also a pattern reported for meadow voles (Grant 1971, Adler and Wilson 1989). Long-tailed voles gnaw on roots and tree butts in times of nutritional distress; typically during winter (Spencer 1984). Root gnawing may be a useful indicator of peak vole numbers (Danell *et al.* 1981); however, the high incidence of root and tree-butt-gnawing of subalpine fir reported at the beginning of the study at the Sicamous study area (H. Merler, *pers. comm.*) could not be directly linked to long-tailed voles. Unfortunately, my study started as populations were declining and ended as they were increasing so I do not have data for an entire cycle; however, the data available suggest that long-tailed voles likely cycle at the study area.

4.5 Conclusions, Management Implications, and Suggestions for Future Research

This study supports previous work that has suggested that *Microtus* respond positively to increasing complexity of habitats, and that they might have different thresholds of response for different cover attributes.

Meadow vole population density was related to the amount of shrub cover, but not to herb and grass, which is the vole's primary food source (Getz 1985). The lack of a relationship between meadow vole density and herb and grass cover suggests that the minimum requirement for these components were met on the heavily-vegetated clear-cuts, but that shrub cover provided an important additional form of cover. Meadow vole population density did not change with the removal of downed wood from treatment areas. It is possible that downed wood could be an important cover component for meadow voles in areas with sparse cover, but because of the overall high ground cover by vegetation on the clear-cuts, I was not able to address this aspect in my study. Therefore, retaining shrub cover during harvesting might provide useful cover for meadow voles on clear-cuts for the first few years post-harvest. Where

meadow voles might become a pest by feeding on seedlings, controlling the amount of shrub cover on harvested areas in combination with a reduction in the grass layer, might reduce populations. Where large populations of meadow voles are not a concern, retention of shrubs on harvested areas could be accomplished by limiting site preparation, or by retaining clumps of shrubs throughout the clear-cut, and thus providing areas of denser vegetation. Maintaining or removing downed wood on clear-cut areas does not appear to adversely affect meadow voles, so no specific downed wood management for these voles is necessary.

Density of long-tailed voles was related to the number of pieces of downed wood on an area, rather than to downed wood volume or to percent ground cover by vegetation. Clear-cuts on the study area were relatively sparsely vegetated, which might have temporarily increased the value of downed wood to long-tailed voles. The importance of downed wood to long-tailed voles might not be solely due to lack of alternative cover, because Van Horne (1982) also reported the relationship in areas with greater ground cover by vegetation. Therefore, downed wood might be an important habitat component for long-tailed voles regardless of other types of cover, but further research is required.

In the interim, in high-elevation or otherwise slow-growing areas, and in areas with long-tailed voles, downed wood should be left after harvesting to provide cover and structure. Cover by downed wood from all size classes ranged from approximately 5% to 19% at Sicamous. Although the lower levels were inadequate to support long-tailed voles, ground coverage of at least 15-20% as suggested by Carey and Johnson (1995) should be suitable. This would result in approximately 280-450 m³/ha of downed wood on the area. Logs should be spread evenly over the site to provide cover and travel corridors over the area. Burning, which is occasionally used as a site preparation tool in spruce-fir forests, should be avoided because it removes the

vegetation remaining after harvest, along with some of the downed wood, and negatively affects long-tailed voles (Sullivan *et al.* 1999a).

Future research could include:

1. Continued sampling of meadow vole populations at Opax. This:
 - a) Will provide longer-term data on the population dynamics of meadow voles to determine whether these voles cycle in the dry interior of B.C.; and,
 - b) Could be combined with vegetation control (treatments) at Opax. Removal of vegetation will provide the ability to determine whether downed wood could be an important component for meadow voles in areas of sparse vegetation. This could also provide important data on minimum cover requirements of meadow voles.
2. Continued sampling of long-tailed vole populations at Sicamous. This:
 - a) Will provide information on the longer-term response of voles to downed wood treatments in high-elevation forests;
 - b) Will provide additional information about whether the population cycles on the study area. Following the population through a peak year might provide information about the response of voles to treatments in forested areas;
 - c) Should include placing traps outside of treatment areas or using radio-telemetry to identify whether voles move outside treatment areas, and whether this varies across treatments; and,
 - d) Will provide information on the response of voles to downed wood treatments when the areas are more heavily vegetated.

3. Additional research should be conducted to investigate the relationship between long-tailed voles and downed wood. It should:

- a) Be conducted on larger treatment areas, at least 5 ha in size and preferably larger (>10 ha);
- b) Have treatments designed to relate the amount of ground cover by downed wood to population dynamics;
- c) Investigate whether population dynamics vary with average piece size;
- d) Investigate whether the response to downed wood varies with the amount of vegetation; and,
- e) Include radio-telemetry or other tracking methods to determine if and how long-tailed voles use downed wood at a microhabitat scale. Data should be collected on minimum piece size required by these voles.

Chapter 5. Population Dynamics of Red-backed Voles in Relation to Downed Wood

5.1 Introduction

As more old-growth forests are harvested, increasing attention is being focused on the consequences of losing important habitat attributes, such as large amounts of downed wood, understorey cover, or multi-layered forest canopies (Hunter 1990, Carey and Johnson 1995, Angelstam 1997, Bunnell *et al.* 1999, Wilson and Carey 2000). Managed forests have very different structural characteristics than old-growth forests (Triska and Cormack 1980, Spies *et al.* 1988, Spies and Franklin 1991, Rosenberg *et al.* 1994, Carey and Johnson 1995), and may provide less suitable habitat for many vertebrate species (Bunnell *et al.* 1999). To maintain structural diversity as well as biodiversity across the managed landscape, recent research has focused on understanding the function of important habitat components for wildlife so that their functions can be maintained in a managed forest context (Carey and Johnson 1995, Bunnell *et al.* 1999). Downed wood in particular has been identified as an important habitat component that provides important structural features across seral stages for a wide variety of organisms (Harmon *et al.* 1986, Carey and Johnson 1995, Bunnell *et al.* 1999, Wilson and Carey 2000).

Downed wood has long been identified as an important habitat component for many small mammals (Goodwin and Hungerford 1979, Maser *et al.* 1979, Thomas 1979, Maser *et al.* 1981, Kaufman *et al.* 1983, Maser and Trappe 1984, Harmon *et al.* 1986, Hayes and Cross 1987, Graham *et al.* 1994, Carey and Johnson 1995, Bunnell *et al.* 1999, Wilson and Carey 2000). It is thought to be particularly important for red-backed voles (*Clethrionomys* spp.; Tevis 1956, Merritt 1981, Harmon *et al.* 1986, Carey and Johnson 1995), which is considered to be associated with late seral forests (Merritt 1981). Most research on habitat relationships of red-backed voles has focussed on the California red-backed vole (*C. californicus*), which may have

different habitat requirements than the southern red-backed vole. Although much of this research has suggested that downed wood is an important habitat component (*e.g.*, Maser and Trappe 1984), some have questioned this relationship (Ure and Maser 1982, Rosenberg *et al.* 1994, Mills 1995). Carey and Johnson (1995) suggested that downed wood is not as important in northern, more mesic forests as in southern forests, and further suggested that forest floor and understorey vegetation are more important factors. Other authors have also suggested that other forest floor characteristics such as a deep organic soil layer or dense understorey cover may be more strongly related to red-backed vole abundance than the amount of downed wood (Nordyke and Buskirk 1991, Rosenberg *et al.* 1994). However, studies have generally been conducted on areas with relatively abundant downed wood, perhaps greater than a required threshold amount to maintain vole abundance (Bunnell *et al.* 1999).

There has not been an experimental evaluation of the effects of downed wood on the southern red-backed vole in forested habitat. One recent study examined the effect on voles of removing downed wood from clear-cuts in a young boreal aspen mixedwood forest, and found that retention of downed wood on the area did not compensate for the loss of the forest canopy (Moses and Boutin 2001). This is the first study to experimentally examine the relationship between downed wood and red-backed voles in both forested and clear-cut habitat in a coniferous forest landscape.

In this chapter, I report the results of a multi-year study of the relationship between manipulated volumes of downed wood and red-backed vole population dynamics, in both forested and clear-cut habitats, and in two distinct ecosystems. I test the hypotheses: 1) that red-backed vole population dynamics will be positively associated with downed wood; specifically, that density, survival rates and reproductive rates will be lower on areas with less downed

wood; 2) that retention of downed wood on clear-cuts will mitigate harvest effects; specifically, that red-backed vole populations will decline faster on clear-cut areas without downed wood than on areas with downed wood; and 3) that downed wood is an important, unique component for red-backed voles; specifically, that a positive relationship between red-backed vole populations parameters and downed wood will not depend on the presence of alternative forms of cover.

5.2 Methods

The study took place at the Opax Mountain and Sicamous Creek Silvicultural Systems Project study areas described in Chapter 1. I studied red-backed vole populations on areas where downed wood was manipulated to provide a range in volume across sampling grids far greater than normally available. The methods used to manipulate downed wood, and the resulting volumes of downed wood on treatment areas are described in Chapter 2. Red-backed voles were monitored on the downed wood treatment areas with an intensive mark-recapture study, following the same protocols described in Chapter 3.

The research was conducted in unharvested treatment areas at two study areas [D, I, and N at Opax, Chapter 2, Fig. 3; and A1, B2, and C4 at Sicamous Creek, Fig. 4] and on clear-cut treatment areas [1.7-ha patch-cuts, blocks E, J, and N at Opax, Fig. 2, and the 10-ha clear-cuts on A4, B5, and C3 at Sicamous Creek, Fig. 4].

5.2.1 Analyses

5.2.1.1 Red-backed Vole Population Dynamics

I analysed mark-recapture data of red-backed voles using the same methodology outlined in Chapter 3 for deer mice. I generated Jolly-Seber population estimates of red-backed vole populations for each sampling session, and analysed the data with a split-plot in time ANOVA

(see Chapter 3 for details). To analyse survival and recapture rates, I used an iterative modelling procedure in Program MARK. The procedures I used are outlined more fully in Chapter 3. For analyses of reproduction indices, juvenile red-backed voles were defined as those individuals weighing ≤ 14 g at first capture at Opax, and ≤ 16 g at Sicamous. I used these cut-offs because they were the smallest weights of red-backed voles known to emigrate from sampling grids (16 g, but voles were normally >16 g), and was less than the weight of male over-wintered red-backed voles (Opax, $\bar{x} = 21.8 \pm 0.6$ g, range 17-30 g, $n = 126$; Sicamous, $\bar{x} = 28.8 \pm 0.5$ g, range 22-36 g, $n = 108$). I analysed reproductive data with split-plot ANOVAs following the procedure detailed in Chapter 3.

Unless otherwise stated, all means are presented ± 2 standard errors (SE) of the mean.

5.3 Results

5.3.1 Red-backed Vole Populations at Opax

I captured 3148 red-backed voles a total of 9283 times during the study; trap mortalities comprised less than 1% of captures. Mean ETA was 1.36 ± 0.04 ha (range: 1.10-1.65 ha), which was smaller than the treatment area of 1.7 ha. ETA among clear-cut downed wood treatment areas was similar ($F_{2,24} = 0.72$, $P > 0.05$), but ETA declined during the study ($F_{3,24} = 5.8$, $P < 0.05$) from a mean of 1.32 ha to 1.14 ha. ETA on forested treatment areas did not vary across years or downed wood treatment ($F_{2,24} = 0.17$, $P > 0.05$, $F_{3,24} = 2.35$, $P > 0.05$).

Eighty-two red-backed voles (2.6% of individuals captured) were captured on more than one sampling grid. Most of these movements (54/82) were one-way movements. Number of voles known to emigrate was similar among downed wood treatments on both forested ($F_{2,6} = 1.55$, $P > 0.1$) and clear-cut treatment units ($F_{2,6} = 1.00$, $P > 0.1$). Rates of immigration were also similar among downed wood treatments on forests and clear-cuts ($F_{2,6} = 0.12$, $P > 0.5$; $F_{2,6} =$

0.5, $P > 0.5$). Twenty-eight voles (0.9%) were captured primarily on one sampling grid, but were captured at least once on another sampling grid and subsequently returned to the primary grid. The proportion of voles that moved back and forth at least once was similar among downed wood treatments on both forested ($F_{2,6} = 0.19$, $P > 0.5$) and clear-cut units ($F_{2,6} = 0.50$, $P > 0.5$).

On clear-cuts, only the *high* treatment on block J had relatively large volumes of downed wood. Therefore, for survival and recapture analyses, data from E and M *high* treatment areas were grouped with *medium* areas. Data for *low* grids were also compared with data combined for all *medium* and *high* grids (*medium/high*). Because of the difficulty of analysing an unbalanced split-plot design, I analysed population density using *low*, *medium*, and *high* groupings, and identified significant downed wood effects by examining graphs of population means. For forest data, I considered the *medium* treatment site on N block to be *low*, and the *high* site on N block to be *medium* for analyses of survival and captures rates. Split-plot analyses require a balanced design, so I could not reclassify sampling grids across downed wood treatment classes. Therefore for analysis of population density, I analysed data for D and I blocks only.

5.3.1.1 Population Density

5.3.1.1.1 Forest

Mean population density of red-backed voles declined during the study, becoming very low by 1996 (year following treatment) and remained low in 1997 (Table 10a, Fig. 25a, Appendix 2g). Population density tended to be higher on *high* treatments ($\bar{x} = 19.7 \pm 4.8$ voles/ha) than on *medium* ($\bar{x} = 13.1 \pm 3.7$ voles/ha) or *low* ($\bar{x} = 14.6 \pm 3.9$ voles/ha) areas post-treatment (P value = 0.08, Table 10a).

Table 10. Results of split-plot analysis of red-backed vole density from the Opax study area for a) forest, and b) clear-cut sampling grids. Split-plot data are presented for i) split-plot in time (time) with individual samples as split-plots and ii) mean density of voles across years (year) as split-plot. An * indicates effects that are statistically significant.

a) i) Forest

Effect	Error term	Test
Pre-treatment		
Downed wood	B ($F_{2,3} = 2.65, P > 0.1$)	$F_{2,3} = 2.49, P > 0.1$
Block*	B	$F_{1,3} = 16.25, P < 0.05$
Time*	B	$F_{1,3} = 11.15, P < 0.05$
Downed wood x time interaction	B	$F_{2,3} = 0.43, P > 0.5$
Post-treatment		
Downed wood	B ($F_{2,3} = 1.53, P > 0.1$)	$F_{2,3} = 7.19, P < 0.1$
Block*	B	$F_{1,3} = 30.37, P < 0.05$
Time*	B	$F_{1,3} = 8.68, P < 0.1$
Downed wood x time interaction	B	$F_{2,3} = 0.92, P > 0.1$

ii) Forest (year)

Effect	Error term	Test
Downed wood	B ($F_{2,3} = 3.92, P > 0.1$)	$F_{2,3} = 0.58, P > 0.5$
Block	B	$F_{1,3} = 21.32, P > 0.05$
Year*	B	$F_{1,3} = 38.17, P < 0.01$
Downed wood x year interaction	B	$F_{2,3} = 1.95, P > 0.1$

b) i) Clear-cut

Effect	Error term	Test
Downed wood	A ($F_{4,6} = 12.35, P < 0.05$)	$F_{2,4} = 3.56, P > 0.1$
Block	A	$F_{2,4} = 1.03, P > 0.1$
Time*	B	$F_{1,6} = 19.39, P < 0.005$
Downed wood x time interaction	B	$F_{2,6} = 2.62, P > 0.1$

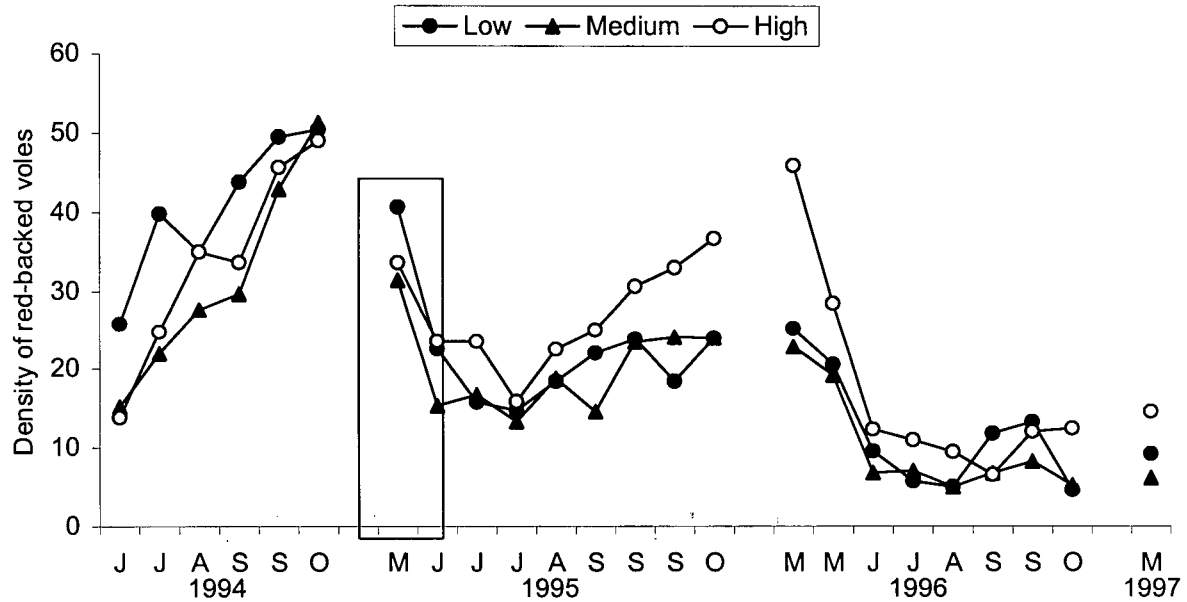
ii) Clear-cut (year)

Effect	Error term	Test
Downed wood*	B ($F_{4,6} = 2.23, P > 0.1$)	$F_{2,6} = 8.35, P < 0.05$
Block	B	$F_{2,6} = 1.84, P > 0.1$
Year*	B	$F_{1,6} = 4.01, P < 0.1$
Downed wood x year interaction*	B	$F_{2,6} = 32.64, P < 0.005$

5.3.1.1.2 Clear-cut

Population densities on *low* (overall $\bar{x} = 4.4 \pm 1.2$ voles/ha) treatment areas were lower than on *medium* (overall $\bar{x} = 12.0 \pm 3.4$ voles/ha) or *high* treatments (overall $\bar{x} = 13.3 \pm 3.2$ voles/ha, Table 10b, Fig. 25b, Appendix 2h). Densities on *medium* and *high* areas were approximately four times those on *low* treatment areas in 1994 (first year post-harvest), and were approximately twice as high in 1995. By 1996 red-backed voles were rare on all clear-cuts.

a) Forest



b) Clear-cut

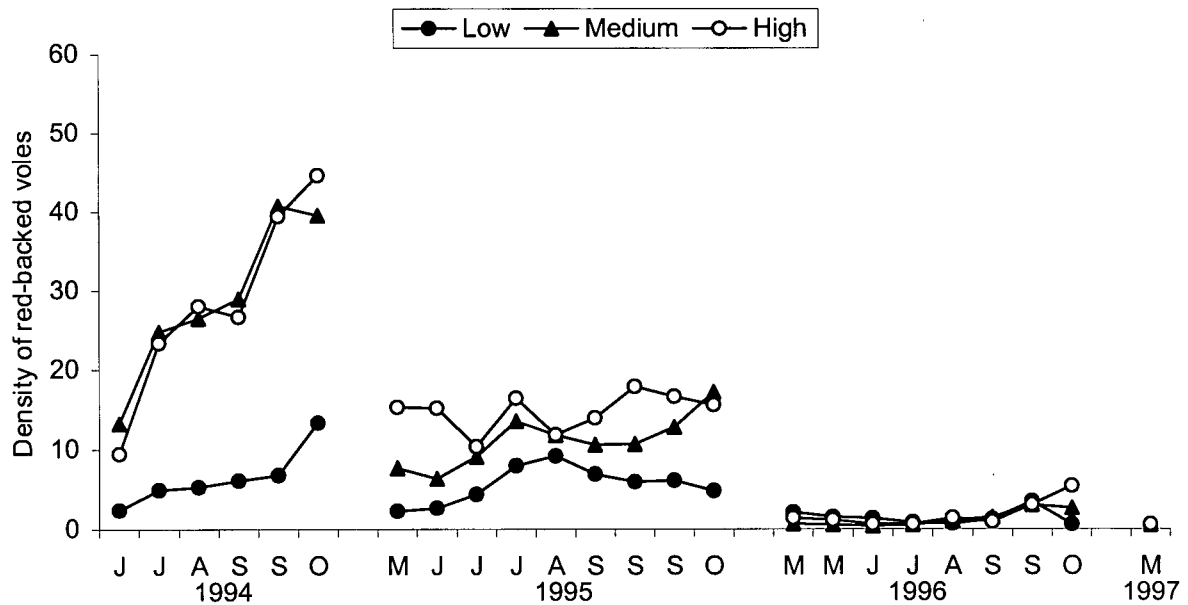


Figure 25. a) Mean density of red-backed voles on forested grids at Opax on D and I block *low*, *medium* and *high* treatment areas, and b) mean density of red-backed voles on Opax clear-cut grids on downed wood treatment areas. Downed wood manipulations on forested areas occurred in summer 1995. Harvest and downed wood manipulations on clear-cuts occurred in winter 1993/4 to spring 1994 before trapping began. Downed wood manipulations on forested areas are indicated by an outlined area. Error bars were omitted for readability; population estimates are presented separately for each sampling grid in Appendix 2.

5.3.1.2 Downed Wood, Vegetation, and Litter and Moss Sampling

I examined scatterplots to examine relationships between population density and habitat characteristics. This was a more appropriate method of looking at general differences among grids than using statistical tests because of the large number of variables I measured, over relatively few sampling grids (nine per seral stage).

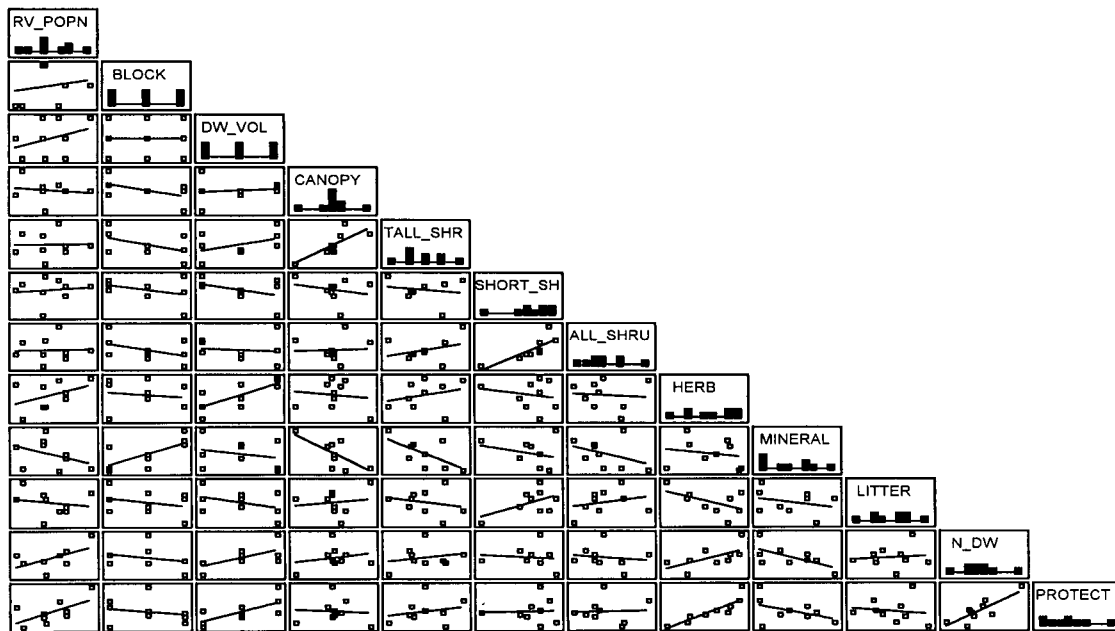
5.3.1.2.1 Forest

Scatterplots of mean post-treatment population density with habitat components and grouping variables suggested that density tended to increase with increasing protective cover, as well as herb cover and number of pieces of downed wood (Fig. 26a). Mean protective cover, which was positively correlated with herb cover and the amount of downed wood, explained approximately 33% of variability in red-backed vole density across sampling grids (adjusted $r^2 = 0.33$, $F_{1,7} = 4.89$, $P = 0.06$).

5.3.1.2.2 Clear-cut

Scatterplots of mean post-treatment population density with habitat components and grouping variables suggested that the habitat variable most closely correlated with vole population density across sampling grids was downed wood volume treatment categories, with a jump between *low* (population densities were very low, along the bottom of the axis) and *medium/high* treatments (Fig. 26b). Downed wood treatments explained approximately 42% of the variability in vole density (adjusted $r^2 = 0.42$, $F_{1,7} = 6.78$, $P < 0.05$). Grouping grids by *low* and *medium/high* explained more variability (adjusted $r^2 = 0.49$, $F_{1,7} = 8.66$, $P < 0.05$). No other significant correlations between density and habitat components were evident.

a) Forest



b) Clear-cut

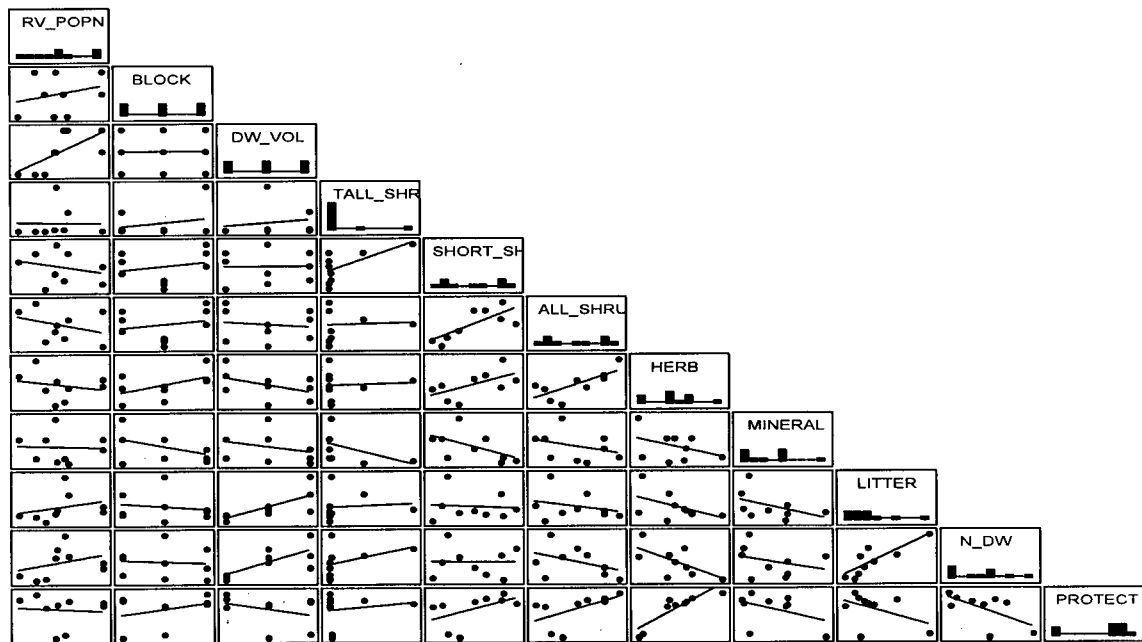


Figure 26. Scatterplot and frequency distribution histogram (and trend line) of red-backed vole population density, block, and downed wood volume treatment class (9 sampling grids) with habitat components including: tall, short, and overall shrub cover, herb and grass cover, mineral soil, litter layer, mean number of pieces of downed wood (N_DW), and protective cover from all habitat components. a) Opax forest b) Opax clear-cut. The trend line in each section is meant as a guide only; it does not signify a statistically significant relationship. The scatterplots are for exploratory purposes only, because the scale of each correlation is different, depending on the habitat variable involved. Density of red-backed voles is on the X axis, habitat component is on the Y axis.

5.3.1.3 Survival and Recapture Rates

5.3.1.3.1 Forest

Initial modeling indicated that recapture rates varied strongly over time, but did not vary among blocks. Recapture rates could not be more parsimoniously modeled by including season or year; however, including *fox* disturbance in the model was better supported than using time alone. Capture effort (number of traps set) was identified as the most important variable for modeling recapture rates. Reintroducing *fox* disturbance along with capture effort was not supported. All recapture rates were $\geq 71\%$ ($\bar{x} = 72\%$); however, recapture rates increased slightly as capture effort decreased. Although unexpected, I used capture effort as the best model for recapture rates when modeling survival rates.

Initial models of survival rates indicated that both grid and time variability were important. Time could not be suitably modeled by including season or year. Modelling grid variability by block was supported; models including downed wood treatment were not. Survival rates of red-backed voles were best modeled by $\phi_{\text{block}+\text{time}} p_{\text{capture effort}}$. Survival rates varied similarly over time, but survival rates of red-backed voles on D block were slightly lower and were parallel on a logit scale to survival rates on I and N block sampling grids. Difference in survival rates was $2\% \text{ wk}^{-1}$. Survival rates were generally $>80\% \text{ wk}^{-1}$.

5.3.1.3.1 Clear-cut

Initial modeling of recapture rates indicated that the model $\phi_{\text{grid}+\text{time}} p_{\text{grid}+\text{time}}$, where recapture rates varied in parallel (on a logit scale) across time, was better supported by the data than including only grid or time. It was also more parsimonious than assuming that recapture rates were constant across grids and time. Grouping grids by block (*i.e.*, E, J, and M) or downed wood treatments, or grouping periods by year or season, did not improve model parsimony. Including *fox* or capture effort also did not improve model parsimony. Thus, recapture rates

were best modelled using the recapture term $p_{\text{grid}+\text{time}}$. Recapture rates were moderately high during the study ($\bar{x} = 60.4\%$).

Modelling survival rates indicated that time was an important factor. The model assuming constant survival rates was not supported, nor was a model where survival rates were different on each sampling grid. Grouping sampling grids by block and downed wood treatment was better supported than assuming each grid varied independently ($\phi_{\text{grid}+\text{time}}$), but less than modelling survival rates with time alone. Modelling time with year and season had less support than modelling time alone. Reintroducing sampling grid grouping by block along with year and season had support. Including a response to downed wood treatments in only the first two years post-harvest (1994-1995) on *low* treatment areas received more support than modelling by block. Weekly survival rates were generally $\geq 80\%$. Survival rates varied across seasons and years; however, the rate was 3-5% wk^{-1} lower on *low* sites than on *medium/high* sites. Survival rates were higher over-winter ($\bar{x} = 91.1\%$) than in the summer ($\bar{x} = 84.9\%$). The final model was ($\phi_{94-5 \text{ low vs med/hi} + \text{season}+\text{year } p_{\text{grid}+\text{time}}$).

5.3.1.4 Reproduction

Weights of over-wintered male red-backed voles at first capture were similar on forests and clear-cuts ($F_{1,124} = 3.09$, $P > 0.05$; forest, 17–30 g, $n = 99$; clear-cut, 18–28, $n = 27$). The breeding season lasted approximately 19 weeks/year for females. Mean length of breeding season was similar on forested and clear-cut sampling grids ($t_{13} = 2.16$, $P > 0.10$).

5.3.1.4.1 Forest

On forested areas, the proportion of reproductive females did not differ significantly across downed wood treatments (*low* $\bar{x} = 9.8\% \pm 2.0$, *medium* $\bar{x} = 13.0\% \pm 3.9$, *high* $\bar{x} = 8.7\% \pm 2.0$) or across years (Table 11). The proportion of juveniles did not differ significantly across downed wood treatments (*low* $\bar{x} = 36.9\% \pm 12.9$, *medium* $\bar{x} = 29.9\% \pm 15.9$, *high* $\bar{x} = 37.3\% \pm$

7.8) but did vary across years (Table 11; $\bar{x}$ proportion of juveniles = 29.9% in 1994 to 41.5% in 1995, and 22.7% in 1996).

5.3.1.4.2 Clear-cut

The proportion of reproductive females was higher on *low* ($\bar{x} = 15.2\% \pm 5.6$) than on *medium* ($\bar{x} = 8.5\% \pm 4.8$) or *high* ($\bar{x} = 6.6\% \pm 3.6$) areas in 1995 and 1996 (Table 11) increasing from 13.9% in 1994 to 22.4% in 1995, and then declining to 9.3% in 1996. The proportion of reproductive females on *medium* and *high* areas declined from 13.7% and 10.1% in 1994, to 12.0% and 9.7% in 1995, respectively. No females in reproductive condition were captured on *medium* or *high* areas in 1996 (only one was captured on *low* areas). The proportion of juveniles

Table 11. Results of split-plot analysis of red-backed vole reproductive parameters from the Opax study area. a) Proportion of population comprised of reproductive females, and b) Proportion of population comprised of juveniles. An * indicates effects that are statistically significant.

a) Reproductive females

Effect	Error term	Test
Forest		
Downed wood	B ($F_{2,3} = 4.49, P > 0.1$)	$F_{2,3} = 2.63, P > 0.1$
Block	B	$F_{1,3} = 2.86, P > 0.1$
Year	B	$F_{1,3} = 0.81, P > 0.1$
Downed wood x year interaction	B	$F_{2,3} = 1.92, P > 0.1$
Clear-cut		
Downed wood*	B ($F_{4,6} = 0.55, P > 0.1$)	$F_{2,6} = 5.90, P < 0.05$
Block	B	$F_{2,6} = 1.28, P > 0.1$
Year*	B	$F_{1,6} = 26.44, P < 0.005$
Downed wood x year interaction	B	$F_{2,6} = 1.48, P > 0.1$

b) Juveniles

Effect	Error term	Test
Forest		
Downed wood	A ($F_{2,3} = 9.13, P < 0.1$)	$F_{2,2} = 0.67, P > 0.5$
Block	A	$F_{1,2} = 0.33, P > 0.5$
Year*	B	$F_{1,3} = 51.89, P < 0.01$
Downed wood x year interaction	B	$F_{2,3} = 4.29, P > 0.1$
Clear-cut		
Downed wood	A ($F_{4,6} = 0.49, P > 0.1$)	$F_{2,6} = 2.61, P > 0.1$
Block	B	$F_{2,6} = 0.51, P > 0.5$
Year	B	$F_{1,6} = 1.02, P > 0.1$
Downed wood x year interaction	B	$F_{2,6} = 0.94, P > 0.1$

doubled from 1994-1996 on *medium* and *high* treatment areas (from 16% to 39%), but stayed relatively constant on *low* treatment areas (12%-15%); however, differences were not statistically significant across years or downed wood treatments (Table 11).

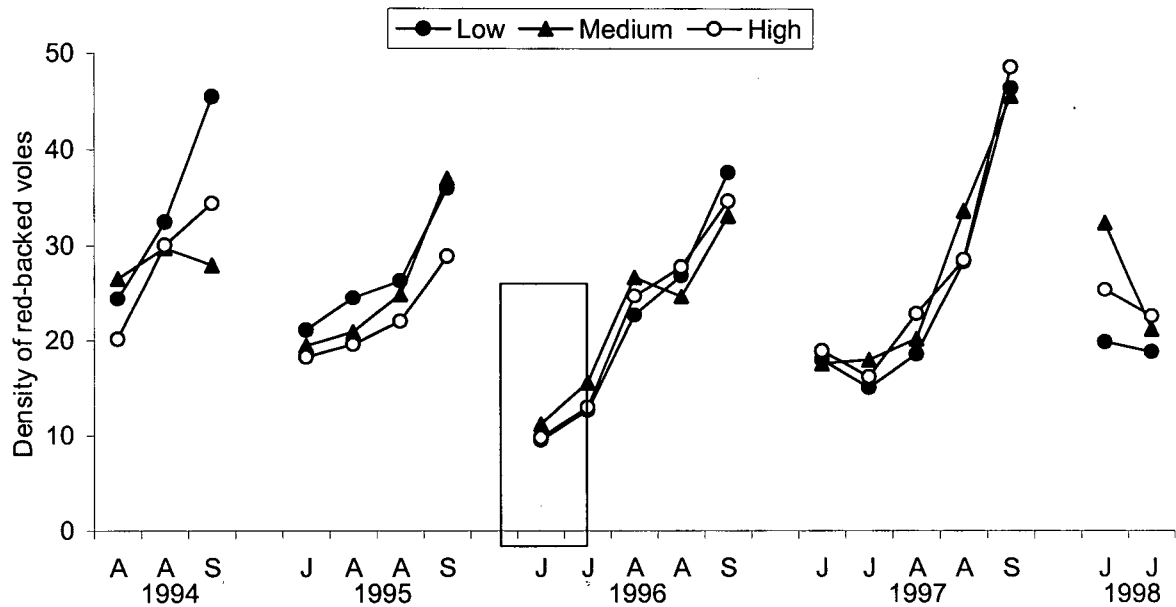
5.3.2 Red-backed Vole Populations at Sicamous

During the study at the Sicamous study area (1994-1998), I had 10,418 total captures of 3,733 different red-backed voles. Accidental trap mortalities comprised approximately 1% of captures. Mean ETA of all grids and years was 1.29 ± 0.01 ha. I captured 113 red-backed voles (3.0% of 3,733) on >1 grid. The majority of these captures (77 voles) were emigrants; voles tagged on one grid that subsequently moved, and were captured at least once on another grid. Three times as many voles emigrated from *medium* or *high* forested treatment areas than *low* areas post-treatment, and 2-4 times the number of voles immigrated to *low* areas than to *high* or *medium* areas. Thirty-six voles (1% of 3,733) were captured on >1 sampling grid; most were captured on one sampling grid, and were captured only once on a second grid. The proportion of voles that moved between sampling grids was similar across downed wood treatments on both forested and clear-cut areas (1-way ANOVA on square root transformed proportion data, $F_{2,6} = 0.38$, $P > 0.5$, $F_{2,6} = 0.00$, $P > 0.5$).

5.3.2.1 Population Density

Population density was higher on forested treatment areas than on clear-cuts during the study (Fig. 27, Appendix 2). Although mean population density stayed relatively high and constant on forested sites, populations on clear-cuts declined after harvesting (winter 1994-1995) and were very small (<5 voles/ha) by 1996. Based on trends in downed wood volume across sampling grids, I compared population parameters for red-backed voles among *low*, *medium* and *high* treatments for survival, recapture and density estimates, as well as *low* versus *medium/high* areas (survival and recapture estimates only).

a) Forest



b) Clear-cut

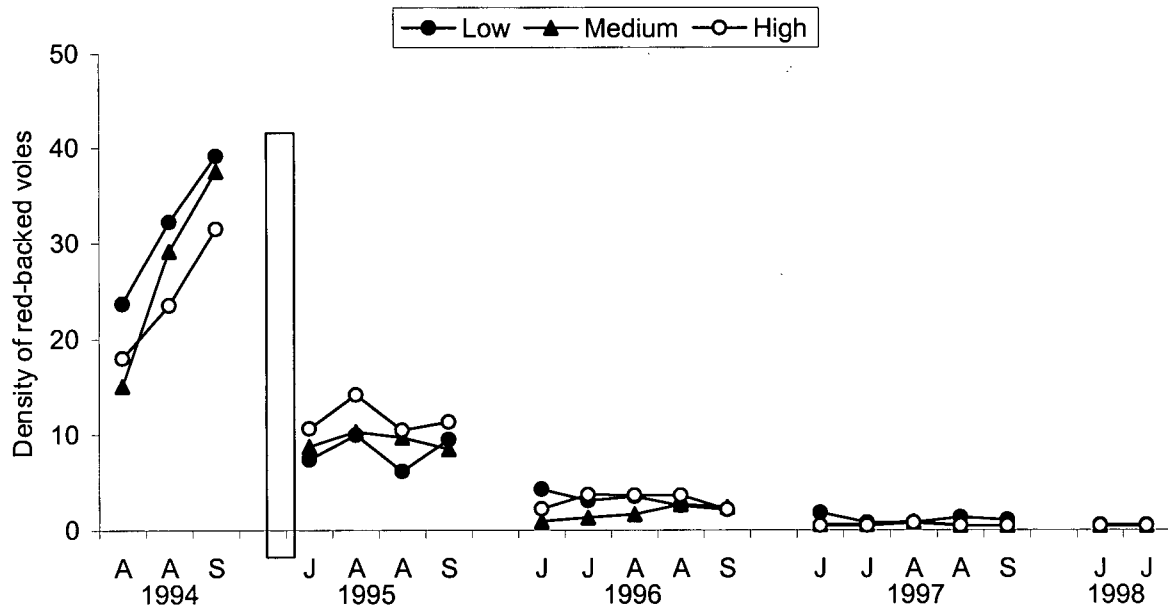


Figure 27. Mean density of red-backed voles on a) forested, and b) clear-cut sampling grids at Sicamous on *low*, *medium* and *high* treatment areas. Downed wood manipulations on forested areas occurred during summer 1996, and manipulations on clear-cuts occurred during harvesting in winter 1994-1995 (indicated by outlined area). Error bars were omitted for readability; population estimates are presented separately for each sampling grid in Appendix 2.

5.3.2.1.1 Forest

Population densities on forested treatment areas varied over time, but did not vary significantly with downed wood treatment (Table 12a, Fig. 27a, Appendix 2i). Densities had a distinct annual cycle, with a large increase in population size throughout the trapping season and a decline over winter. This pattern continued throughout the study, and did not change after downed wood treatments (which occurred during the trapping season in 1996). Mean post-treatment population density was similar on *low* (25.3 ± 3.9), *medium* (27.4 ± 3.9), and *high* (27.1 ± 4.0) areas. Population density declined from 1994 to 1996 ($\bar{x}$ across forested treatment areas = 32.9 ± 5.8 , 25.3 ± 3.0 , 21.9 ± 1.4 , during the three years, respectively), increased again in 1997 (25.9 ± 4.0), and declined slightly in 1998 (incomplete sampling year 22.6 ± 2.7).

5.3.2.1.2 Clear-cut

Population densities declined after harvesting in winter 1994-1995, continued to decline in 1996, and remained at very low levels (<5 voles/ha) through 1997-1998 (Table 12b, Fig. 25b, Appendix 2j). Densities were similar across downed wood treatment areas post-harvest (*low* $\bar{x} = 3.5 \pm 1.1$, *medium* $\bar{x} = 3.1 \pm 1.2$, *high* $\bar{x} = 4.1 \pm 1.5$, Table 12b).

5.3.2.2 Downed Wood, Vegetation, and Litter and Moss Sampling

Scatterplots of mean red-backed vole population density in forests with abundance of forest floor components did not suggest any strong correlations (Fig. 28a). On clear-cuts, although population density did not vary significantly with downed wood volume classes, densities did vary with mean protective cover (primarily composed of cover by short shrubs and herbs) and with the amount of exposed mineral soil (Fig. 28b). Red-backed vole population density tended to be lower on areas with more protective cover, herb and shrub cover (which were highly correlated with protective cover and each other), and exposed mineral soil. Herb cover had the strongest correlation with mean red-backed vole density; variability in herb cover explained

Table 12. Results of split-plot analysis of red-backed vole density from the Sicamous study area for a) forest, and b) clear-cut sampling grids. Split-plot data are presented for i) split-plot in time (time), and ii) split-plots across years (year). An * indicates effects that are statistically significant.

a) i) Forest

Effect	Error term	Test
Pre-treatment		
Downed wood	A ($F_{4,6} = 5.09, P < 0.05$)	$F_{2,4} = 0.12, P > 0.5$
Block	A	$F_{2,6} = 0.95, P > 0.1$
Time*	B	$F_{1,6} = 19.76, P < 0.005$
Downed wood x time interaction	B	$F_{2,6} = 1.40, P > 0.1$
Post-treatment		
Downed wood	A ($F_{4,6} = 4.11, P < 0.1$)	$F_{2,4} = 0.22, P > 0.5$
Block	A	$F_{2,4} = 0.73, P > 0.5$
Time*	B	$F_{1,6} = 16.41, P < 0.01$
Downed wood x time interaction	B	$F_{2,6} = 0.55, P > 0.5$

ii) Forest (year)

Effect	Error term	Test
Downed wood	B ($F_{4,6} = 0.61, P > 0.1$)	$F_{2,6} = 0.08, P > 0.5$
Block	B	$F_{2,6} = 0.70, P > 0.5$
Year*	B	$F_{1,6} = 4.65, P < 0.1$
Downed wood x year interaction	B	$F_{2,6} = 0.69, P > 0.5$

b) i) Clear-cut

Effect	Error term	Test
Pre-harvest/treatment		
Downed wood	B ($F_{4,6} = 1.59, P > 0.1$)	$F_{2,6} = 3.32, P > 0.1$
Block	B	$F_{2,6} = 0.50, P > 0.5$
Time*	B	$F_{1,6} = 17.89, P < 0.01$
Downed wood x time interaction	B	$F_{2,6} = 0.56, P > 0.5$
Post-treatment		
Downed wood	A ($F_{4,6} = 3.84, P < 0.1$)	$F_{2,4} = 0.31, P > 0.5$
Block	A	$F_{2,4} = 2.12, P > 0.1$
Time*	B	$F_{1,6} = 14.11, P < 0.01$
Downed wood x time interaction	B	$F_{2,6} = 0.68, P > 0.1$

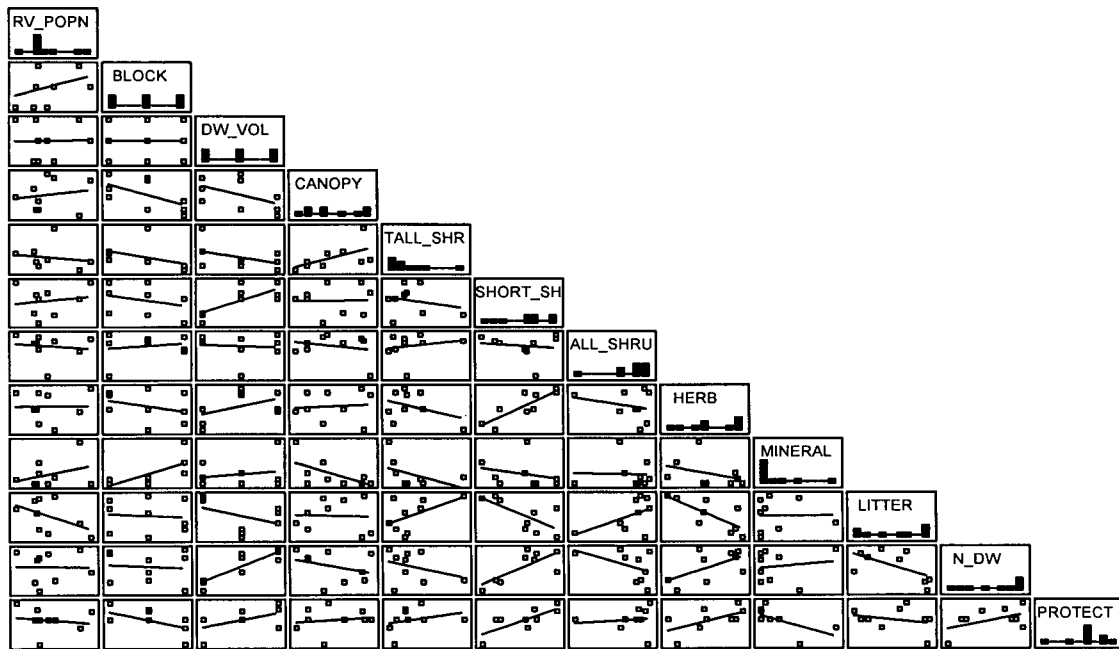
ii) Clear-cut (year)

Effect	Error term	Test
Downed wood	B ($F_{4,6} = 1.54, P > 0.1$)	$F_{2,6} = 1.35, P > 0.1$
Block	B	$F_{2,6} = 2.57, P > 0.1$
Year*	B	$F_{1,6} = 160.51, P < 0.001$
Downed wood x year interaction	B	$F_{2,6} = 1.24, P > 0.1$

62.5% of the variability in red-backed vole density (adjusted $r^2 = 0.625$, $F_{1,7} = 14.34$, $P < 0.01$).

The range in mean population density across clear-cut treatment areas was small (1.7-5.6 voles/ha) so it not clear whether this relationship is biologically significant.

a) Forest



b) Clear-cut

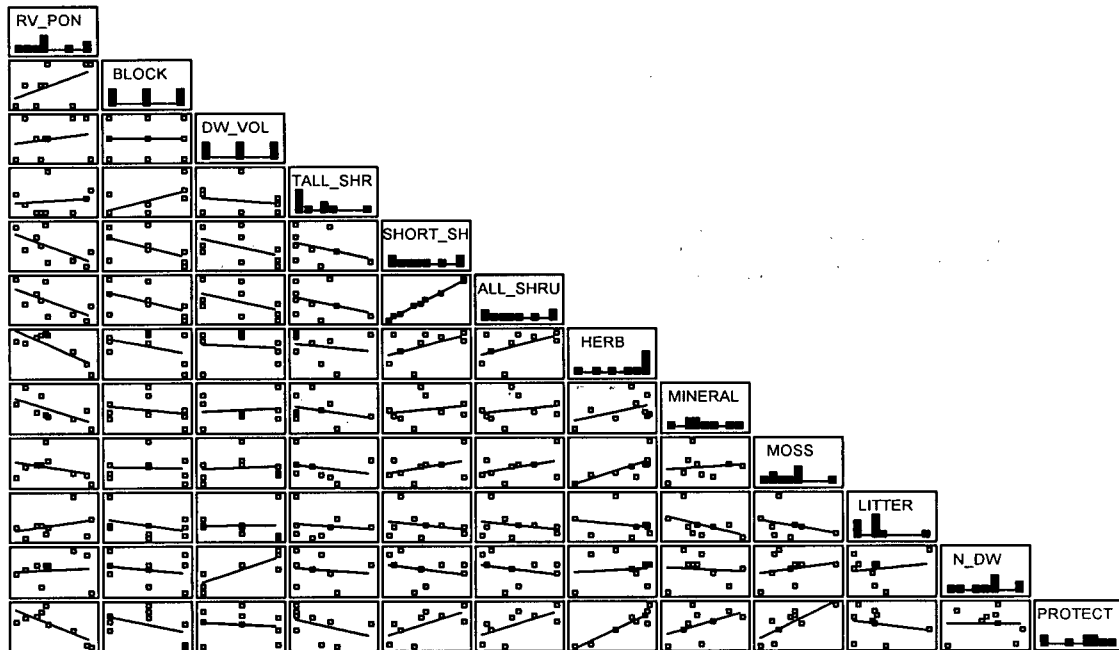


Figure 28. Scatterplots (and trend line) of mean red-backed vole population density, block, and downed wood volume treatment class with habitat components including: tall, short, and overall shrub cover, herb and grass cover, mineral soil, moss and litter layer, mean number of pieces of downed wood (N_DW), and mean protective cover on a) Sicamous forest, and b) Sicamous clear-cut. The trend line in each section is meant as a guide only; it does not signify a statistically significant relationship. The scatterplots are for exploratory purposes only, and the scale of each correlation is different, depending on the habitat variable involved. Density of red-backed voles is on the X axis, habitat component is on the Y axis.

5.3.2.3 Survival and Recapture Rates

5.3.2.3.1 Forest

Analyses identified some overdispersion in the data. Accordingly, $\hat{c}$ was adjusted to 1.45. Initial models of recapture rates indicated that variability among sampling grids and time was important; the $p_{\text{grid}+\text{time}}$ model was best supported among the general models. Grouping grids by downed wood treatment was better supported. Modelling variability across time with season and year was better supported than allowing each time period to vary independently. Reintroducing downed wood treatment groupings to the season+year model received support. The most parsimonious model included variability by season and year, and downed wood treatment. Recapture rates improved after 1994 (from 63% in 1994 to 83% 1995-1998) and stayed relatively constant for the rest of the study. After downed wood treatments, recapture rates were highest on unmanipulated *medium* treatment sites (86.0%), and slightly lower on *low* (81.4%) and *high* (82.7%) treatment areas for the rest of the study.

Modelling survival rates indicated that both grid and time were important sources of variability. Modelling time variability by including year or season was not supported. However, variability in survival rates across grids could be more parsimoniously modelled by including block in the model. The final model was $(\phi_{\text{block}+\text{time}} p_{\text{pre/post treatment by downed wood treatment}+\text{season}+\text{year}})$. Survival rates averaged $>90.0\% \text{ wk}^{-1}$. Survival rates tended to be highest on C block, and lowest on B; the difference between the two was $2\% \text{ wk}^{-1}$.

5.3.2.3.2 Clear-cut

Analyses identified some overdispersion in the data; $\hat{c}$ was adjusted to 1.1. Initial models of recapture rates indicated that both grid and time were important variables. There was some support for modelling time by year and season. Introducing block and downed wood treatment effects indicated that the best model for recapture rates was $\phi_{\text{grid}*\text{time}} p_{\text{downed wood treatments}}$. Mean

recapture rates were all >71% but were lowest on *low* treatment areas (71.6%), moderate on unmanipulated *medium* treatment areas (74.5%) and highest on *high* areas (82.9%). Survival rates tended to vary across grids and across sampling periods; both time and grid models were better supported than assuming constant survival rates. Modelling variability across time by including season or year was better supported; grouping years pre- and post-harvest was better supported. The most parsimonious model was $\phi_{\text{pre/post harvest+season}} p_{\text{downed wood treatment}}$. Summer and fall survival rates pre-harvest were similar (90.3% wk⁻¹, 91.0% wk⁻¹, respectively). Survival rates dropped approximately 10% post-harvest (to 80.2% wk⁻¹ and 81.5% wk⁻¹ for summer and fall respectively). Winter survival remained high (93.9% wk⁻¹).

5.3.2.4 Reproduction

Male over-wintered red-backed voles were similar in weight on unmanipulated clear-cuts and unmanipulated forested areas (weights at first over-wintered capture: $n = 12$, $\bar{x} = 31.0 \pm 2.2$ g; $n = 55$, $\bar{x} = 29.4 \pm 1.1$ g; $t_{65} = 1.2$, $P > 0.1$).

5.3.2.4.1 Forest

Proportion of reproductive females post-treatment on forested grids varied over time, but not across downed wood treatments (*low* $\bar{x} = 36.1\% \pm 9.2$, *medium* $\bar{x} = 35.6\% \pm 9.1$, *high* $\bar{x} = 28.2\% \pm 10.4$, Table 13a). The proportion of reproductive females in 1996 was 40.4%, but declined to 26.2% in 1997. Proportion of juveniles followed the trend in reproductive females (*low* $\bar{x} = 17.7\% \pm 8.3$, *medium* $\bar{x} = 15.9\% \pm 7.3$, *high* $\bar{x} = 12.7\% \pm 8.5$). Juveniles declined from 21.9% in 1996 to 9.1% in 1997. The proportion of juveniles did not differ significantly across downed wood treatments (Table 13b).

5.3.2.4.2 Clear-cut

Proportion of reproductive females on clear-cut areas followed a trend similar to that on forested areas. Proportion of reproductive females increased post-harvest from 28.5% in 1995 to

Table 13. Results of split-plot analysis of red-backed vole reproductive parameters from the Sicamous study area. a) Proportion of population comprised of reproductive females, and b) proportion of juveniles in the population. An * indicates that the effect is statistically significant.

a) Reproductive females

Effect	Error term	Test
<u>Forest (post-treatment)</u>		
Downed wood	B ($F_{4,6} = 1.19, P > 0.1$)	$F_{2,6} = 1.79, P > 0.1$
Block	B	$F_{2,6} = 2.00, P > 0.1$
Year*	B	$F_{1,6} = 12.19, P < 0.05$
Downed wood x year interaction	B	$F_{2,6} = 0.64, P > 0.5$
<u>Clear-cut (post-treatment)</u>		
Downed wood	B ($F_{4,6} = 0.3, P > 0.5$)	$F_{2,6} = 1.61, P > 0.1$
Block	B	$F_{2,6} = 1.51, P > 0.1$
Year*	B	$F_{1,6} = 9.37, P < 0.05$
Downed wood x year interaction	B	$F_{2,6} = 0.08, P > 0.5$

b) Juveniles

Effect	Error term	Test
<u>Forest (post-treatment)</u>		
Downed wood	B ($F_{4,6} = 1.58, P > 0.1$)	$F_{2,6} = 1.06, P > 0.1$
Block	B	$F_{2,6} = 1.34, P > 0.1$
Year*	B	$F_{1,6} = 15.57, P < 0.01$
Downed wood x year interaction	B	$F_{2,6} = 0.55, P > 0.5$
<u>Clear-cut (post-treatment)</u>		
Downed wood	B ($F_{4,6} = 0.57, P > 0.1$)	$F_{2,6} = 1.71, P > 0.1$
Block	B	$F_{2,6} = 1.39, P > 0.1$
Year	B	$F_{1,6} = 2.27, P > 0.1$
Downed wood x year interaction	B	$F_{2,6} = 0.42, P > 0.5$

46.1% in 1996, and then declined in 1997 (8.6%, Table 13a). Proportion of reproductive females did not differ significantly across downed wood treatments (*low* $\bar{x} = 25.4\% \pm 14.7$, *medium* $\bar{x} = 38.1\% \pm 20.7$, *high* $\bar{x} = 19.8\% \pm 13.5$, Table 13a). Proportion of juveniles declined on *low* treatment areas after 1995, but increased in 1996 and declined in 1997 on *medium* and *high* areas; however, these differences were not statistically significant (overall *low* $\bar{x} = 7.6\% \pm 6.7$, *medium* $\bar{x} = 27.6\% \pm 22.7$, *high* $\bar{x} = 11.5\% \pm 8.4$; Table 13b).

5.4 Discussion

5.4.1 Experimental Design

The occasional movement of red-backed voles among sampling grids suggests that treatment areas were not completely independent. Ideally, sampling grids should have been more widely spaced on the landscape. The placement of sampling grids in my study was influenced by the operationally sized harvest treatment blocks established as part of two large silvicultural systems projects. As well, the size of the manipulations, particularly on forested areas, was constrained by the labour-intensive nature of removing downed wood by hand. Rates of movement were similar across downed wood treatments, ETA was smaller than the 1.7-ha treatment area size, and 97% of voles studied were within one treatment area which suggests that most voles were not moving among treatment areas. However, if a few voles were moving off the treatment area to access a habitat component, such as downed wood, it would reduce variability in red-backed vole densities across downed wood treatments within blocks. This would hamper my ability to detect a treatment effect.

Red foxes were present on the Opax study area, but did not cause a problem until 1996. Foxes in 1996 and 1997 cued in to live-trapping grids and broke open traps. Foxes disturbed traps on every sampling grid in my study, but were particularly active on clear-cut sampling grids. Traps were not disturbed every sampling session, and generally $\leq 10\%$ of traps would be disturbed when a fox visited the grid (the maximum level of disturbance was 30%). When I analysed survival and recapture data, I included a covariate to test whether survival rates or recapture rates were significantly lower during trapping sessions when the fox had disturbed traps on the grid. Fox disturbance did not appear to significantly affect recapture or survival rates across forested or clear-cut sampling grids. The combination of similar levels of fox

disturbance across sampling grids within seral stages, and the lack of a significant fox effect on survival or recapture rates suggests that observed patterns in red-backed vole population density across downed wood treatment areas was not influenced by trap disturbance by foxes.

5.4.2 Red-backed Vole Populations

5.4.2.1 Forest

At Opax, mean population density on *high* areas tended to be higher than on *medium* or *low* areas, but at Sicamous I did not detect any changes in population density with downed wood treatment. I did not detect significant changes in survival rates or reproductive rates within two years (three summers) of the removal of downed wood on forested areas at either study area. The result at Sicamous is contrary to my hypothesis that red-backed vole population density, survival rates, and reproductive rates would be lower on areas with less downed wood. Results of the red-backed vole study at Opax appeared to provide some support for the hypothesis that downed wood is an important habitat component for red-backed voles.

Red-backed voles presumably associate with downed wood to satisfy many of their requirements (Harmon *et al.* 1986, Doyle 1987, Bunnell *et al.* 1999). Voles consume mycorrhizal fungi, lichens, and occasionally insects (Martell 1981, Gunther *et al.* 1983) all of which are often associated with downed wood (Harmon *et al.* 1986, Amaranthus *et al.* 1994, Clarkson and Mills 1994, Waters *et al.* 1997, Carey *et al.* 1999, Gagné *et al.* 1999, Pyare and Longland 2001). Voles often nest under logs and in stumps (Harmon *et al.* 1986). As well, voles are often captured next to logs, which suggests that downed wood provides red-backed voles with an important structural component of their habitat, similar to that described for other small mammals (Lovejoy 1975, Doyle 1987, Hayes and Cross 1987, Graves *et al.* 1988, Barnum *et al.* 1992, Planz and Kirkland 1992, McMillan and Kaufman 1995).

My ability to detect a response to downed wood treatments at Opax might have been hampered by the low population densities across the entire study area beginning in 1996, the year following downed wood treatments. The large decline in population density in 1996 likely made it more difficult to detect any potential treatment effects on the study area. In addition, edge effects might have reduced the treatment effect, also making a response more difficult to detect. Despite these potential effects, I did determine that population densities on *high* treatment areas tended to be larger than on *low* or *medium* areas by the end of the trapping season in 1995 and beginning of 1996. The fact that densities were apparently higher on *high* than *medium* sites suggests that even a 50% (as opposed to >80% on *low* treatments) reduction in naturally occurring levels of downed wood negatively influences red-backed vole populations in these forests.

It is not clear why red-backed voles declined on the Opax study area in summer 1996. Populations of deer mice also declined from 1994-1996 on forested areas, but increased on clear-cuts during the same period, along with meadow voles. Predators appeared to increase on the study area after 1994; weasel captures were highest in 1995, and red foxes were active in 1996 and 1997. However, both weasels and foxes appeared to be most active on clear-cuts. *Clethrionomys* population size in other studies is also very variable across years (Rosenberg *et al.* 1994, Boutin *et al.* 1995, Von Treba *et al.* 1998, Sullivan *et al.* 2000).

At the Sicamous study area, population densities were high across all forested treatment areas during the study. Even with the removal of >90% of downed wood on *low* treatment areas, population density, survival rates, and reproductive rates did not differ from unmanipulated areas over the three summers that voles were monitored following treatment. There was indirect evidence that red-backed voles responded differently to *low* than to *medium*

or *high* treatments. The rate of known immigration to *low* treatment areas was higher than to *medium* or *high* areas, and the rate of emigration was higher on *medium* and *high* areas than *low* areas. This suggests that *low* areas were potentially sink habitats (Van Horne 1983), but without concurrent changes in density, survival rates, or reproductive rates, the data are inconclusive. Recapture rates were slightly lower on *low* and *high* areas than on *medium* treatments, suggesting that voles became less trappable after the site was disturbed. These changes were not sufficient to affect overall population density or survival rates, which suggests that red-backed voles were not immediately negatively affected by the removal of downed wood from the treatment sites.

The removal of downed wood from *low* sites likely decreased the availability of insects, fungi, and lichens associated with downed wood (especially moderately to heavily decayed logs; Amaranthus *et al.* 1994, Clarkson and Mills 1994, Harmon *et al.* 1986, *c.f.* Luoma 1988); however, the effect might not have been immediate. I removed practically all of the intact downed wood (a few logs could not be removed for safety reasons) from *low* treatment areas and destroyed the structure of decayed downed wood (decay class 4 and 5, Maser *et al.* 1979) and scattered debris over the surrounding area. This would prevent voles from traveling in tunnels associated with decayed wood, and would destroy the favourable moist microclimate on which insects and fungi depend (Harmon *et al.* 1986, Amaranthus *et al.* 1989, Waters *et al.* 1997, Carey *et al.* 1999). The microclimate associated with downed wood was likely particularly important at the dry, hot Opax site, similar to that reported by Clarkson and Mills (1994) for a site in southwestern Oregon. The remaining debris might have provided some suitable characteristics for fungi and insects for a period of time, which would have reduced the immediate effect of the treatment on red-backed voles. However, this does not adequately

explain the lack of response to the treatments at Sicamous because the scattered chunks of downed wood likely would not provide suitable microclimates for insects and fungi over the three summers I monitored red-backed vole populations post-downed wood manipulation.

The removal of downed wood would have had an immediate, but probably short-term effect on the availability of lichens to red-backed voles. Long branches, where most arboreal lichens are found, were removed from *low* treatment areas along with logs. Lichen can form the majority of red-backed voles' diets (Gunther *et al.* 1983), and appeared to be an important component of the diet of voles at Opax (Chapter 6). Forests at both study areas contained abundant lichens in the tree canopy, which would fall and eventually replace lichens removed during the treatment.

Downed wood was potentially an important source of thermal cover for red-backed voles. Thermal cover is important in mediating temperature extremes in the local environment (Getz 1971), and might be especially important at Opax. High summer temperatures at Opax may increase stress on vole species with poor kidney efficiencies, like red-backed voles (Miller and Getz 1977, Getz 1985), which are generally considered to be associated with mesic environments (Martell and Radvanyi 1977). Downed wood also might be important in providing structure under the snowpack. Access to subnivean spaces, where temperatures remain relatively warm and stable (Pruitt 1978, Anderson 1986), is critical to overwinter survival of small mammals (Schlegl-Bechtold 1980, West *et al.* 1980, Pruitt 1984). Access to subnivean spaces would be especially important on the Sicamous study area, where snow 1-2 m deep covered the site for 7-9 months of the year.

Previous research has suggested that other forest features, such as shrubs, might also influence vole abundance (Nurdyke and Buskirk 1991, Rosenberg *et al.* 1994, Carey and

Johnson 1995). Red-backed voles are sensitive to changes in the forest microclimate. Previous research on the response by red-backed voles to alternative silvicultural systems indicated that red-backed voles benefit from a combination of canopy cover as well as understory cover. Red-backed voles respond positively, at least initially, to light-entry harvesting systems such as shelterwoods, which open the forest canopy, often have greater percent ground cover from shrubs and downed wood, and retain much of the microclimate characteristics of uncut forest (Von Treba *et al.* 1998, Steventon *et al.* 1998). The positive response to shelterwood harvest is absent if the understory is burned, which removes downed wood, shrubs, and truffles (Waters and Zabel 1995, Waters and Zabel 1998). The strong relationship with shrub cover is not always apparent. Silvicultural systems that remove more of the canopy, such as partial-cuts or seed-tree systems, tend to negatively affect red-backed voles, even though shrub and downed wood cover increase (Sullivan *et al.* 2000, *c.f.* Monthey and Soutiere 1985).

The depth and characteristics of the organic soil layer have also been suggested as an important habitat component for red-backed voles because it might influence truffle abundance or the soil microclimate (Rosenberg *et al.* 1994, Wilson and Carey 2000). I measured the depth of the organic litter layer, which varied between 1.5 and 8 cm at Sicamous and was ≤ 2 cm at Opax. I did not detect a correlation between depth of the layer and red-backed vole abundance at either study area.

At Sicamous, red-backed vole population density, survival rates, and reproductive rates were similar across downed wood treatments even though the abundance of downed wood, shrub, herb and mean protective cover was much lower on *low* treatment areas than on *medium* or *high* areas. This suggests that characteristics of all sampling grids met some minimum threshold required to maintain abundant red-backed vole populations. All of the sampling grids had $\geq 65\%$

protective cover. Although canopy cover was low (approximately 11%), understory cover from shrubs (43-63%), herbs (9-63%) and moss (32-78%) was relatively high.

Vegetation can function in similar ways to downed wood for small mammals. It provides protection from predators (Kotler *et al.* 1988, Longland and Price 1991, Korpiimäki *et al.* 1996, Rohner and Krebs 1996, Sheffield *et al.* 2001), mediates temperature and microclimate (Spencer 1984, D'Anieri *et al.* 1987, Santillo *et al.* 1989, Taylor and Buskirk 1996), and creates subnivean spaces (Spencer 1984, Taylor and Buskirk 1996). This suggests that in cool, moist ecosystems where the understory is dense and structurally diverse, downed wood might not be required to maintain red-backed voles, at least in the short term.

Results from a radio-telemetry study of female red-backed voles at Opax (Chapter 6) suggested that edge effects might have hampered my ability to detect treatment effects. Radio-telemetry data indicated that downed wood was an important habitat component for red-backed voles at Opax, which supports the weak treatment effect identified at the population level. Vole home ranges on both *low* and *high* treatment areas were in areas with much greater amounts of downed wood than regularly available in the surrounding treatment area. Radio-telemetry data indicated that the voles on *low* treatment areas established home ranges around the few remaining pieces of downed wood on the area, or moved at least partially off of the treatment area where they associated with downed wood. Therefore, they were able to satisfy their requirements for downed wood while remaining at least partially on the treatment area. The low population densities at Opax also likely made it difficult to detect treatment effects. Although the few voles on the area were able to satisfy their requirements for downed wood, it is unclear how red-backed voles would have responded during periods of higher vole density. Female red-backed voles are territorial, and limit the rate at which juvenile females become reproductive,

although at peak densities home ranges of females may overlap (Bondrup-Nielsen 1985, 1986). They have fairly stable home ranges, which are sensitive to changes in habitat quality, but do not change in size with population density (Bondrup-Nielsen 1986). If downed wood was perceived as high quality habitat by voles, as the radio-telemetry data suggests, then the fewer pieces on *low* treatment areas would support fewer voles. As vole densities increase, the difference in the number of voles, or at least the number of reproductive females, might become detectable.

I did not detect a response by red-backed voles at the Sicamous Creek study area to the removal of downed wood on forested areas. My ability to detect a treatment effect was not hampered by low population densities; populations were large during the study at Sicamous. The downed wood manipulations removed more than 90% of the downed wood on *low* treatment areas, but a few pieces remained, which likely provided habitat for a few voles on the area, as at Opax. If red-backed voles depended on downed wood, it is unlikely that the small amount of downed wood remaining could support the high population densities observed. It is possible that red-backed vole populations on *low* treatment areas were being maintained by individuals moving partially off of the sampling grid, as at Opax. To examine whether it was likely that this occurred, I compared the proportion of resident voles (voles captured >1 time) that were captured at least once on edge traps (traps on the periphery of the sampling grid) the year following treatment (1996 at Opax, 1997 at Sicamous). At Opax, 11% more voles were captured at least once on edge traps on *low* treatment areas than on *high* treatment areas. This was similar to the trend I found with my telemetry data that suggested that voles on *low* treatment areas accessed downed wood off of the sampling grid. At Sicamous, 4% fewer voles were captured in edge traps on *low* treatment areas than control areas. Although this is not a

rigorous test, the patterns suggest that red-backed voles on low treatment areas at Sicamous were not more likely to be moving at the edge of the sampling grid. Thus, I can not determine from my data whether the lack of a detectable response to the removal of downed at Sicamous was caused by edge effects, where most of the voles on the area (mean estimated population density ranged from 15 to 40 voles/ha through the sampling season) were accessing downed wood off the treatment area. The fact that the proportion of voles captured in edge traps was not much larger on *low* areas than *high* areas suggests that, perhaps, the results were accurate. This would mean that similar population densities of red-backed voles were maintained on areas with only 3% of the volume of downed wood found on control areas.

5.4.2.2 Clear-cut

Populations of red-backed voles on clear-cuts at both my study areas declined to very low levels within two years post-harvest. Although Kirkland (1990) reported that red-backed voles tend to increase in abundance after clear-cutting, red-backed vole populations in western North America tend to be negatively affected by removal of the canopy (Ramirez and Hornocker 1981, Smith 1999, Sullivan *et al.* 1999 a and b, Moses and Boutin 2001). The response of red-backed voles to clear-cutting is likely influenced by the amount of downed wood and vegetation left on the area post-harvest (Martell 1983, Sullivan and Boateng 1996), which would affect the forest floor microclimate and, potentially, mycorrhizal fungi (Sullivan *et al.* 1999a). The results of my study suggest that the response is also influenced by the ecosystem in which harvesting occurs.

Although clear-cutting negatively affected red-backed voles at both study areas, the ability of downed wood to mitigate the initial effects of clear-cutting varied. At Opax, the immediate impact of clear-cutting was partially mitigated, at least in the short term, by maintaining >80 m³/ha of downed wood on the site, in agreement with my second hypothesis. Population

densities and survival rates were higher for the first two years post-harvest on *medium* and *high* areas than *low* areas. Although there appeared to be a higher proportion of reproductive females on *low* areas in 1995, it was likely an artifact of the low densities on *low* treatment areas (only one reproductive female vole was captured in 1995 on one *low* treatment area). The positive response to the retention of downed wood existed even though the site was sparsely vegetated immediately post-harvest, but became heavily vegetated within two years. This result is in agreement with my third hypothesis, that downed wood is an important and unique habitat component for red-backed voles.

The importance of downed wood in mitigating the initial effects of clear-cutting at Opax is likely related to its importance as a moisture reservoir, especially in a dry, hot ecosystem. Downed wood can hold up to twice its weight in water (Amaranthus *et al.* 1989), and provides an important microenvironment for epigeous fungi (truffles), which tend to be more abundant close to decayed downed wood (Clarkson and Mills 1994, Waters *et al.* 1997, Carey *et al.* 1999, Pyare and Longland 2001). Although population densities on *medium* and *high* treatment areas were still higher than on *low* treatment areas in 1995 (one year post-harvest), they were lower than in 1994. Perhaps the favourable microclimate associated with downed wood in 1994 had declined somewhat by 1995. Mycorrhizae often remain alive on clear-cuts for one year after harvesting (Perry *et al.* 1987); however, they do not produce sporocarps (Jones and Durall 1997). Thus, truffles that were associated with downed wood in 1994 were likely less abundant by the end of the second year post-harvest. As well, percent ground cover by vegetation was high on all clear-cuts by 1995 (82% protective cover, 35% shrub cover, 69% herb cover). This would likely compensate, to some extent, for the lack of downed wood on *low* areas by fulfilling some of the same cover (thermal and security) roles (Spencer 1984, D'Anieri *et al.*

1987, Kotler *et al.* 1988, Santillo *et al.* 1989, Longland and Price 1991, Korpimäki *et al.* 1996, Rohner and Krebs 1996, Taylor and Buskirk 1996, Sheffield *et al.* 2001). The decline in the population was faster and more complete on clear-cuts than on forested areas, but it is possible the decline in 1995 could have been related to the overall decline in red-backed vole abundance across the study area. In years of greater abundance, clear-cut sites with downed wood might have supported larger populations for a longer period.

Hayward *et al.* (1999) suggested that red-backed voles might perceive small patch-cuts (0.6 to 3.9 ha) differently than large clear-cuts, because they captured red-backed voles in the interior of smaller patch-cuts even though voles are often reported to decline after harvesting on larger clear-cuts. In my study, red-backed voles declined on patch-cuts as well as larger openings. My data suggest that the response to patch-cutting reported by Hayward *et al.* (1999) is not universal, and the response of red-backed voles may be influenced more by the amount of downed wood and vegetation left after harvesting. The patch-cuts in Hayward *et al.*'s (1999) study had abundant downed wood and saplings <15 cm in diameter left on site, which likely helped to ameliorate some of the initial effects of clear-cutting within the two-year sampling frame of their study. Therefore, depending on the intensity of the harvest treatment and subsequent site modification, red-backed voles might be considerably more sensitive to habitat perforation caused by placing small patch-cuts throughout the landscape than suggested by Hayward *et al.*'s (1999) study.

Retaining downed wood on clear-cut sites at Sicamous had no measurable benefit for red-backed vole populations within the first two years after harvesting, contrary to my hypothesis. The proportion of resident red-backed voles (captured > once) captured in edge traps was lower on *low* treatment areas than on *medium* or *high* areas, which suggests that voles were not

moving outside the grid to access downed wood. Downed wood volumes on clear-cuts at Sicamous were substantially higher than at Opax; volumes on *high* treatments were 3-4 times that on Opax clear-cuts. Even while populations on forested areas remained high, populations on clear-cuts declined to low levels immediately after harvesting, and red-backed voles were rare on clear-cuts within two years post-harvest. The rate of decline was not influenced by the amount of downed wood, unlike at Opax. This result is similar to that reported by Moses and Boutin (2001) from a study in a boreal mixedwood forest where post-harvest abundance of red-backed voles was similar on areas where downed wood had been removed to areas where downed wood was retained. Although downed wood volume on clear-cuts at Sicamous was relatively high, the percent ground cover by vegetation was low, even in the second growing season post-harvest. Mean protective cover was <50%, with very low shrub (15%), herb (27%) and moss cover (3%). At this high elevation site, downed wood does not appear to influence the immediate response of red-backed voles to clear-cutting, at least within the downed wood levels studied. In this case, additional vegetation or protective cover might have been more important than retention of downed wood (Sullivan *et al.* 1999a, Walters 1991, Hayward *et al.* 1999). Conversely, in periods of greater vole abundance (perhaps where minimum vegetation requirement were met), downed wood might be an important component for voles in these forests.

Previous research has indicated that red-backed voles on clear-cuts are sensitive to the abundance of shrub and herb cover. The use of herbicide to reduce herbaceous and shrub vegetation on clear-cuts generally results in a reduction in red-backed vole density (D'Anieri *et al.* 1987, Santillo *et al.* 1989, Sullivan 1990, Lautenschlager 1993, Sullivan *et al.* 1998a). Red-backed voles at higher elevations may require a threshold amount of vegetation or cover to

remain on clear-cuts, which was not met on the Sicamous study area. Retaining more vegetation after harvesting may mitigate some of the immediate effects of clear-cutting on red-backed voles.

5.5 Conclusions, Management Implications, and Suggestions for Future Research

The results of my study suggest that the southern red-backed vole might depend on the presence of downed wood; however, the relationship with downed wood varies depending on the ecosystem and other habitat components available in the area.

In dry ecosystems, such as the Opax study area in the interior of B.C., downed wood might be particularly important as a moisture reservoir and cover component (Clarkson and Mills 1994, Carey and Johnson 1995). On clear-cuts at Opax, the removal of downed wood resulted in lower red-backed vole population densities, and lower survival rates for at least the first two years post-harvest. On forested areas, despite edge effects, population densities on *high* areas tended to be higher than on *medium* or *low* treatment areas. This suggests that even a moderate reduction in the amount of downed wood in these forests could negatively affect red-backed voles.

On the high-elevation spruce-fir forest study area, red-backed vole abundance was not influenced by the abundance of downed wood. On forested areas with heavy cover from shrubs, herbs, and moss cover (>65%), red-backed voles were as abundant on different treatment areas with more than a 10-fold range in the volume of downed wood. The effect of harvesting on red-backed voles at the high-elevation system was also not related to the abundance of downed wood. Removal of the forest canopy resulted in the almost complete loss of red-backed voles from clear-cuts. Retention of downed wood did not modify the site enough to maintain populations, or slow the decline as at Opax. In this system, voles might require a threshold

amount of some other habitat component such as vegetation before they become abundant on forest openings.

Removing downed wood from forested areas was meant to mimic the potential long-term consequences of intensive forest management (Angelstam 1997); however, there are important differences, which my study was unable to address. In unharvested stands, forest floor characteristics, including shrub, herb, and litter cover, as well as downed wood are different from those found in managed forests (Triska and Cormack 1980, Spies *et al.* 1988, Spies and Franklin 1991, Rosenberg *et al.* 1994, Carey and Johnson 1995). Although red-backed vole populations were not negatively affected by the removal of downed wood within the short time frame of this study, the longer-term effects of the loss of downed wood could be more severe. The loss of downed wood at a large scale and over a long timespan would likely affect red-backed voles by negatively affecting many other attributes of the ecosystem on which they rely, such as fungal communities, forest floor characteristics, and understorey vegetation. As well, the heavy lichen growth on trees in old-growth forests, important for red-backed voles, is often not found in younger managed forests. Therefore, although other forest floor components in old-growth forests might fulfill the requirements of red-backed voles in the absence of downed wood, these components might be sparse or absent in managed forests. My study was able to address only the short-term response of voles to the removal of downed wood in an old forest ecosystem.

Based on my results I conclude that it is important to retain downed wood in dry ecosystems, where it might be particularly important as a moisture reservoir. Red-backed vole abundance and survival rates were lower on clear-cut areas with only 5% ground cover by downed wood (≥ 7.5 cm in diameter), compared to sites with 9-15% ground cover by downed

wood. In addition, on forested areas, red-backed voles were negatively affected by the reduction of downed wood below approximately 80 m³/ha. Therefore, after harvesting, at least 10% of the ground should be covered by downed wood ≥ 7.5 cm in diameter. This amount of ground cover resulted in downed wood volumes of 80-200 m³/ha. This is a minimum requirement, to ensure the presence of adequate levels of downed wood in later seral forests. For downed wood to be maintained through time, larger pieces should be left on site after harvesting. Larger pieces provide greater amounts of cover, retain more moisture, and also decay more slowly. It takes 80-190 years for a log to fully decompose in this dry ecosystem (Feller 1997). Maintaining larger logs, which take longer to decompose, on harvested areas will increase the abundance and diversity of downed wood in later seral stages. If the presence of wood-boring beetles is a concern, bark could be stripped from a few large logs, or more medium-sized logs could be left on site. Instead of piling and burning downed wood left after harvesting, distribute the material throughout the harvest block to create additional habitat. Previous research indicated that burning reduces the amount of downed wood and vegetation, negatively affecting some species of small mammals (Martell 1984, Sullivan *et al.* 1999a).

On the high-elevation site, red-backed vole abundance on forested areas, and perhaps clear-cuts, might be more strongly related to vegetation or protective cover than to downed wood alone. Once minimum requirements for cover are met, downed wood might be an important component for voles; this question needs further research. To encourage diversity in vegetation, a variety of harvesting techniques should be used across the managed landscape (Carey and Johnson 1995, Sullivan *et al.* 1999b). Harvesting and site-preparation removed most of the vegetation from harvested areas at the study area. Leaving patches of shrubs and other vegetation would provide structure, and may help to mitigate some of the initial effects of clear-

cutting on red-backed voles. Burning should be avoided because it removes much of the remaining vegetation and downed wood, and alters the forest floor. Large logs take 330-390 years to decompose completely in high-elevation ecosystems of interior B.C. (Feller 1997), so logs left on clear-cuts will provide an important legacy across seral stages, as well as ensure a diversity of log decay classes and sizes over time. If partial-cutting or other management to promote tree growth occurs in these forests, some large logs should be left behind to compensate for the reduced tree mortality in the stand (which will reduce future downed wood input).

Research on the relationship between red-backed voles and downed wood should continue to identify important minimum requirements. Research could include:

1. Continued sampling of red-backed vole populations at Opax and Sicamous. This:
 - a) Will provide information about the response of red-backed voles to treatments with forest succession;
 - b) Will provide information on the response of voles to treatments on Sicamous clear-cuts as they become more heavily vegetated;
 - c) Should include trapping at the edges of treatment areas or radio-telemetry to determine whether voles are moving outside treatment areas. This is especially important on Sicamous forested areas to determine whether populations on *low* areas are being maintained by accessing downed wood off the treatment area;
 - d) Should consider removing the vegetation from Sicamous forested treatment areas if red-backed voles continue to show no response to treatments and do not demonstrate edge effects. This will provide information about the substitutability

and potential minimum requirements of red-backed voles for downed wood and vegetation in moist environments; and,

- e) Should consider diet studies of red-backed voles at Opax and Sicamous. This study should include a component on the importance of downed wood at the Opax site as a moisture reservoir.

2. Research elsewhere should:

- a) Include studies in dry and wet ecosystems to determine whether the apparent difference in response by red-backed voles to downed wood is due to ecosystem differences. Initial studies should focus on comparing sites where downed wood is removed with natural sites. Vegetation should be removed or controlled as a factor;
- b) Include larger treatment areas of at least 5 ha and preferably larger (>10 ha); and,
- c) Investigate whether voles will respond to higher levels of downed wood than normally available in the surrounding habitat. This is particularly important in dry habitats where downed wood is more sparsely distributed, and where downed wood might be a limiting factor.

Chapter 6. Microhabitat Associations of Southern Red-backed Voles at Two Spatial Scales

6.1 Introduction

Recent research has focussed on identifying important habitat features for small mammals in forested habitats, to better predict the impacts of forest management. Researchers have determined the response of small mammal population and community dynamics to many forest management practices through mark-recapture studies, which provide information at the forest stand scale (*e.g.*, Van Horne 1981, Kirkland 1990, Rosenberg *et al.* 1994, Sullivan *et al.* 1998a, Von Treba *et al.* 1998, Loeb 1999, Sullivan *et al.* 2000 among others). Fewer studies have focussed on finer-scale spatial relationships between individuals and components of their habitats, relationships that might be obscured at larger scales (Wiens *et al.* 1993, Bunnell *et al.* 1999).

Downed wood is a habitat component that is considered important to numerous species of small mammals, and particularly important to red-backed voles (*Clethrionomys* spp., Harmon *et al.* 1986, Carey and Johnson 1995); but the extent to which red-backed voles depend on downed wood is unclear (Ure and Maser 1982, Gunther *et al.* 1983, Maser and Trappe 1984, Nordyke and Buskirk 1991, Rosenberg *et al.* 1994, Carey and Johnson 1995, Mills 1995). With intensive forest management, the amount of downed wood decreases with each harvest rotation (Angelstam 1997). This long-term reduction in the amount of downed wood in forested stands has the potential to affect small mammals that rely on downed wood for habitat. Studies to date on the relationship between small mammals and downed wood have likely been hampered by attempts to detect relationships in study areas with relatively large amounts of downed wood (Bunnell *et al.* 1999).

As part of a larger study examining the relationship between red-backed voles and downed wood, I examined spatial relationships between southern red-backed voles (*C. gapperi*) and components of their habitat, with particular emphasis on downed wood. In Chapter 5, I examined the response of red-backed voles at the population level to the manipulation of downed wood on forested sites in two different ecosystems. In this chapter, I report the results of a study of microhabitat associations of red-backed voles at two scales in a dry, Douglas-fir-lodgepole pine ecosystem. I compared habitat within vole home ranges with that available in the surrounding habitat (forest stand), and examined microhabitat associations of voles within home ranges. My hypotheses were: 1) if downed wood is an important component for red-backed voles, then vole home ranges will be associated with downed wood, 2) if downed wood is an important habitat component, then vole home ranges on *low* treatment areas will be larger than on *high* treatment areas, because *low* areas would represent poorer quality habitat (Bondrup-Nielsen 1985, Bondrup-Nielsen and Karlsson 1985), and 3) if downed wood is an important habitat component, then vole locations within home ranges will be associated with downed wood more than expected at random.

6.2 Methods and Analyses

I studied the microhabitat associations of southern red-backed voles using radio-telemetry, on forested areas at the Opax study area described in Chapter 1. The study was conducted on *low* and *high* treatment areas on two replicate forested areas (blocks D and I, Fig. 3, Chapter 2) that were part of a larger study on the population-level response of deer mice, meadow voles, and red-backed voles to downed wood treatments (reported in Chapters 3, 4, and 5).

6.2.1 Radio-telemetry

I attached radio-transmitters (Holohil Systems, Carp Ontario, model MD-2C) to female red-backed voles on forested downed wood treatment areas. I selected red-backed voles for radio-tracking because they are considered to be closely associated with old seral forest and downed wood (Tevis 1956, Merritt 1981). Female red-backed voles appear to be territorial and tend to have smaller, better-defined home ranges than males (Bondrup-Nielsen 1985, 1986), which might make them more dependent on local microhabitat features. Originally, I planned to radio-track red-backed voles on both forested and clear-cut areas to study their microhabitat associations across a range of habitat. Unfortunately, although red-backed voles were reasonably numerous overall on clear-cuts in 1994 and 1995, populations declined across the study area, and they became rare on clear-cuts by 1996. Small mammal sampling grids on each area were live-trapped approximately every three weeks from May to October 1996 and May to July 1997 as part of the study on the relationship between downed wood and red-backed vole population dynamics (Chapter 5). Voles were selected for collaring if they were resident on a sampling grid (had been captured at least twice), and were ≥ 22 g in weight, such that radios (approximately 1.2 g with collar) were $\leq 5.5\%$ of their body weight. Radios were strung on cable ties and carefully tightened on the necks of voles. Any extra length of cable tie was cut off. I briefly anaesthetized the first few voles with methoxyfluorane before attaching collars; however, with practice I was able to collar voles quickly without anaesthetic. Once collars were attached, voles were placed back in a livetrapp and held until the end of the trapping session (at least 0.5 h). I examined voles before release to ensure that collar attachments were secure.

A reference grid for triangulating telemetry locations was superimposed on small mammal sampling grids where radio-collared voles were resident. Telemetry reference points were 7.5 m apart. Voles were located immediately after I arrived on the grid. While locating voles, I

remained at least 5 m away from the vole and took compass bearings towards the vole from three points on the grid. After taking bearings I approached some voles to identify their exact locations and to check the accuracy of compass bearings. After recording the initial location of the vole, I waited for 15 minutes to determine if the vole was active. If she was active I took locations every 15 min, as well as opportunistically (if she was sighted). If a vole was sighted, I recorded her general behaviour and flagged the site. I collected locations on radio-collared voles for >2 weeks at different times of day. At least one night-time telemetry session was conducted for each vole. I attempted to collect ≥ 35 telemetry locations for each vole.

Home ranges were calculated using the 95% minimum convex polygon (MCP, Mohr 1947) using the Animal Movement Extension (Hooze and Eichenlaub 1997) in ArcView 3.2 (Environmental Systems Research Institute (ESRI), Redlands, CA). Bootstrap analyses of 95% minimum convex polygon (MCP) home ranges for voles with ≥ 60 telemetry locations suggested that home range size began to asymptote at approximately 35 locations. Thus, home range sizes were only calculated for voles with ≥ 35 locations. I also calculated 95% and 50% kernel home ranges for each vole in ArcView, to visually determine how activity patterns were distributed throughout the home range.

6.2.2 Broader-scale habitat associations

Broader-scale habitat data (Table 14) were collected in 5.65-m-radius sampling plots within each vole home range, and around every second trap station on the sampling grid (25 plots per sampling grid) as described in Chapter 1. Downed wood data were also collected along a triangular transect superimposed over the plot. The number of plots placed within vole home ranges was constrained such that the sampling intensity was similar within home ranges and

Table 14. Habitat variables for which data were collected in 5.65-m-radius plots.

Variable	Description
Canopy	Percent ground cover
Mineral soil	Percent ground cover
Moss	Percent ground cover and depth
Litter layer	Percent ground cover and depth
Herbs and Grass	Percent ground cover
Tall shrubs (>2 m tall)	Percent ground cover
Short shrubs (<2 m tall)	Percent ground cover
Number of pieces	Number of pieces of downed wood that cross the transect
Diameter of downed wood	Diameter for each piece of downed wood that crosses transect
Height of downed wood	Height off ground for each piece of downed wood
Length of downed wood	Length of each piece of downed wood
Decay class of downed wood	Decay class (following Maser <i>et al.</i> 1979), for each piece of downed wood
Number of trees	Number of trees within the plot

within grids. One plot was placed around the nest of each vole, and other plots were distributed systematically throughout the home range.

I used multiple logistic regression best subsets analysis (*Statistica* version 5, StatsSoft Inc.) to distinguish differences between data from habitat plots in vole home ranges and plots on the sampling grid. Because of the small number of plots per vole, I pooled plots within treatment types (*i.e.*, *low* and *high* downed wood). Logistic regression allows the identification of a model that includes a subset of habitat components that vary (in this case) between vole home ranges and the surrounding area.

Habitat variables were screened for multicollinearity and the threshold for variable exclusion was set at $r = 0.5$. I used Akaike's Information Criterion adjusted for small sample size (AICc; Akaike 1985, Burnham and Anderson 1998) to identify models best supported by the data. Unlike likelihood ratio testing, AIC allows comparison between non-nested models (Lebreton *et al.* 1992). Models within 2 Δ AICc of the most parsimonious model were considered to have support (Anderson *et al.* 1994). Once I identified the variables best supported by the data, I performed Type 1 and Type 3 Likelihood tests, which indicated the contribution each variable made to the model. Variables that did not improve the model with P

≤ 0.05 were excluded from future tests. Overall model goodness of fit was also assessed with odds ratios, where ratios $>1:1$ indicated models unlikely by chance. Running the data through the selected model also provided information about the proportion of each group of data (vole home range vs. surrounding habitat) that was correctly classified with the model.

6.2.3 Fine-scale habitat associations

I collected fine-scale habitat data in vole home ranges defined by telemetry using two methods: plots and habitat maps. Habitat data were collected in 2-m-diameter plots around randomly selected vole locations and in plots placed systematically throughout the vole's home range (Table 15). I used multiple logistic regression to distinguish habitat differences between vole locations and random locations within each vole home range, following the method described above. Again, because of small sample sizes I pooled data for individual voles within a given downed wood treatment.

6.2.4 Home range habitat maps

I mapped the habitat characteristics of 10 vole home ranges in 1 m x 1 m cells (Fig. 29, Appendix 3). For the mapping I chose voles with well-established home ranges (few long-range excursions). I recorded habitat data on cover classes of vegetation, as well as information on size, number of pieces, and decay class of downed wood (Table 16). Cover data were recorded

Table 15. Habitat data collected in 2-m-diameter plots within vole home ranges

Variable	Description
Mineral soil	Percent ground cover
Moss	Percent ground cover and depth
Litter layer	Percent ground cover and depth
Grass	Percent ground cover
Herbs	Percent ground cover
Shrubs	Percent ground cover
Distance to dw ¹	Distance from plot centre to closest piece of downed wood
Diameter (dw) ¹	Diameter of the closest piece of downed wood
Height (dw) ¹	Height of the closest piece of downed wood
Length (dw) ¹	Length of the closest piece of downed wood
Distance to tree	Distance to the closest tree ≥ 7.5 cm in diameter

¹dw is an abbreviation for downed wood ≥ 7.5 cm in diameter

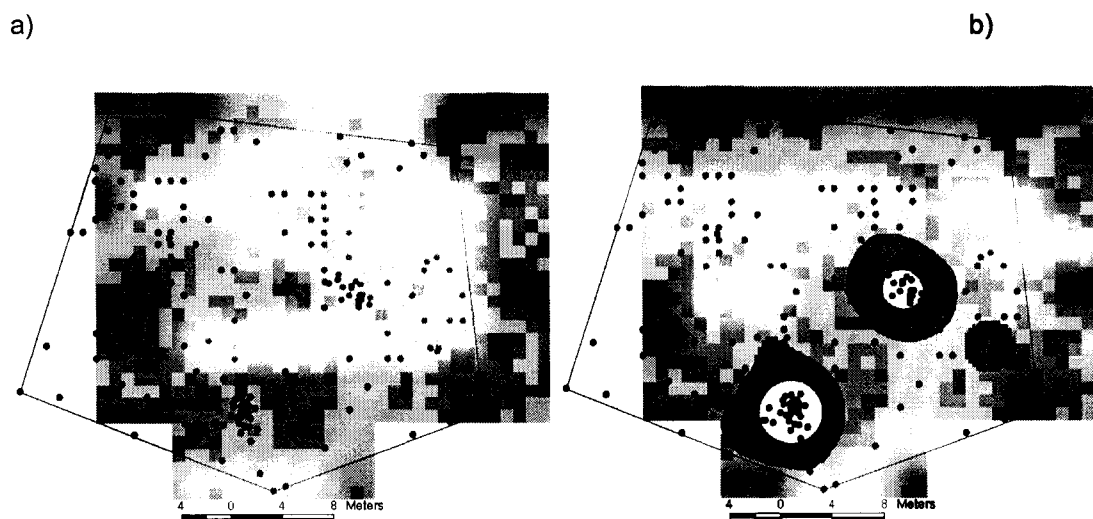


Figure 29. Examples of home range maps for voles, each pixel is 1m x 1m in size a) This map indicates the placement of large (>20 cm) diameter downed wood on the site. The lightest colour indicates that there is none in that cell, the darker the colour of grey, the more number of pieces within the cell. Dots indicate vole locations, and the outlined area is the vole home range estimate by 95% MCP. b) The same map illustrating the 95% and 50% Kernel home range estimate. The large dark circle is the 95% estimate, and the lighter, smaller circle the 50% Kernel home range estimate. This vole's nest was in the 50% Kernel estimator in the bottom left part of the map.

as belonging to one of three cover classes, and downed wood in one of five diameter classes, height classes and decay classes.

To determine whether habitat components interacted to provide important habitat for voles, I constructed several composite variables to include in the analyses. These included a 'minimum cover' estimate, where cells were scored as '1' if they contained at least 10% cover from herbs or shrub, or one piece of downed wood >10 cm in diameter, or two pieces of downed wood >5 cm in diameter. I also constructed a 'dense cover' variable, where cells were scored as '1' if they had >50% cover from shrubs or herbs, or had one piece of downed wood >20 cm in diameter, two pieces of downed wood >10 cm in diameter, or three pieces of downed wood >5 cm in diameter. These composite variables were also screened against other variables for multicollinearity. I combined counts of logs from decay classes 1 and 2 into one group, and decay classes 4 and 5 into one group.

Table 16. Categories used to classify habitat in each grid cell for home range maps

	Category	Description
Grass	0,1,2	Grass cover in 3 categories (<10% cover, 11-50% cover, >50% cover)
Herb	0,1,2	Herb cover in 3 categories (as above)
Moss	0,1,2	Moss cover in 3 categories (as above)
Shrub	0,1,2	Shrub cover in 3 categories (as above)
Tree	0,1,2	Tree canopy cover in 3 categories (as above)
Tree Stem	count	No. tree stems in each grid cell
Stump	count	No. stumps in each grid cell (data were too sparse to be included in analyses)
	count	No downed wood
Downed wood (6 categories)		Number of pieces <5 cm in diameter
		Number of pieces 5-10cm in diameter
		Number of pieces 10-20 cm in diameter
		Number of pieces 20-30 cm in diameter
		Number of pieces >30 cm in diameter
DC1	count	Number of pieces of downed wood in DC 1
DC2	count	Number of pieces of downed wood in DC 2
DC3	count	Number of pieces of downed wood in DC 3
DC4	count	Number of pieces of downed wood in DC 4
DC5	count	Number of pieces of downed wood in DC 5

I assembled maps for each vole home range in ArcView and calculated 95% minimum convex polygon (MCP) home ranges based on all locations for each vole (even where locations were close together in time). However, only locations collected >30 min apart were used in the analyses. An equal number of random locations located in the home range were used to represent “available” habitat in the analyses. Map layers were queried for habitat values for each vole and random location. I built separate regression models for each vole, following methods described above for plot data.

Unless otherwise stated, all means are presented ± 2 standard errors.

6.3 Results

6.3.1 Downed Wood

Approximately 83% and 92% of downed wood volume was removed from the two *low* treatment areas (Fig. 5, Chapter 2). Most of the larger logs were removed on *low* areas. Larger pieces of downed wood remaining on *low* treatment areas were generally <20cm in diameter

(Fig. 6, Chapter 2). The distribution of logs by decay class indicated that *low* treatment areas had a greater proportion of logs in more advanced stages of decay (decay classes 4 and 5, Fig. 6, Chapter 2). However, the overall number pieces of decayed wood on *low* areas was smaller, and remaining pieces tended to be scattered chunks from the destruction of decayed logs, whereas on *high* areas they were intact.

6.3.2 Radio-telemetry

Unfortunately, red-backed vole population density was low during the years I conducted the radio-telemetry study, which limited my ability to capture suitable individuals. There were on average six and nine voles (total) ha^{-1} on *low* grids, and 11 and 15 voles (total) ha^{-1} on *high* sampling grids. Six red-backed voles were successfully collared and radio-tracked in 1996, and 11 in 1997; six of these voles were on *low* treatment areas, and 11 on *high* areas. Nine of 17 voles radio-tracked had some portion of their home range at the boundary of, or off the downed wood treatment area.

MCP vole home ranges varied in size from 0.012 ha to 0.2 ha (Table 17). MCP generally provides the largest estimate of home range size, and includes some areas seldom used by voles (Fig. 29). Kernel home ranges were much smaller, and reflected the intense use of the nest area. There was no indication that home range size varied with downed wood treatment (*low* grids $\bar{x}$ home range = 0.12 ± 0.05 ha; *high* $\bar{x}$ = 0.10 ± 0.04 ha).

6.3.3 Nest Site Characteristics

All radio-tracked voles had well-defined nest areas where they spent a large proportion of their time. All nests were in, or under, downed wood (a log or stump). Downed wood at nest sites was 8-91 cm in diameter (Table 18). Both mean and median nest log size was 38 cm in

Table 17. Home range characteristics of red-backed voles at the Opax study area

Downed Wood Treatment	Grid	Vole	No. of locations	95% MCP Home range (ha)	95% Kernel Home range (ha)	50% Kernel home range (ha)
Low	D1	41-2	175	0.200	0.061	0.004
Low	D1	19	56	0.166	0.046	0.007
Low	D1	57	41	0.136	0.079	0.015
Low	D1	73	43	0.069	0.014	0.003
Low	I2	95	44	0.083	0.018	0.004
Low	I2	31	42	0.043	0.013	0.002
High	D2	41-1	99	0.198	0.043	0.007
High	D2	87	30	Not calculated, no. points <35		
High	D2	21	40	0.156	0.154	0.010
High	D2	51	56	0.067	0.064	0.007
High	D2	90	47	0.094	0.049	0.004
High	D2	92	40	0.054	0.041	0.007
High	D2	72	29	Not calculated, no. points <35		
High	I3	49	48	0.101	0.017	0.002
High	I3	23	65	0.142	0.077	0.009
High	I3	55	35	0.012	0.012	0.002
High	I3	84	90	0.066	0.020	0.002

diameter. Lengths of nest logs also varied from short, heavily decayed pieces to firmer 16.5 m logs. All nests were in logs or stumps of decay class 3-5.

I did not collect detailed behaviour information; however, I did have the opportunity to watch voles on occasion. Voles spent much of their time at their nest, returning to it often in between periods of activity. On five occasions (three different voles), I observed other voles interacting with the collared vole. None of the encounters appeared to be antagonistic. In addition, I had the opportunity to watch some voles foraging. I observed voles digging, eating fungi (white, unknown species), a heart-leaved arnica (*Arnica cordifolia*) leaf, and witch's hair lichen (*Alectoria* spp.). The majority of foraging observations were of voles eating bunches of horsehair lichens (*Bryoria* spp.) that were hanging from downed branches, small trees, or on the ground.

Table 18. Nest site characteristics of radio-tracked red-backed voles.

DW Treatment ¹	Grid	Vole	DW ¹ species	Diameter (cm)	Length (m)	Decay class	Comments
Low	D1	41-2	DF ²	60	6.0	3	Decayed stump
Low	D1	19	DF ²	50	3.5	4.5	
Low	D1	57	Unknown	45	1.5	5	
Low	D1	73	Unknown	22	3.0	3	
Low	I2	95	DF ²	60	2.0	4	
Low	I2	31	Unknown	8	1.5	5	
High	D2	41-1	Unknown	10	1.0	5	
High	D2	87	Unknown	20	8.5	3.5	
High	D2	21	DF ²	60	1.14	3	
High	D2	51	DF ²	91	9.4	3.5	
High	D2	90	Unknown	22	9.5	4	
High	D2	92	DF ²	38	9.5	3	
High	D2	72	DF ²	45	4.0	3	
High	I3	49	DF ²	39	16.5	3	
High	I3	23	DF ²	25	11.5	3	
High	I3	55	Unknown	24	1.3	5	
High	I3	84	Unknown	31	2.9	4	

¹ DW is an abbreviation for downed wood

² DF = Douglas-fir

Red-backed voles were active throughout the day and night. The likelihood of encountering voles at their nest did not appear to be influenced by time of day. Voles often moved quickly through their home range, and were able to travel up to 30 m in five minutes.

6.3.4 Broader-scale habitat associations of red-backed voles

Identifying important habitat components at the home range scale involved comparing habitat characteristics of known vole home ranges with characteristics of the surrounding area. Data for the surrounding area likely included both suitable and unsuitable vole habitat, permitting me to detect only the strongest relationships.

Seven models were supported by the data ($<2 \Delta AICc$ of the most parsimonious model) for voles on *high* treatment areas. All of the top models identified canopy cover and number of pieces of downed wood as important variables. The amount of tall shrub cover also showed up consistently in the top models (and was identified along with canopy cover and number of pieces of downed wood in the most parsimonious model). Other habitat variables such as

downed wood length (longer in vole home ranges), short shrub cover (less in vole home ranges), and herb cover (less in vole home ranges) were identified inconsistently. Based on the best-supported variables, vole home ranges on *high* treatment areas had greater canopy cover, less tall shrub cover, and had more pieces of downed wood ≥ 7.5 cm in diameter than available on the treatment area (Table 19, Table 20a). The analysis correctly classified 92% of vole home range plots and 96% of treatment area plots (odds ratio 1:276 meaning that this level of accuracy was very unlikely to happen by chance).

On *low* treatment sites, the mean number of pieces of downed wood was higher on vole home ranges ($\bar{x} = 11.9 \pm 3.2$) than on the treatment area ($\bar{x} = 2.5 \pm 0.8$, Kolmogorov-Smirnov test $P < 0.001$); however, distribution of the data was very skewed. Even after different transformations, the data could not be normalized to be included in regression models. In future discussions I include downed wood as an important component. An analysis without this variable identified three models within 2 $\Delta AICc$ of the most parsimonious model. Canopy cover and tall shrub cover were identified as important variables in the best-supported model, and short shrub cover (less on vole home ranges), downed wood length (longer on vole home ranges), and percent litter cover (less cover on vole home ranges) were variables identified in the other models. The model including only the most parsimonious variables (canopy cover and tall shrub cover) indicated that vole home ranges had more canopy cover and less tall shrub cover than on the surrounding treatment area (Table 19, Table 20b). The analysis correctly classified 94% of plots in vole home ranges, and 96% of plots on the treatment area (1:416 odds).

Vole home ranges on *low* and *high* areas had similar attributes. Mean number of pieces of downed wood per plot on *low* treatment areas was similar to that on *high* treatment areas (Table

Table 19. Means (± 2 SE) for broader-scale habitat plots for each downed wood treatment area. Data are presented for plots in vole home ranges, and plots placed in the surrounding treatment area.

Downed wood treatment	<i>Low</i>		<i>High</i>	
	Vole home range	Treatment area	Vole home range	Treatment area
Variables				
Canopy cover	36.0 (7.5)	15.7 (1.5)	36.2 (6.6)	14.7 (1.6)
% Mineral soil	2.9 (1.1)	0.5 (0.5)	1.6 (0.9)	0.02 (0.02)
Moss depth (cm)	1.3 (0.2)	1.8 (0.3)	1.2 (0.1)	1.7 (0.3)
% Moss	11.3 (4.8)	17.4 (4.3)	19.0 (8.1)	21.8 (5.1)
Duff depth (cm)	1.1 (0.1)	1.5 (0.2)	1.1 (0.2)	1.4 (0.2)
% Duff	32.6 (7.6)	38.0 (4.8)	31.7 (5.9)	27.5 (5.2)
% Herb and grass	40.8 (8.5)	52.9 (4.1)	41.3 (9.3)	65.4 (4.0)
% Shrubs <2 m tall	25.3 (8.2)	37.6 (4.3)	19.3 (6.2)	39.6 (5.4)
% Shrubs >2 m tall	1.6 (1.1)	16.2 (3.4)	4.3 (2.4)	20.8 (4.2)
No. pieces DW ¹	11.9 (3.3)	2.5 (0.7)	12.4 (2.1)	5.1 (1.0)
DW diameter (cm) ¹	18.1 (2.3)	15.1 (2.7)	21.3 (3.5)	18.9 (2.0)
DW length (m) ¹	3.8 (0.9)	3.1 (1.2)	6.7 (1.3)	5.0 (0.8)
DW height (cm) ¹	4.5 (2.9)	18.7 (6.4)	6.6 (4.4)	23.7 (3.5)
Number of trees ²	8.8 (2.0)	8.7 (1.4)	11.7 (2.1)	9.8 (1.2)
Protective cover ³	83.2 (4.3)	75.9 (3.6)	81.4 (5.1)	84.4 (2.4)

¹ DW is an abbreviation for downed wood pieces ≥ 7.5 cm in diameter

² Trees ≥ 7.5 cm in diameter

³ Protective cover was a visual estimate made at each plot of the total amount of ground cover from all sources, including vegetation, downed wood, and canopy cover

19). The same was true of canopy cover and tall shrub cover, the other two variables identified as important in the analysis.

6.3.5 Fine-scale habitat associations

As with the broader-scale habitat association analyses, random plots within vole home ranges likely included suitable vole habitat. Therefore, I likely detected only the strongest associations.

I measured habitat components in 2m-radius plots at 15-39 vole locations in each vole home range. Analyses for voles on *high* treatment areas identified 13 models supported by the data (Table 21, Table 22a). Five variables: moss cover, litter depth, distance to the closest piece of downed wood ≥ 7.5 cm in diameter, diameter of closest downed wood, and distance to the closest tree ≥ 7.5 cm in diameter were identified in almost all of the top models. An all-effects logistic regression model suggested that distance to the closest tree (tree distance) contributed

Table 20. Results of logistic regression analysis to distinguish plots on vole home ranges from plots on the sampling grid. Results are presented for a) voles on *high* treatment areas, and b) voles on *low* treatment areas. Std Estimate is the estimates scaled by their SE so that the size indicates the relative strength of the relationship. The sign of the estimate indicates the trend from grid locations to vole home ranges (e.g., on *high* areas, number of pieces of downed wood is higher on vole home ranges than on grid plots).

a) *High* treatment areas

df=71, -2LL = 18.9 $\chi^2(4) = 76.49, P < 0.001$				
Variable	Estimate	SE	Std Estimate	p-level
Intercept	-9.43	3.63	-2.60	0.01
Canopy	0.20	0.07	2.74	0.01
Tall shrub cover	-0.11	0.06	-1.67	0.10
Number of pieces of downed wood	0.60	0.28	2.15	0.03

b) *Low* treatment areas

df=66, -2LL = 14.62 $\chi^2(3) = 68.30, P < 0.001$				
Variable	Estimate	SE	Std Estimate	p-level
Intercept	-4.33	2.13	-2.04	0.04
Canopy	0.34	0.14	2.52	0.01
Tall shrub cover	-0.74	0.33	-2.26	0.02

little to the overall fit of the model. Without tree distance, the model identified 61% of vole locations correctly, and 72% of random locations correctly. The model had an odds ratio of 1:4.

Logistic regression analysis to discriminate vole locations from random locations within vole home ranges on *low* treatment areas also failed to identify a single best model. Twelve models were identified that had support ($\Delta AICc < 2$, Table 22b). Six variables: litter cover, litter depth, shrub cover, distance to downed wood, and diameter and height of the closest piece of downed wood were consistently identified in top models, including the most parsimonious model. An all-effects model using these variables correctly classified 77% of vole locations and 82% of random locations, and had an odds ratio of 1:15.

Table 21. Means (± 2 SE) of each habitat variable measured in 2-m plots around vole and random locations within vole home ranges.

Downed wood treatment	Low		High	
	Vole locations	Random	Vole locations	Random
% Mineral soil	3.0 (2.1)	1.7 (0.9)	0.8 (0.4)	0.9 (0.4)
Moss depth (cm)	1.0 (0.2)	0.9 (0.1)	0.9 (0.1)	1.0 (0.1)
% Moss	11.1 (3.6)	17.5 (4.7)	15.8 (2.8)	13.2 (2.9)
Litter depth (cm)	1.5 (0.3)	1.0 (0.1)	1.7 (0.2)	1.4 (0.1)
% Litter cover	46.7 (5.5)	31.6 (5.5)	54.5 (4.0)	53.7 (3.9)
% Grass cover	19.3 (4.8)	13.2 (3.1)	17.4 (3.1)	22.1 (3.2)
% Herb cover	17.1 (3.1)	15.5 (2.6)	18.7 (2.3)	18.6 (1.7)
% Shrub cover	17.1 (2.9)	20.1 (3.8)	23.9 (3.2)	22.0 (2.8)
Distance to DW (cm) ¹	36.1 (12.2)	101.9 (21.9)	56.2 (15.5)	87.3 (12.3)
DW diameter (cm) ¹	24.6 (3.5)	20.1 (2.6)	34.0 (4.1)	20.5 (2.1)
DW length (m) ¹	6.5 (1.6)	4.8 (1.0)	7.3 (0.8)	5.7 (0.7)
DW height (cm) ¹	17.8 (5.0)	6.9 (3.0)	11.0 (3.3)	6.5 (2.4)
Distance to tree ²	123.1 (22.2)	165.2 (20.2)	139.2 (12.1)	160.6 (15.9)

¹ DW is an abbreviation for downed wood pieces ≥ 7.5 cm in diameter

² Trees ≥ 7.5 cm in diameter

6.3.6 Home Range Habitat Maps

The response among voles to specific habitat components was variable, but in general, voles were associated with some form of cover (Tables 23, 24). Eight of ten voles were associated with areas of denser cover provided by downed wood, shrubs, or a combination of variables. One vole was negatively associated with grass cover, and another was negatively associated with logs 20-30 cm in diameter.

The proportion of vole locations in mapped cells with downed wood >10 cm in diameter was 55%, which was significantly greater than the proportion of random locations associated with cells with downed wood (41%, $t_{2,1} < 0.05$).

6.4 Discussion

Downed wood is widely considered an important habitat component for many species of small mammals, and particularly for red-backed voles (Harmon *et al.* 1986, Carey and Johnson 1995); however, previous research has produced equivocal results. My study supports the hypothesis that downed wood is an important habitat component for red-backed voles, which is

Table 22. Results of logistic regression analysis to discriminate between vole locations and random locations within vole home ranges. Data are presented for voles pooled across a) high treatment areas, and b) low treatment areas. The standardized estimate (Std Estimate) indicates the strength of the relationship. The sign of the estimate indicates the direction of variability from random plots to vole locations (e.g., for high areas, distance to downed wood decreases from random to vole locations).

a) *High treatment areas*

df=425, -2LL = 544.17 $\chi^2(4) = 47.53, P < 0.001$				
Variable	Estimate	SE	Std Estimate	p-level
Intercept	-1.11	0.28	-3.95	0.00
Moss cover	0.01	0.00	2.07	0.04
Depth of litter layer	0.23	0.10	2.25	0.02
Distance to the closest piece of DW ¹	-0.00	0.00	-2.00	0.05
Diameter of the closest piece of DW ¹	0.03	0.01	4.95	0.00

¹DW = downed wood > 7.5 cm in diameter

b) *Low treatment areas*

df=191, -2LL = 207.82 $\chi^2(7) = 66.66, P < 0.001$				
Variable	Estimate	SE	Std Estimate	p-level
Intercept	-1.26	0.51	-2.45	0.01
Litter layer cover	0.02	0.01	2.35	0.02
Depth of litter layer	0.62	0.33	1.85	0.06
Shrub cover	-0.02	0.01	-1.96	0.05
Distance to the closest piece of DW ¹	-0.01	0.00	-4.12	0.00
Diameter of the closest piece of DW ¹	0.03	0.01	-2.19	0.03
Height off the ground of the closest piece of DW ¹	0.03	0.01	3.20	0.00

¹DW = downed wood ≥ 7.5 cm in diameter

selected for at both the home range (broad) and the microhabitat (fine) scales in dry Douglas-fir forests of southern British Columbia. Although my data did not support my second hypothesis (home ranges will be larger on *high* treatment areas), my hypothesis was based on the assumption that voles on *low* treatments would not have access to downed wood. However, voles on *low* areas did access downed wood, which supports the underlying hypothesis that downed wood is an important component for red-backed voles at the Opax study area.

6.4.1 Broader-scale habitat associations

Habitat selection of red-backed voles was most evident at the home range scale. Voles had strong positive relationships with downed wood and canopy cover, and negative relationships with shrub cover on both *high* and in particular, on *low* treatment areas. This result addresses my first hypothesis, which stated that, if downed wood were an important habitat component, voles would associate with it at the home range scale. Vole home ranges on both *low* and *high* treatment areas were associated with higher densities of downed wood than available in the surrounding area. Although the number of pieces of downed wood on *low* vole home ranges could not be included in the logistic regression analysis, vole home ranges had four times the number of pieces of downed wood than available on the *low* treatment area. As well, the number of pieces of downed wood within vole home ranges was similar on *low* and *high* areas (Table 19).

The apparent association of voles with downed wood on *low* treatment areas was influenced by the fact that five of the seven voles on *low* areas had some proportion of their home range at the boundary of, or outside the treatment area. As a result, these voles had access to more downed wood than was generally available on the treatment area. However, voles that had their entire home ranges on the treatment area selected areas where there was as much downed wood as the home ranges of voles that extended beyond the treatment area boundary. These voles were associated with the occasional large piece of downed wood on the *low* treatment areas that could not be removed safely. Therefore, voles on *low* treatment areas still accessed downed wood by selecting areas where downed wood still remained, or by locating their home ranges partly off the treatment area to where downed wood was more available.

Table 23. Results of logistic regression analysis of home range mapping data. The analysis was run to discriminate habitat around vole locations with that around random locations.

Downed wood Treatment	Vole ID	Regression statistics					% correctly classified	
		df	-2LL	$\chi^2(df) =$	<i>P</i>	Odds ratio	vole	random
<i>Low</i>	31	80	85.35	(3)=36.23	<0.001	1:14	83	74
	57	78	88.90	(4)=24.78	<0.001	1:8.4	83	63
	73	78	63.22	(6)=53.23	<0.001	1:55.3	81	93
<i>High</i>	21	75	79.30	(5)=31.60	<0.001	1:9.3	79	80
	23	124	143.41	(6)=36.81	<0.001	1:8.0	75	72
	49	93	116.11	(3)=16.98	<0.001	1:3.7	71	60
	51	108	134.10	(4)=21.17	<0.001	1:6.8	80	63
	55	68	92.35	(2)=4.69	>0.05*	1:2.0	69	51
	84	176	233.11	(4)=16.42	<0.005	1:4.6	89	37
	90	92	126.29	(2)=4.02	>0.10*	1:3.3	23	91

*Note that these logistic regression analyses were not significant at $\alpha = 0.05$

Voies on *high* treatment areas also selected areas where downed wood was more available than the surrounding area. This provides strong evidence that downed wood is an important habitat component influencing the habitat selection of red-backed voles on the study area.

Vole home ranges on both *low* and *high* treatment areas were in areas with greater amounts of canopy cover and less tall shrub cover than the surrounding area. The (primarily) Douglas-fir forest on the study area is very patchy and many small openings are associated with rocky areas that are likely too dry to provide suitable habitat (Getz 1968). Tall shrubs provide security cover and might also moderate the microenvironment with respect to soil moisture. Other researchers have reported a positive relationship between shrub cover and red-backed voles (Nordyke and Buskirk 1991, Rosenberg *et al.* 1994, Carey and Johnson 1995). It is not clear why there was a negative association in my study, although it might reflect the weak negative correlation between shrub cover and downed wood abundance and attributes.

Habitat characteristics measured within home ranges on *high* treatment areas might represent optimal conditions for these voles within the study area because population densities were low and, as a result, competition for suitable habitat was also likely low. Female red-

Table 24. Parameter estimates for habitat components identified as important from logistic regression analysis on map data for each vole. Estimates presented are standardized by their standard error, and therefore indicate the relative strength of the relationship. Blank areas indicate that the vole used the habitat component in relation to its availability. The sign of the parameter indicates how the habitat component varies between random plots and vole locations (e.g., vole 23 vole locations have less grass cover than do random locations in the home range).

Habitat variable	Vole ID									
	31	57	73	21	23	49	51	55*	84	90*
Grass ¹					-2.54			-2.09	2.16	
Herb ¹	-0.49			-2.78	2.10	-2.10				
Moss ¹										
Shrub ¹						2.71	-3.56			
Canopy ¹				2.23						
Tree stem			2.4				-1.98			
DW ² <5 cm ²			3.2							
DW ² 5-10 cm		3.64	2.5							
DW ² 10-20cm		2.14			3.72				-2.16	1.90
DW ² 20-30 cm		3.64	2.9							
DW ² >30 cm				-3.04			2.33			
DC ³ 1 & 2			3.0							
DC ³ 3					-2.16					
DC ³ 4&5					-2.25					
Dense cover ⁴	0.66			3.51						
Minimum cover ⁴	-0.88								2.25	
Intercept	0.45	-3.15	-4.23	-1.58	0.76	-0.89	1.83	1.31	-2.24	-0.79

*Logistic regression analysis not significant ($P > 0.05$, see Table 23)

¹These are percent cover variables

²DW = downed wood

³DC = decay class

⁴Dense cover and minimum cover are composite cover variables, including downed wood, shrub, and herb cover (see text)

backed voles maintain exclusive home ranges, and do not appear to compete with male voles (Mihok 1979, Gilbert *et al.* 1986). As well, the size of female red-backed vole home ranges is apparently sensitive to differences in habitat quality (Bondrup-Nielsen 1984). I occasionally saw interactions among voles, but they did not appear antagonistic. None of the home ranges of females I radio-tracked overlapped. Deer mice were the only other species captured regularly on forested areas, but these species likely co-exist without competing for resources (Galindo and Krebs 1985, Barry *et al.* 1990, Morris 1996).

The 95% MCP home ranges of red-backed voles in my study (0.012-0.2 ha) were within the range of home range size reported for *Clethrionomys* (0.09 to 0.5 ha, Bondrup-Nielsen and Karlsson 1985). They were smaller than Bondrup-Nielsen's (1986) estimate of 0.26 (deciduous habitat) to 0.33 ha (coniferous habitat), and Gillis and Nams' (1998) estimate of a 65-m-diameter home range (0.44 ha), but were similar to Tallmon and Mill's (1994) estimates of 0.06 to 0.30 ha (home ranges of the two females they radio-tracked were 0.06 and 0.09 ha). The kernel estimates illustrated the well-defined nest sites of each vole, where they spent the majority of their time. Voles on *high* and *low* treatment areas had similar home range sizes, which suggests that the voles were satisfying their requirements within a similar sized area. This result is seemingly contrary to my second hypothesis that home ranges would be smaller on *low* treatment areas because of the lower quality habitat (Bondrup-Nielsen (1984, 1985, 1986). My hypothesis was based on the assumption that voles on *low* treatment areas would have little access to downed wood. This was not the case, however, as the voles associated with the few remaining pieces of downed wood on the sampling grid, or moved slightly off the area where they associated with downed wood.

6.4.2 Fine-scale habitat associations

The identification of important habitat components at the fine scale was more difficult than at the home range scale. This was likely due to the fact that voles already showed strong selection for habitat components at the home range scale.

All voles had nest sites in logs or stumps, supporting my third hypothesis that voles would associate with downed wood at the microhabitat scale. Gunderson (1959) also reported a positive association between *C. gapperi* and decayed stumps. I found that voles often used

decayed stumps; however, the patchy distribution of stumps on the landscape made this relationship difficult to detect statistically.

The two methods I used to measure fine-scale habitat selection identified different habitat variables, which probably reflected the different variables included in each analysis as well as the resolution of habitat measures. Plot data included more information on habitat gradients, including the percent ground cover of a number of habitat components, and distance to the closest pieces of downed wood and its attributes. Data from 17 voles were pooled by treatment type, which obscured the relationship of individual voles with habitats in their home range. In contrast, the map data emphasized categories, and included more general information on the number of pieces of all the downed wood within each cell, along with cover classes. Map data were analyzed separately for each of the 10 voles. Although the map data were collected at a finer spatial scale than the plot data, the level of detail on specific habitat elements was lower than the plot data. Still, both data sets revealed a generally positive response by voles to greater amounts of downed wood and other forms of cover.

The analysis of plot data indicated that vole locations were closer to logs than random points, and that the closest downed wood piece was larger near vole locations than random points. Shrub cover was not identified as an important component on *high* areas; however, voles on *low* treatment areas were associated with areas with less shrub cover. Finally, vole locations were positively associated with forest floor attributes such as litter depth and cover.

The analysis of the map data suggested that the relationship between voles and their habitat is complex; habitat components appear to be complementary. Locations of all of the voles were positively associated with some form of cover, usually downed wood, and also the composites dense cover, minimum cover, and shrub cover. Two voles avoided grassy areas. A simple t-test

indicated that voles were more likely to be located in cells with downed wood >10 cm in diameter than random cells. This result is similar in direction, if not scale, to Tallmon and Mills' (1994) study that reported that 98% of telemetry locations of red-backed voles were under logs, even though logs covered only 7% of the area. My analyses of map data did not indicate this relationship clearly, and collecting downed wood data in diameter classes might have obscured the relationship.

The association of voles with downed wood at fine scales likely reflects their use of downed wood for foraging and travelling. Large pieces of downed wood overhang the ground and provide covered travel routes, which are preferred by California red-backed voles (*C. californicus*, Hayes and Cross 1987). Other researchers have either not found a relationship between abundance of voles and downed wood diameter (Nordyke and Buskirk 1991), or have reported a negative relationship between abundance and downed wood >10 cm in diameter (Orrock *et al.* 2000). My analyses suggest that larger logs are important structures. On *low* treatment areas, the height of downed wood off the ground was also identified as an important component for microhabitat associations. The suspension of downed wood slightly off the ground would permit voles to run underneath, creating a protected travel route, similar to the overhang from a large log (Hayes and Cross 1987). Height, as long as the piece was not too far off the ground, likely increases the usefulness of cover provided by downed wood, especially for smaller pieces.

The decay class of downed wood was generally not identified as a component selected for by voles in my study. Lightly to moderately decayed downed wood (classes 1-3) would provide travel corridors for voles (Hayes and Cross 1987), whereas heavily decayed downed wood would be useful for travelling in tunnels, nesting, and foraging (Harmon *et al.* 1986). Because

downed wood of different decay classes serves different functions for voles, identifying preferences for specific decay classes is difficult. A more useful analysis would relate vole activities to particular decay classes. Heavily decayed logs, in particular, are thought to influence red-backed vole activity; however, evidence is contradictory. Although Tallmon and Mills (1994) reported that *C. californicus* was closely related to decayed logs, Hayes and Cross (1987) found no relationship between capture success of *C. californicus* and decay class of log. Bowman *et al.* (2000) reported a positive correlation between capture success and abundance of red-backed voles in managed forests, and the abundance of decay class 5 logs, similar to the relationship between increasing abundance and decay class reported by Nordyke and Buskirk (1991).

The primary function ascribed to decayed wood for red-backed voles is foraging habitat. Downed wood, which can hold up to twice its weight in water (Amaranthus *et al.* 1989), is an important moisture reservoir in forests (especially in the dry interior). Epigeous fungi (truffles) tend to be more abundant close to decayed downed wood (Clarkson and Mills 1994, Waters *et al.* 1997, Carey *et al.* 1999), and can be up to ten times more abundant in decayed wood than adjacent soil. Decayed downed wood is a useful landmark for finding truffles for mycophagist small mammals (Pyare and Longland 2001). Truffles can form up to 90% of the diet of *C. californicus*; however, although *C. gapperi* do eat fungi (Rhoades 1986), they do not appear to rely on truffles to the same extent (Gunther *et al.* 1983, Carey and Johnson 1995).

The removal of downed wood from *low* sites likely reduced the availability of associated fungi and lichens, at least temporarily (especially on decayed logs, Clarkson and Mills 1994, *c.f.* Luoma 1988). However, downed wood removals might not have reduced resources below a critical level. I did not remove decay class 5 material from the treatment area. Instead, I

destroyed the structure of the log to make it unusable for travelling by voles and to disrupt the log microclimate, which is assumed to influence the presence of mycorrhizal fungi (Amaranthus *et al.* 1994). The remaining debris (small chunks) was scattered in the surrounding area. This might temporarily have disrupted the presence of mycorrhizal fungi, which tend to resprout in the same location in successive years (Pyare and Longland 2001). The treatments likely did not result in the complete removal of fungi from the area because Hagerman *et al.* (2000) reported that, at the Opax study area, at least 11 forest understorey plant species act as ectomycorrhizal refugia, which would ensure that fungi remained in the area.

Lichens also comprise a large proportion of the diet of red-backed voles (Ure and Maser 1982, Gunther *et al.* 1983). Red-backed voles that I observed foraging ate primarily lichens associated with downed trees and branches. Removing the downed wood would have resulted in a temporary decrease in the amount of lichens available to voles on large branches of decay class 1 and 2 logs or trees. Long branches, where most arboreal lichens were found, were removed from *low* treatment areas along with logs. Although a few bunches of lichens likely fell off downed wood, the majority were likely removed along with the downed wood. Therefore, the abundance of lichens was likely lower post-treatment. However, voles responded to downed wood removal by selecting home range areas with abundant downed wood, where lichens would continue to be abundant.

Previous research on the relationship between downed wood and red-backed voles indicated that although downed wood was likely an important habitat component for these voles, it was not a robust predictor of vole presence or abundance. Ure and Maser (1982) captured California red-backed voles in areas with relatively few logs. Rosenberg *et al.* (1994) reported small populations of California red-backed voles in areas with abundant downed wood and suggested

that other forest floor components may be more important in determining red-backed vole abundance, such as deep litter layer and quality (decay class, length, diameter) of downed wood. Other researchers have also reported a positive relationship between red-backed voles and forest floor characteristics (Rosenberg *et al.* 1994, Carey and Johnson 1995). My analyses of plot data also identified depth and extent of the moss and litter layers as important habitat components. I did not record data on litter layer attributes for map data, but I did record moss cover class. A deep litter or moss layer is likely associated with greater foraging opportunities (Maser 1981). Two voles in my study were negatively associated with grassy areas, a relationship also reported by Corn *et al.* (1988). Grassy areas at Opax generally were more open, without other forms of cover, which was probably why voles avoided them.

Shrub cover also might influence vole abundance (Nordyke and Buskirk 1991, Rosenberg *et al.* 1994, Carey and Johnson 1995). Both downed wood and understorey vegetation have been identified as important, and complementary sources of cover for small mammals (Barnum *et al.* 1992). Results from my study of red-backed voles and downed wood at the population level (Chapter 5) suggested that in moist forests with abundant shrub cover, downed wood might not be necessary to maintain red-backed voles. Walters (1991) reported that red-backed vole abundance was similar on high-elevation old-growth forests and older clear-cuts (15 years old) where there was dense vegetation ground cover. Moses and Boutin (2001) suggested that retention of some canopy cover and the growth of vegetation post-harvest ameliorated effects of clear-cutting on red-backed voles. Carey and Johnson (1995) reported that downed wood and shrub cover together accounted for 77% of variability in population size of red-backed voles in managed stands. Shrub cover can provide effective protection from predators (Longland and Price 1991), and can favourably modify the microenvironment for red-backed voles (Martell

1983). In my study, red-backed vole locations were negatively associated with shrub cover at the home range scale, and also at the microhabitat scale on *low* areas, which was surprising. These relationships likely reflected the weak negative correlation between shrub cover and downed wood abundance and quality characteristics on the area. Where shrub cover was higher, the amount of downed wood tended to be lower, and the diameter and length of pieces that were present tended to be smaller. The map data indicated that there was some degree of complementarity among habitat components. Although four voles were positively associated with various downed wood size classes, and only one with shrub cover, an additional three voles were positively associated with the composite cover variables (downed wood and shrub and herb cover). Further examination of the data for these voles indicated that downed wood was the major form of cover in the composite cover variables. As well, for the vole where locations were positively associated with shrub cover, 79% of vole locations in cells with shrub cover also had downed wood, whereas only 47% of random locations in cells with shrub cover also contained downed wood. Thus, on my study area, voles selected areas with downed wood, which generally were in areas with less shrub cover. However, in areas where shrub and downed wood cover co-occur, voles associate with these areas of composite cover, likely because of the presence of downed wood. This suggests that downed wood is not a substitutable habitat component for red-backed voles at Opax.

It is clear that on my study area, downed wood fulfilled an important role for red-backed voles that was not easily replaceable. All of the voles' nests were in or under logs or stumps. Voles used downed wood extensively while they were travelling (*pers. obs.*), and both their home ranges and microhabitat use within home ranges was closely associated with downed wood. Similar to the suggestion by Carey and Johnson (1995), downed wood in these dry

forests probably provides an important moisture reservoir associated with mycorrhizal fungi and lichens.

6.5 Conclusions and Management Implications

My study confirms that downed wood is an important habitat component for the southern red-backed vole in the dry interior forest of British Columbia. Voles showed the strongest habitat selection at the home range scale, selecting home ranges within forested stands with substantially greater amounts of downed wood than was generally available. This relationship held even for voles in the control areas, where downed wood was not manipulated. They also preferentially used areas within their home ranges with more downed wood, to the extent of not utilizing other potentially useful cover components such as shrubs if downed wood was scarce. Voles on areas where downed wood was removed did not use other habitat components to satisfy their requirements; instead their home ranges were located in areas where downed wood was available.

These data suggest that the potential long-term consequences of intensive forest management as described by Angelstam (1997) could be severe, especially in dry, warm forests. In areas with widespread loss of downed wood, voles would be unable to respond by moving to areas of more abundant wood, as they did in this study.

Downed wood was naturally quite sparse in these dry Douglas-fir forests. In these forests where downed wood piece size is rarely >20 cm in diameter, and decay rates are relatively high (Feller 1997), retaining downed wood, especially large pieces, on harvested areas will provide downed wood to red-backed voles through older seral stages. During salvage logging operations of fire- or bark beetle-killed stands, retain large logs (if possible), and snags, which will eventually become downed wood, in the area. Special emphasis should be placed on retaining

pieces that are not fully charred, which will decrease their usefulness to voles. Scraping the bark off large logs before they are left on the area will limit their usefulness as bark beetle habitat. Although it will not be possible to do this everywhere, retaining even a few large logs that would normally be removed from the area because of the threat of bark beetle attack would be a valuable addition to the area.

Vole home ranges were in areas with denser canopy cover, and vole locations were associated with components such as greater litter cover and moss cover, that are suggestive of a diverse, well-developed forest floor. The importance of these attributes to red-backed voles suggests that forest management that removes or reduces the forest canopy and disturbs the forest floor might negatively affect voles. Previous research suggested that red-backed voles, at least initially, tolerate some canopy removal with light-entry harvest systems such as shelterwood or light partial-cutting (Martell 1983, Von Treba *et al.* 1998), but decline on more intensively harvested areas (seed-tree silvicultural system, Sullivan *et al.* 2000). A concurrent study on the effect of different silvicultural treatments in dry Douglas-fir forests at the Opax study area suggested that limited removal of the forest canopy in this ecosystem (up to 50% volume removal with a uniform partial-cut) did not negatively impact red-backed vole abundance three years post-harvest (Klenner 1998). Including partial-harvesting systems over the managed landscape will ensure that some large trees will exist in the area, which will potentially provide large downed wood to the area. When the area is harvested, as much downed wood as possible should be retained on site to provide habitat for red-backed voles. Data from Chapter 5 indicated that retention of downed wood on harvested areas was favourable for red-backed voles immediately post-harvest in this system, and that voles were negatively affected by the reduction of downed wood volumes on forested areas by as little as

50%. Retaining abundant downed wood post-harvest will ensure that downed wood remains in later seral forested stands, where it continues to be an important habitat component for red-backed voles. Data from the population-level study of red-backed voles (Chapter 5) suggested that at least 10% ground cover by downed wood ≥ 7.5 cm in diameter should be maintained post-harvest, and that volumes on forested areas should be $>80 \text{ m}^3/\text{ha}$.

Chapter 7. Conclusions and Management Implications

Downed wood is an integral component of the forest environment, providing a substrate for plants and animals, nutrients to the environment, and an important legacy across forest seral stages (Thomas 1979, Maser and Trappe 1984, Harmon *et al.* 1986, Bunnell *et al.* 1999, Wilson and Carey 2000). Downed wood is an important reservoir of nutrients and moisture, and central to energy flow and nutrient cycling in forest ecosystems (Maser *et al.* 1979, Harmon *et al.* 1986, Amaranthus *et al.* 1994, Bunnell *et al.* 1999). It provides a necessary substrate for many species of microbes, fungi, plants, as well as invertebrate and vertebrate species (Maser *et al.* 1979, Maser and Trappe 1984, Harmon *et al.* 1986), and an important legacy on the forest floor connecting stands through time.

Downed wood has long been proposed as an important, even critical, habitat component for some species of small mammals (Tevis 1956, Carey and Johnson 1995), but the evidence so far has been equivocal (Mills 1995, Loeb 1999, Moses and Boutin 2001). My study encompassed two very different ecosystems, two seral stages, and a range in the amount of downed wood far greater than typically found at either study area. This provided me with the unique opportunity to study the response of a select group of small mammal species with downed wood across a wide range of conditions. My results suggest that:

- 1) Downed wood in warm, dry ecosystems appears to be particularly important for the southern red-backed vole, but perhaps less important in moist environments with abundant alternate cover

Red-backed voles on forested areas were associated with downed wood at the low-elevation dry site, but not at the high elevation site. The relatively low abundance of downed wood on dry forested sites in this study likely increases the importance of downed wood for voles as cover

and as a moisture reservoir. Downed wood could potentially be a limiting factor for red-backed voles in these dry forests. Carey and Johnson (1995) suggested that *C. californicus*, which lives on drier forests to the south, might be more closely tied to downed wood than *C. gapperi* because of the importance of downed wood in dry forests as a moisture reservoir. My research suggests that this relationship may be more general. Downed wood might not have been necessary to maintain red-backed vole populations on forested areas at the higher and wetter Sicamous site. I was unable to determine if voles were accessing downed wood outside the treatment area, which would have reduced the treatment effect, and hampered my ability to detect a response. Therefore, additional research (addressed in Chapter 5) on the relationship between red-backed voles and downed wood in moist ecosystems is required to more fully address this question.

2) Red-backed voles appear to have different minimum thresholds of response to downed wood and vegetation in different ecosystems

Retaining downed wood on Opax clear-cuts helped to mitigate the initial effects of clear-cutting on red-backed voles (even while vegetation was sparse on clear-cuts immediately post-harvest); however, it did not serve a similar function at Sicamous, where clear-cuts remained sparsely vegetated throughout the study. This suggests that at low elevations, the retention of downed wood is sufficient to mitigate some of the initial effects of clear-cutting, but at higher elevations, voles may require a minimum level of ground cover from vegetation before they increase in abundance on an area. Once minimum requirements for voles to become abundant are met, voles might respond to the abundance of downed wood, as at Opax. Further research on this question is required (addressed in Chapter 5).

3) Meadow voles appear to have different thresholds of response to different types of cover

Previous research suggested that *Microtus* require $\geq 30\%$ cover in the grass and herb layer before voles will become abundant on an area (Getz 1985, Adler and Wilson 1989, Kirkland 1990, Getz *et al.* 2001). My study suggests that meadow voles also benefit from shrub cover up to a threshold of 20-25%, once requirements for herb and grass cover are met.

- 4) Deer mice behaved as habitat generalists in my study, as expected; however, in cooler, moister environments, such as a high-elevation site with short growing seasons and heavy snow cover through much of the year, deer mice might require a higher amount of vegetation cover to become abundant on clear-cuts

Deer mice at the low-elevation study area became abundant on clear-cuts, but failed to increase with clear-cutting on the high-elevation site. The high-elevation site had up to three to four times as much downed wood on clear-cuts as at Opax, but very low ground cover by vegetation ($< 20\%$ shrub cover, and $< 30\%$ herb cover compared to $> 30\%$ shrub cover and $> 60\%$ herb cover at Opax). These data suggest that deer mice in high elevation systems require some threshold amount of ground cover by vegetation above that available at Sicamous. Once deer mice become more abundant on the area, downed wood might be an important habitat component for mice, but further research is required (addressed in Chapter 3).

- 5) Downed wood may be an important habitat component for long-tailed voles regardless of the abundance of vegetation cover

My data indicated that long-tailed vole density in the sparsely vegetated high elevation study area was correlated with the number of pieces of downed wood on an area. This relationship was also reported by Van Horne (1982) on well-vegetated older openings, so the relationship that I observed may not exist solely because of lack of ground cover from vegetation.

- 6) Downed wood should be maintained on harvested areas

Recommendations for the minimum amount of downed wood that should be maintained on harvested areas varied across ecosystems. Naturally occurring levels of downed wood were up to four times higher at Sicamous than Opax and recommendations for one area are not suitable for another. I identified one species of small mammal at each study area (red-backed voles at Opax, and long-tailed voles at Sicamous) whose population dynamics were related to the abundance of downed wood. Population dynamics of deer mice and meadow voles appeared to be more closely related to vegetation patterns than to the abundance of downed wood. Based on patterns in population dynamics of red-backed and long-tailed voles I recommend:

- a) At least 10% ground cover by downed wood ≥ 7.5 cm in diameter (>80 m³/ha) be maintained on harvested sites at the Opax study area;
- b) That downed wood volumes of at least 80 m³/ha be maintained on forested areas at the Opax study area; and,
- c) At least 15-20% ground cover by downed wood ≥ 7.5 cm in diameter (>300 m³/ha) be maintained on harvested sites at the Sicamous study area.

Trees should be de-limbed on site, and woody debris spread over the area. Downed wood should not be piled and burned. There is no evidence that leaving large volumes of downed wood negatively affects small mammals. In fact, the consequences of reduced downed wood input during harvesting include possible reduced site productivity (Harmon *et al.* 1986) and reductions in the quantity and changes in the characteristics of downed wood in future rotations (Angelstam 1997). The consequences of this are unknown, but would likely affect every aspect of the forest ecosystem from the presence of soil microbes, to the presence of invertebrates, and plant and fungi growth. These changes will negatively affect small mammals and ultimately those species that rely on small mammals as a food source. During stand management (spacing

etc.) or partial-cutting, additional downed wood should be added to the system to ensure that the amount of ground covered by downed wood remains higher than the minimum levels outlined above.

Thus, the results of my study suggest that both downed wood and vegetation are important habitat components for many forest-dwelling small mammals, but the strength of the relationship is influenced by the ecosystem and the availability of other habitat components. Consequently, it is difficult to identify the various contributions of potentially substitutable resources.

Future research on the relationship of small mammals with habitat components, or the response of small mammals to changes in the structure of their habitat should be explicit about the conditions being examined. It is possible that some of the contradictory results that have been reported on habitat relationships of small mammals in the past were merely descriptions of different aspects of the relationship. Kirkland (1990), who examined patterns in the response of small mammal species to clear-cutting, and Lautenschlager (1993), who reviewed the literature on the response of small mammals to herbicide treatments, make it clear that the same management activities (clear-cutting, herbicide treatment) can have very different outcomes depending on the species, ecosystem, and the intensity of the treatment applied. To facilitate the identification of important minimum requirements and the potential for substitution among habitat components, future research should provide information on the abundance of important habitat components, such as downed wood and vegetation.

In the preceding chapters I made recommendations for forest management and future research for deer mice, meadow voles, long-tailed voles, and red-backed voles. Management recommendations varied for different species and different ecosystems. Developing general

management recommendations for large areas is difficult because the same type of harvest treatment will most likely affect each group differently, and the response will likely vary in different ecosystems. Developing and implementing management recommendations becomes even more difficult if the rarer species known to occur on the site (for example heather voles, jumping mice, shrews, bog lemmings, and weasels, to name but a few) are considered.

Focusing on species most likely to be negatively affected by forest management over the longer-term simplifies the task somewhat. Retention of old seral structures and habitat heterogeneity in managed stands is currently the focus of much research. However, even the current, relatively focused emphasis on the retention of old seral structures (such as a layered canopy, snags, downed wood) in managed stands becomes complicated when different methods used to attain this goal effect very different results (Wilson and Carey 2000).

All of the species of small mammals that I studied appeared to show a response to habitat components that are typically patchy within forest stands (downed wood, shrubs, and forest openings). Little is known about the ability of small mammals to move across the landscape to associate with novel habitat patches. Gillis and Nams (1998) suggest that distances as little as 60-70 m between habitat patches could isolate red-backed vole populations. Deer mice and meadow voles appear better able to find and exploit small habitat patches (as in my study). My study was not designed to address the challenges of maintaining habitat heterogeneity in the environment, or questions of scale. My study, however, does illustrate the difficulties of trying to determine the "best" harvesting treatment that will retain small mammal biodiversity or biodiversity in general across the landscape.

Additional and longer-term research is required on the effects of alternative silvicultural systems on small mammals as well as other animals and habitat components. Long-term

research projects such as the Opax Mountain and the Sicamous Creek Silvicultural Systems projects will provide valuable information about a variety of harvesting techniques designed to mimic patterns of natural disturbance on the landscape.

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Appendix I

Appendix 1a. Mean habitat components (± 2 SE) for each clear-cut downed wood treatment area at the Opax Mountain study area.

	Downed wood treatment level, replicate								
	Low			Medium			High		
	Block E	Block J	Block M	Block E	Block J	Block M	Block E	Block J	Block M
% Mineral soil ¹	15.6 (3.6)	15.6 (4.8)	8.02 (2.8)	24.2 (8.2)	15.9 (3.2)	6.6 (2.2)	5.8 (1.6)	7.8 (4.8)	11.8 (4.0)
Moss depth (cm)	0.6 (0.1)	0.7 (0.1)	0.7 (0.1)	0.6 (0.1)	0.5 (0.1)	0.6 (0.1)	0.8 (0.2)	1.1 (0.3)	0.9 (0.1)
% Moss ¹	2.9 (1.0)	1.0 (0.6)	2.7 (1.0)	1.3 (1.2)	1.4 (0.6)	2.5 (1.2)	3.0 (1.6)	0.5 (0.4)	3.1 (1.6)
Litter depth (cm)	1.1 (0.2)	1.2 (0.2)	0.9 (0.1)	1.0 (0.1)	0.8 (0.1)	1.4 (0.2)	1.8 (0.1)	1.5 (0.2)	1.6 (0.3)
% Litter ¹	11.7 (2.6)	9.6 (1.8)	11.0 (2.8)	12.0 (4.0)	14.0 (4.4)	13.0 (3.8)	17.4 (4.0)	22.3 (5.8)	12.4 (3.6)
% Herb & grass ¹	74.1 (4.2)	67.1 (7.0)	82.1 (2.8)	59.5 (5.4)	69.3 (3.8)	71.6 (4.6)	68.0 (6.6)	60.7 (9.4)	72.4 (5.0)
% Shrubs <2 m tall ¹	37.5 (6.6)	17.3 (3.6)	44.0 (9.8)	27.9 (6.8)	21.5 (5.6)	49.6 (9.2)	43.4 (7.2)	23.0 (5.6)	33.8 (6.6)
% Shrubs ≥2 m tall ¹	0 (-)	0 (-)	0 (-)	0.1 (0.2)	0.0 (0.0)	2.2 (2.8)	0.9 (1.0)	0.1 (0.2)	0 (-)
Number pieces DW ²	1.3 (0.6)	0.9 (0.4)	0.6 (0.4)	6.8 (1.2)	5.4 (1.6)	8.2 (1.6)	7.5 (1.6)	13.7 (2.8)	4.9 (1.0)
DW diameter (cm) ²	13.9 (3.2)	11.2 (3.0)	10.9 (1.6)	13.3 (1.6)	11.3 (1.4)	12.5 (1.2)	16.5 (2.6)	13.6 (1.4)	12.0 (1.0)
DW length (m) ²	0.7 (0.2)	0.9 (0.2)	0.6 (0.2)	2.2 (0.4)	2.0 (0.4)	2.5 (0.2)	2.5 (0.4)	2.5 (0.4)	1.5 (0.2)
DW height (cm) ²	10.6 (2.2)	11.0 (2.6)	9.7 (2.2)	17.0 (1.8)	13.0 (2.0)	17.0 (2.0)	19.1 (2.4)	17.5 (1.8)	16.0 (2.0)
Number of stumps ³	6.1 (1.2)	7.0 (1.8)	6.9 (1.8)	7.3 (1.4)	7.8 (1.8)	5.9 (1.8)	6.3 (1.2)	4.0 (1.4)	7.3 (1.2)
DBH stumps (cm) ³	25.9 (5.4)	23.8 (3.2)	28.1 (5.2)	26.7 (3.8)	22.4 (5.0)	31.0 (4.6)	30.5 (3.8)	28.5 (5.8)	18.3 (3.4)
Height stumps (m) ³	0.3 (0.4)	0.3 (0.04)	0.3 (0.1)	0.3 (0.04)	0.2 (0.04)	0.3 (0.04)	0.3 (0.04)	0.3 (0.10)	0.3 (0.04)
% Protective cover ⁴	87.0 (3.0)	83.8 (3.8)	89.0 (3.2)	71.4 (3.8)	84.3 (3.8)	84.8 (3.4)	86.2 (3.2)	72.3 (8.0)	85.7 (4.2)

¹ % cover estimates

² DW = downed wood pieces ≥7.5 cm in diameter where they cross the transect

³ Trees ≥7.5 cm in diameter (diameter at breast height)

⁴ % protective cover was a visual estimation at each plot of the amount of ground covered by vegetation (including canopy cover) and downed wood

Appendix 1b. Mean habitat components (± 2 SE) for each forested downed wood treatment area at the Opax Mountain study area.

	Downed wood treatment level, replicate								
	Low			Medium			High		
	Block D	Block I	Block N	Block D	Block I	Block N	Block D	Block I	Block N
% Canopy ¹	17.1 (2.3)	14.5 (2.1)	11.7 (1.7)	13.9 (1.8)	14.5 (2.8)	14.4 (2.3)	15.2 (1.9)	14.3 (2.1)	15.0 (2.4)
% Mineral soil ¹	0.1 (0.2)	1.1 (0.0)	2.8 (3.4)	1.7 (0.6)	0.8 (2.3)	1.8 (0.1)	0.0 (1.8)	0.0 (2.7)	2.1 (2.1)
Moss depth (cm)	2.4 (0.6)	1.4 (0.4)	1.0 (0.4)	1.8 (0.2)	1.2 (0.3)	1.7 (0.4)	1.9 (0.5)	1.6 (0.1)	0.6 (0.3)
% Moss ¹	20.7 (10.0)	17.9 (8.1)	16.1 (6.9)	20.8 (4.9)	15.2 (5.3)	14.7 (2.9)	32.6 (4.2)	11.9 (5.3)	11.7 (9.7)
Litter depth (cm)	1.9 (0.4)	1.2 (0.2)	1.5 (0.3)	1.5 (0.2)	1.3 (0.3)	1.6 (0.4)	1.2 (0.4)	1.7 (0.1)	0.9 (0.3)
% Litter ¹	39.3 (10.3)	36.0 (7.4)	31.6 (7.4)	33.9 (6.5)	37.3 (6.5)	29.2 (4.9)	35.5 (6.8)	18.5 (6.1)	25.8 (3.9)
% Herb & grass ¹	44.3 (6.9)	58.2 (3.7)	50.3 (5.2)	62.1 (5.8)	54.9 (5.9)	50.6 (7.1)	64.3 (5.8)	65.2 (7.5)	61.6 (10.7)
% Shrubs <2 m tall ¹	38.4 (6.9)	38.1 (7.9)	43.1 (9.3)	35.3 (7.3)	31.8 (6.8)	34.2 (7.7)	41.0 (5.4)	37.9 (5.7)	20.2 (8.8)
% Shrubs $\geq$ 2 m tall ¹	21.9 (2.3)	14.8 (2.1)	2.9 (1.7)	10.8 (1.8)	10.2 (2.8)	11.2 (2.3)	27.8 (1.9)	14.7 (2.1)	20.8 (2.4)
Number pieces DW ²	3.2 (1.4)	3.3 (1.2)	2.1 (1.5)	4.1 (1.2)	4.5 (0.9)	3.6 (1.5)	4.2 (0.9)	6.1 (0.8)	3.5 (1.0)
DW diameter (cm) ²	15.3 (5.3)	15.0 (3.3)	17.1 (5.4)	20.6 (3.2)	16.6 (2.7)	17.7 (2.5)	18.9 (3.7)	18.7 (3.6)	17.1 (6.6)
DW length (m) ²	2.5 (1.6)	3.7 (1.1)	0.9 (0.7)	1.7 (1.1)	5.1 (1.7)	2.8 (1.0)	3.9 (0.8)	6.0 (1.4)	5.1 (0.7)
DW height (cm) ²	13.4 (7.1)	23.8 (3.9)	3.4 (4.1)	15.0 (6.1)	26.4 (10.3)	16.8 (4.9)	18.2 (5.2)	28.6 (3.4)	17.9 (2.6)
Number of trees ³	9.2 (1.9)	8.3 (2.5)	9.1 (5.2)	10.1 (1.7)	11.5 (2.3)	8.3 (2.3)	10 (1.5)	9.6 (1.9)	9.8 (2.3)
DBH trees (cm) ³	20.2 (4.4)	21.1 (8.8)	16.9 (4.6)	19.7 (4.1)	20.2 (2.9)	22.4 (3.8)	19.4 (2.7)	19.8 (3.2)	20.3 (2.5)
Height trees (m) ³	13.2 (2.5)	8.7 (2.1)	10.3 (2.9)	9.8 (1.2)	10.1 (1.3)	10.4 (1.3)	9.1 (1.6)	11.7 (1.4)	10.3 (1.1)
%Protective cover ⁴	72.6 (6.7)	78.3 (3.6)	74.2 (3.9)	79.8 (4.3)	76.9 (3.6)	75.7 (3.1)	81.7 (5.2)	86.9 (5.6)	77.8 (11.6)

¹ % cover estimates

² DW = downed wood pieces ≥ 7.5 cm in diameter where they cross the transect

³ Trees ≥ 7.5 cm in diameter (diameter at breast height)

⁴ % protective cover was a visual estimation at each plot of the amount of ground covered by vegetation (including canopy cover) and downed wood

Appendix 1c. Mean habitat components (± 2 SE) for each downed wood clear-cut treatment area at the Sicamous Creek study area.

	Downed wood treatment level, replicate								
	Low			Medium			High		
	Block A	Block B	Block C	Block A	Block B	Block C	Block A	Block B	Block C
% Mineral soil ¹	30.2 (10.2)	26.7 (5.6)	16.4 (5.2)	21.1 (6.0)	18.9 (5.0)	18.4 (5.8)	17.6 (4.4)	27.4 (4.8)	18.9 (5.8)
Moss depth (cm)	0.90 (0.02)	0.88 (0.14)	1.11 (0.26)	1.44 (0.22)	0.94 (0.18)	1.46 (0.30)	1.23 (0.16)	0.77 (0.16)	1.20 (0.34)
% Moss ¹	1.2 (0.6)	4.1 (1.6)	0.8 (0.6)	3.4 (3.0)	6.5 (3.8)	2.7 (2.0)	2.0 (1.0)	2.3 (1.6)	1.7 (1.0)
Litter depth (cm)	3.9 (0.8)	3.5 (0.4)	1.3 (1.8)	3.1 (0.4)	8.4 (2.6)	1.2 (3.4)	2.2 (1.2)	12.3 (0.2)	7.7 (2.6)
% Litter ¹	36.7 (6.6)	37.4 (4.4)	47.3 (6.4)	35.7 (7.8)	32.0 (6.2)	40.8 (4.6)	56.9 (7.4)	32.0 (5.2)	34.6 (7.2)
% Herb & grass ¹	25.3 (6.4)	35.6 (4.6)	13.8 (6.0)	31.8 (6.8)	31.8 (6.8)	32.1 (6.2)	25.2 (4.8)	29.2 (4.6)	16.8 (5.8)
% Shrubs <2 m tall ¹	15.7 (6.8)	18.2 (3.6)	16.7 (5.8)	19.1 (6.2)	22.3 (4.2)	11.8 (3.6)	13.8 (2.6)	15.3 (3.6)	11.8 (4.0)
% Shrubs ≥ 2 m tall ¹	0.1 (0.2)	0 (-)	0.4 (0.4)	0.3 (0.6)	0.0 (-)	0.3 (0.4)	0.0 (-)	0.1 (0.1)	0.18 (0.2)
Number pieces DW ²	5.4 (3.0)	4.2 (1.2)	2.3 (0.6)	10.2 (1.4)	9.7 (2.0)	10.4 (2.4)	14.3 (1.6)	8.8 (1.8)	13.8 (1.8)
DW diameter (cm) ²	17.1 (3.8)	14.1 (2.4)	15.3 (2.8)	19.0 (1.8)	17.3 (2.0)	19.4 (2.4)	22.5 (1.8)	20.3 (1.6)	18.5 (1.6)
DW length (m) ²	1.1 (0.4)	0.9 (0.2)	1.3 (0.8)	3.2 (0.6)	2.4 (0.6)	3.7 (1.0)	2.6 (0.4)	3.4 (0.8)	3.2 (0.4)
DW height (cm) ²	14.4 (4.6)	9.5 (1.4)	8.3 (2.4)	24.5 (3.2)	16.4 (2.6)	22.9 (4.0)	24.7 (4.4)	20.9 (3.4)	21.5 (2.6)
Number of stumps ³	3.6 (1.0)	5.6 (0.8)	5.1 (1.0)	5.7 (1.0)	4.8 (1.0)	8.2 (1.2)	5.2 (1.0)	4.8 (1.0)	6.1 (0.8)
DBH stumps (cm) ³	30.2 (5.6)	36.1 (4.0)	33.0 (1.8)	31.3 (2.4)	34.2 (3.4)	31.5 (2.6)	33.6 (4.4)	35.4 (4.4)	32.6 (2.6)
Height stumps (m) ³	0.57 (0.2)	0.42 (0.0)	0.79 (0.4)	0.54 (0.2)	0.47 (0.0)	0.87 (0.4)	0.56 (0.2)	0.48 (0.2)	0.46 (0.0)
% Protective cover ⁴	39.7 (5.4)	63.8 (5.0)	37.8 (8.2)	58.2 (7.8)	64.6 (5.6)	47.6 (8.0)	47.7 (4.2)	54.0 (6.8)	34.4 (7.0)

¹ % cover estimates

² DW = downed wood pieces ≥ 7.5 cm in diameter where they cross the transect

³ Trees ≥ 7.5 cm in diameter (diameter at breast height)

⁴ % protective cover was a visual estimation at each plot of the amount of ground covered by vegetation (including canopy cover) and downed wood

Appendix 1d. Mean habitat components (± 2 SE) for each downed wood forested treatment area at the Sicamous Creek study area.

	Downed wood treatment level, replicate								
	Low			Medium			High		
	Block A	Block B	Block C	Block A	Block B	Block C	Block A	Block B	Block C
% Canopy ¹	11.7 (1.9)	12.7 (2.2)	10.6 (1.8)	13.1 (1.8)	12.6 (1.5)	9.8 (1.8)	10.9 (2.0)	9.7 (1.7)	9.2 (1.9)
% Mineral soil ¹	0 (-)	0.1 (0.2)	0.4 (0.5)	0 (-)	0 (-)	0.2 (0.3)	0.1 (0.1)	0 (-)	0.8 (1.0)
Moss depth (cm)	1.2 (0.1)	1.2 (0.1)	0.9 (0.1)	1.4 (0.2)	1.2 (0.3)	1.1 (0.2)	1.0 (0.2)	1.3 (0.2)	0.8 (0.1)
% Moss ¹	53.5 (7.6)	62.4 (6.1)	32.3 (8.1)	47.0 (5.6)	58.5 (7.8)	38.2 (5.6)	77.2 (5.2)	78.8 (4.3)	49.4 (9.5)
Litter depth (cm)	1.8 (0.5)	1.8 (0.4)	1.3 (0.2)	1.5 (0.7)	1.7 (0.7)	1.7 (0.5)	0.6 (0.1)	0.6 (0.1)	0.9 (0.2)
% Litter ¹	54.8 (7.4)	58.0 (5.9)	56.1 (5.9)	18.8 (3.1)	13.9 (2.8)	21.8 (3.4)	44.5 (10.0)	40.6 (5.4)	29.8 (5.6)
% Herb & grass ¹	37.3 (5.6)	9.9 (5.7)	16.5 (4.1)	55.3 (6.1)	63.0 (5.1)	57.5 (5.4)	59.5 (4.6)	35.5 (5.8)	32.5 (7.8)
% Shrubs <2 m tall ¹	47.9 (5.1)	46.5 (6.3)	42.7 (5.9)	57.4 (4.1)	62.7 (5.9)	54.3 (5.1)	62.6 (5.9)	56.8 (5.6)	54.6 (5.2)
% Shrubs $\geq$ 2 m tall ¹	4.8 (2.0)	9.6 (2.3)	1.4 (0.8)	3.0 (1.1)	2.6 (0.7)	1.7 (0.5)	4.5 (1.6)	2.7 (1.1)	0.8 (0.5)
Number pieces DW ²	4.0 (1.3)	4.6 (0.9)	2.6 (0.6)	9.9 (1.3)	6.3 (0.8)	9.4 (1.4)	10.6 (1.6)	8.6 (1.6)	10.7 (1.4)
DW diameter (cm) ²	17.2 (3.2)	17.9 (2.6)	15.8 (3.1)	20.7 (1.6)	22.7 (1.8)	24.1 (2.4)	23.1 (1.9)	22.9 (2.5)	23.1 (1.8)
DW length (m) ²	1.4 (0.5)	1.4 (0.4)	3.3 (3.9)	7.2 (1.1)	7.0 (1.2)	7.5 (0.7)	5.3 (0.7)	6.7 (1.4)	6.5 (0.7)
DW height (cm) ²	12.7 (3.4)	9.6 (1.6)	8.0 (2.1)	30.8 (3.1)	25.9 (4.3)	26.8 (3.3)	28.8 (3.7)	23.1 (3.4)	26.5 (3.9)
Number of trees ³	12.4 (1.8)	18.3 (2.4)	8.4 (1.1)	12.5 (1.9)	10.0 (1.4)	5.9 (0.9)	9.6 (1.5)	9.7 (1.5)	6.5 (1.5)
DBH trees (cm) ³	25.1 (1.3)	19.8 (1.4)	28.4 (2.2)	24.3 (1.8)	23.9 (1.5)	29.0 (2.8)	22.8 (1.6)	24.7 (1.4)	28.9 (3.4)
Tree height (m) ³	10.0 (1.2)	10.8 (0.9)	12.4 (1.6)	15.0 (1.2)	14.6 (1.3)	15.1 (2.6)	13.9 (1.7)	14.1 (1.6)	12.0 (1.6)
% Protective cover ⁴	82.7 (3.5)	82.8 (2.7)	67.4 (6.3)	82.5 (4.2)	88.1 (3.9)	82.8 (4.2)	93.4 (2.6)	90.2 (2.2)	77.5 (4.2)

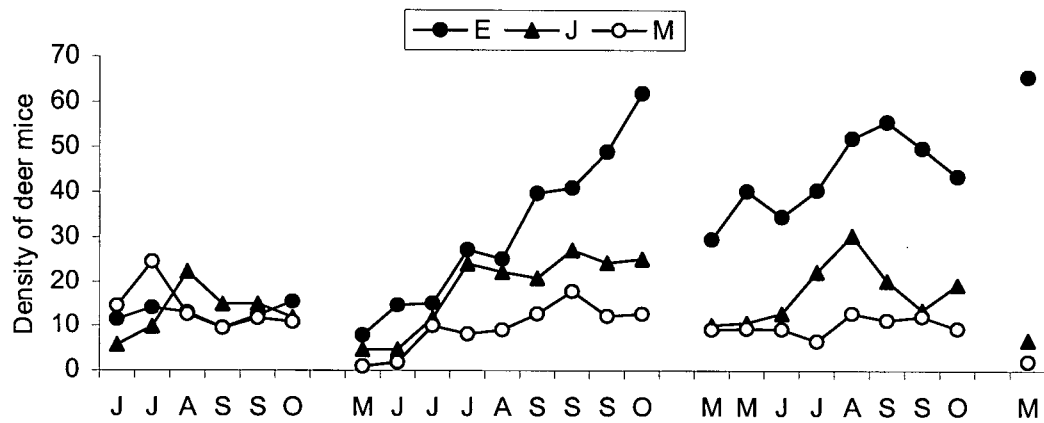
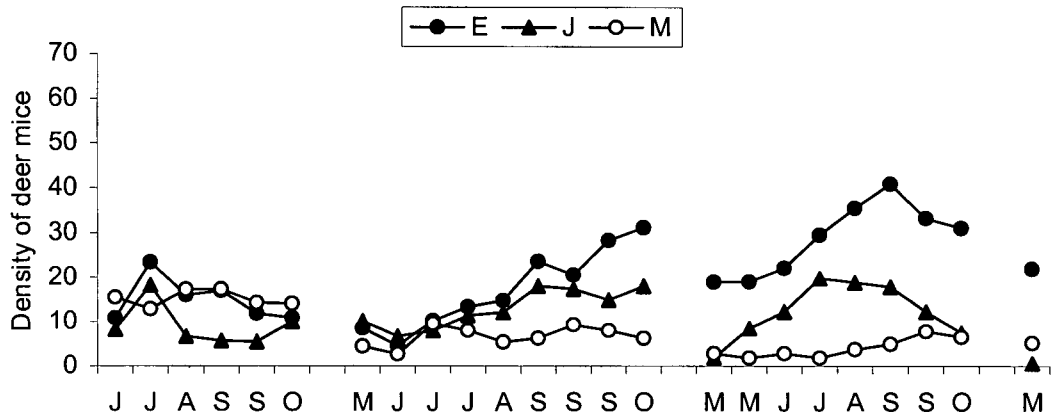
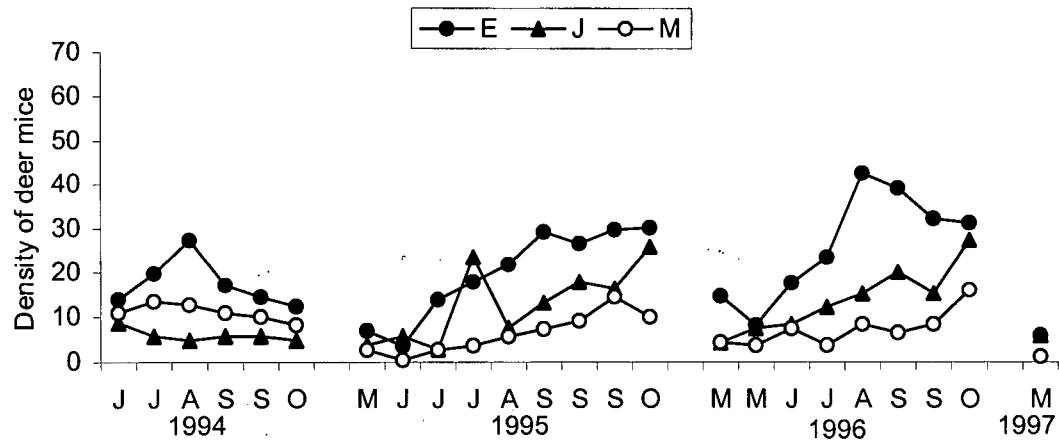
¹ % cover estimates

² DW = downed wood pieces ≥ 7.5 cm in diameter where they cross the transect

³ Trees ≥ 7.5 cm in diameter (diameter at breast height)

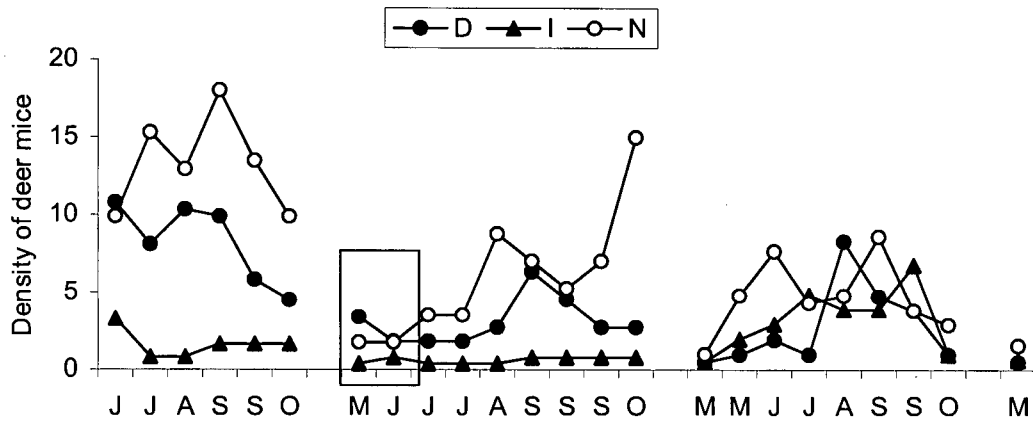
⁴ % protective cover was a visual estimation at each plot of the amount of ground covered by vegetation (including canopy cover) and downed wood

Appendix II

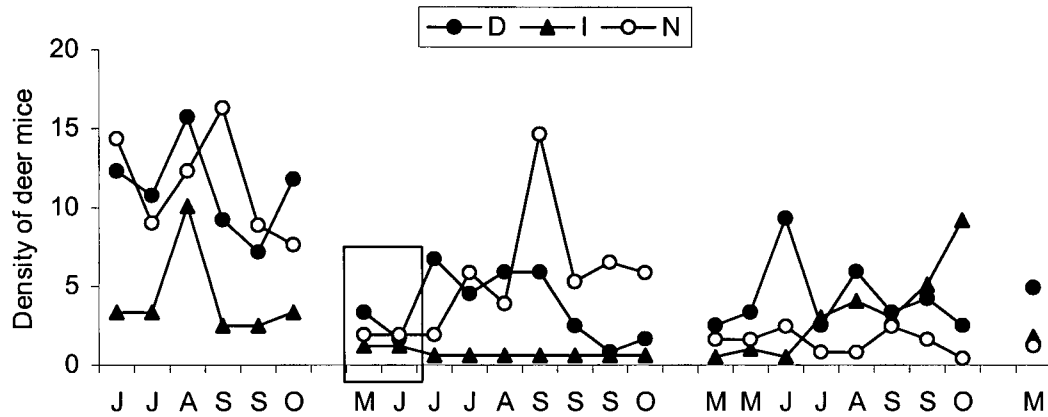
a) *Low*b) *Medium*c) *High*

Appendix 2a. Estimated density of deer mice on clear-cut sampling grids at Opax on a) *low*, b) *medium*, and c) *high* treatment areas for each replicate separately. Harvest and downed wood manipulations occurred in winter 1993/4 to spring 1994.

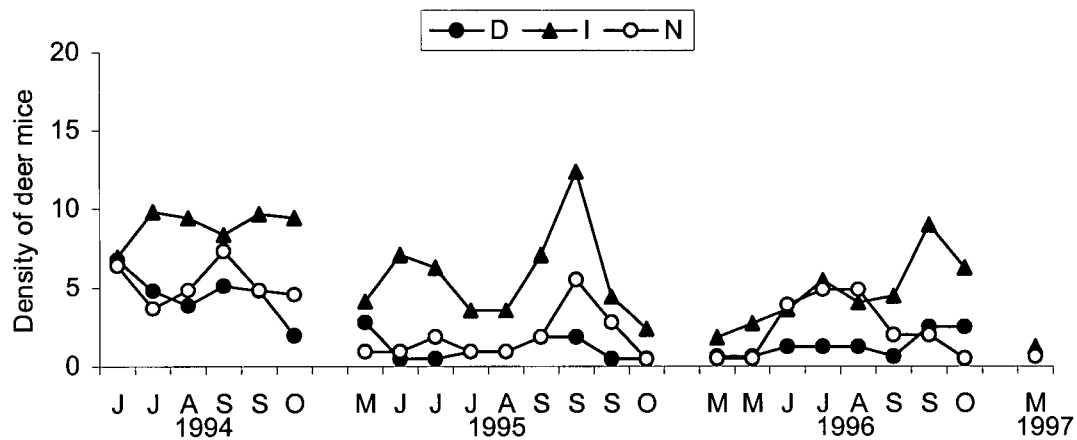
a) Low



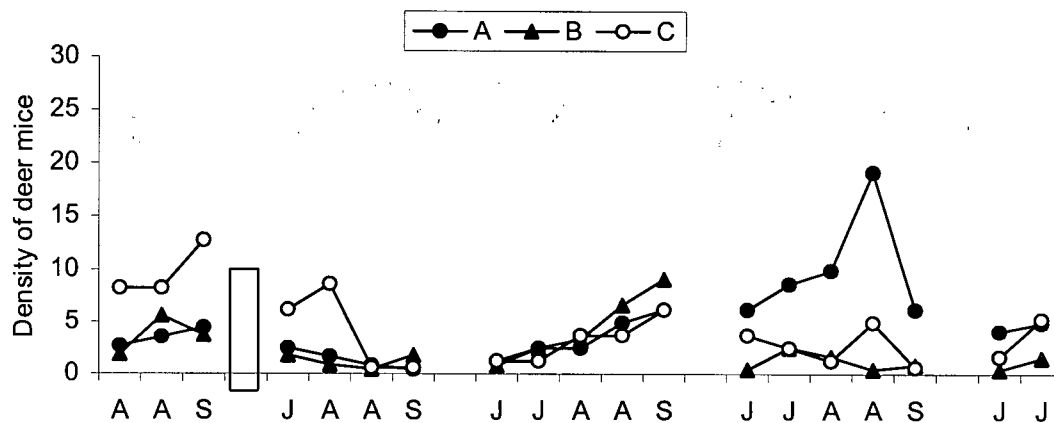
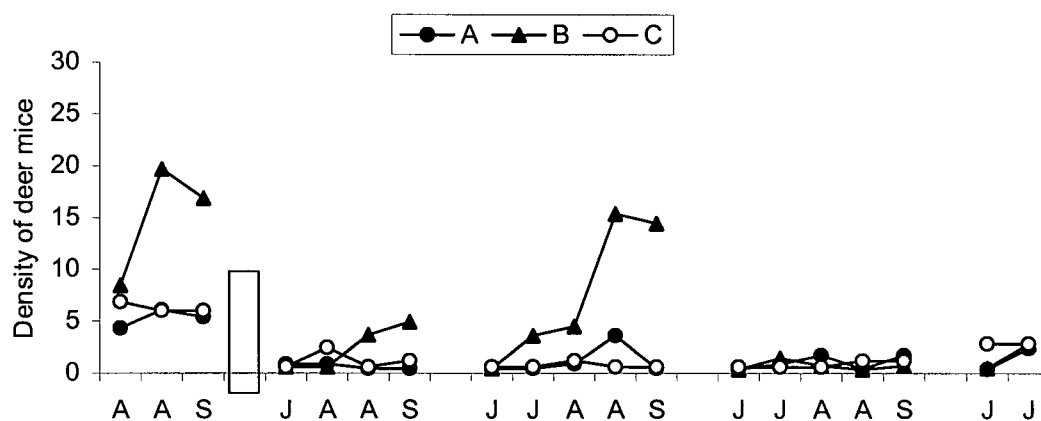
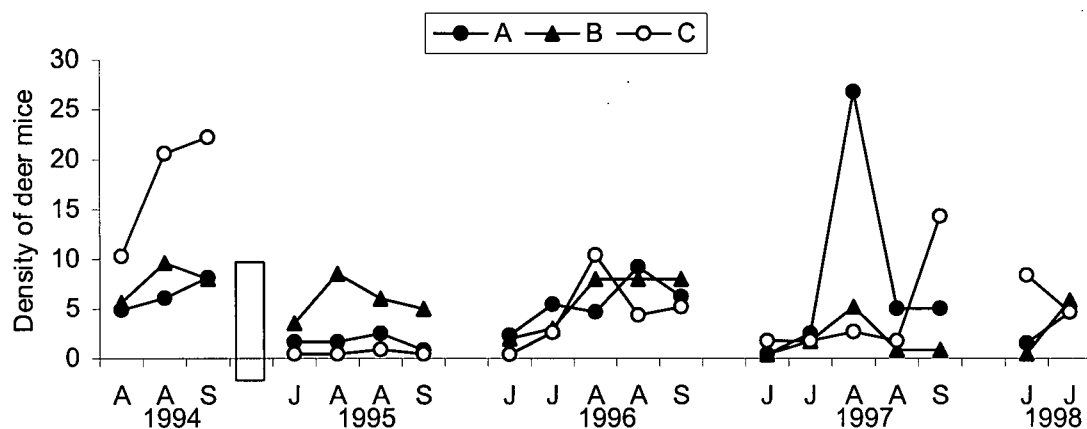
b) Medium



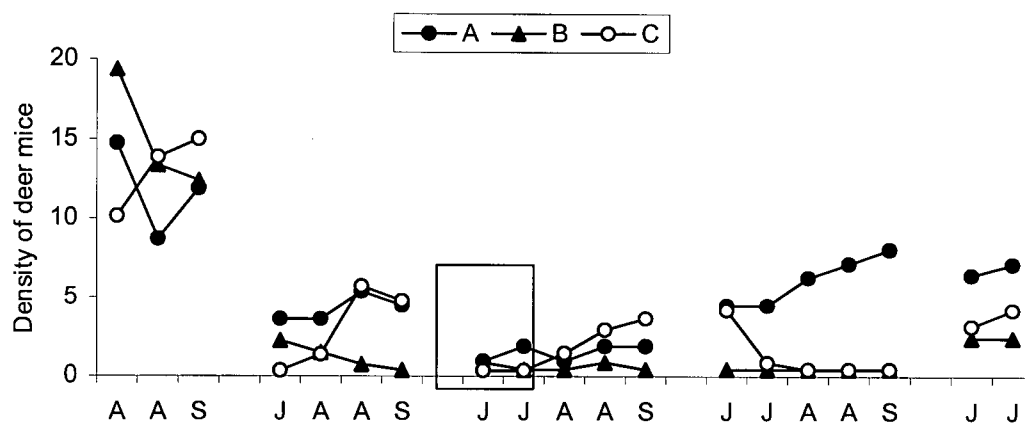
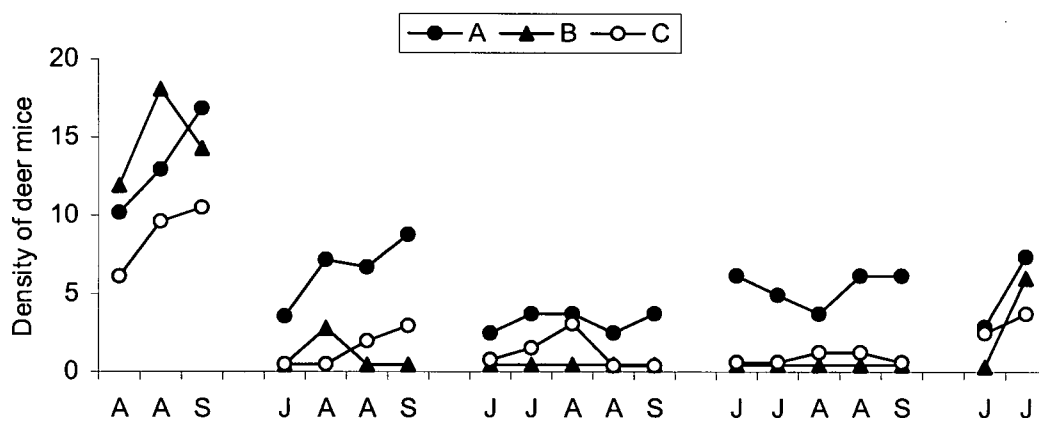
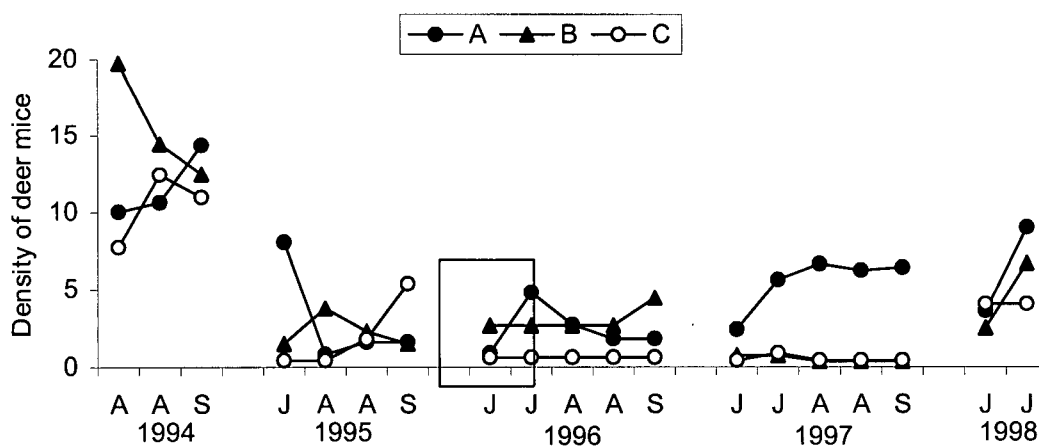
c) High



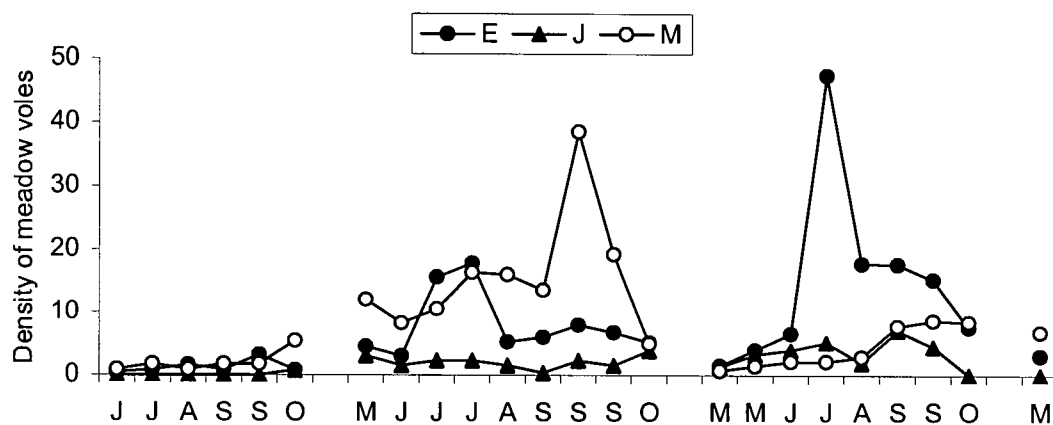
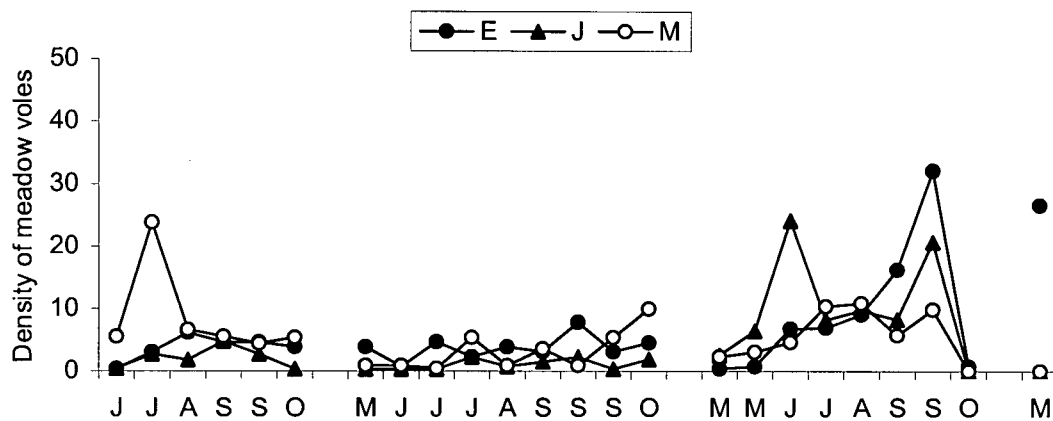
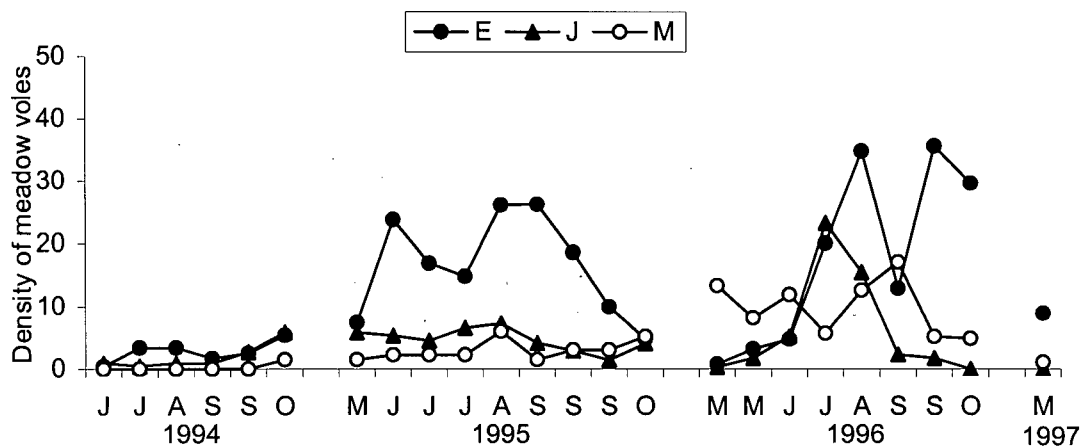
Appendix 2b. Estimated density of deer mice on forested sampling grids at Opax on a) *low*, b) *medium*, and c) *high* (control) treatment areas for each replicate individually. The outlined area indicates time during which downed wood was being manipulated on the treatment areas.

a) *Low*b) *Medium*c) *High*

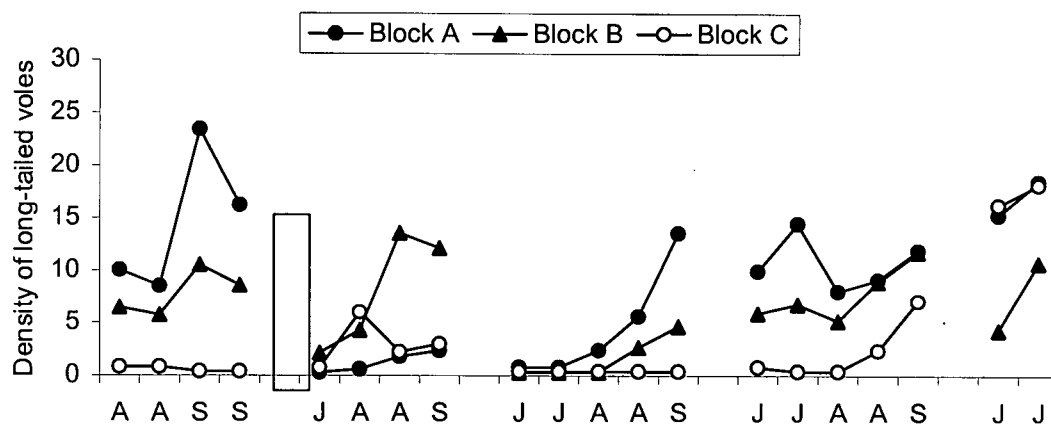
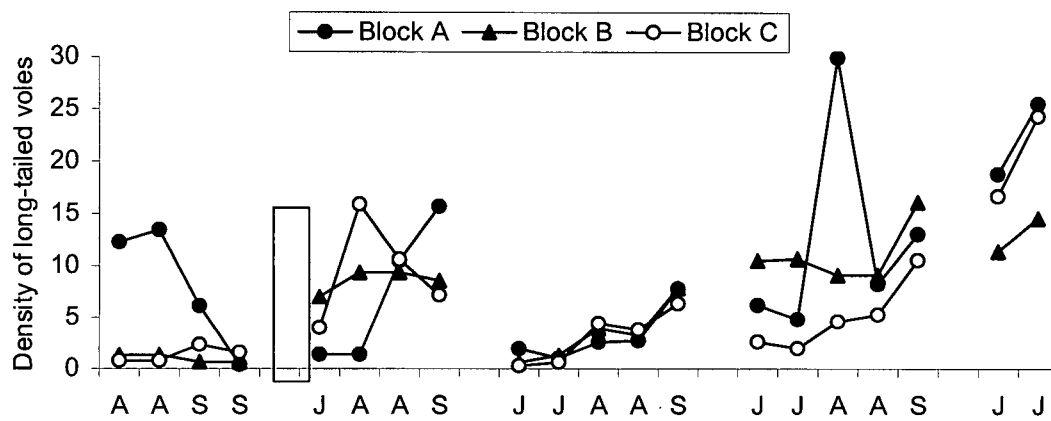
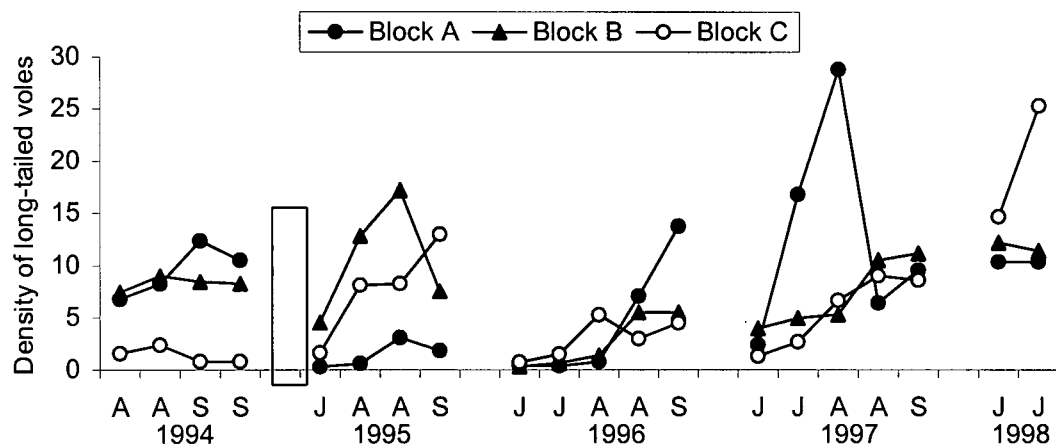
Appendix 2c. Estimated density of deer mice on clear-cut sampling grids at Sicamous on a) *low* b) *medium* and c) *high* treatment areas for each replicate separately. Downed wood was manipulated during harvesting in winter 1994/5 and spring 1995 (indicated by outlined area).

a) *Low*b) *Medium*c) *High*

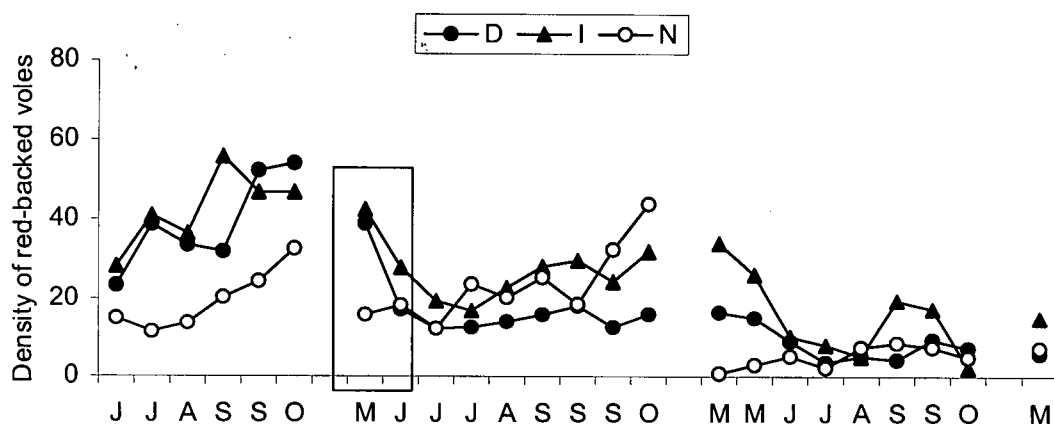
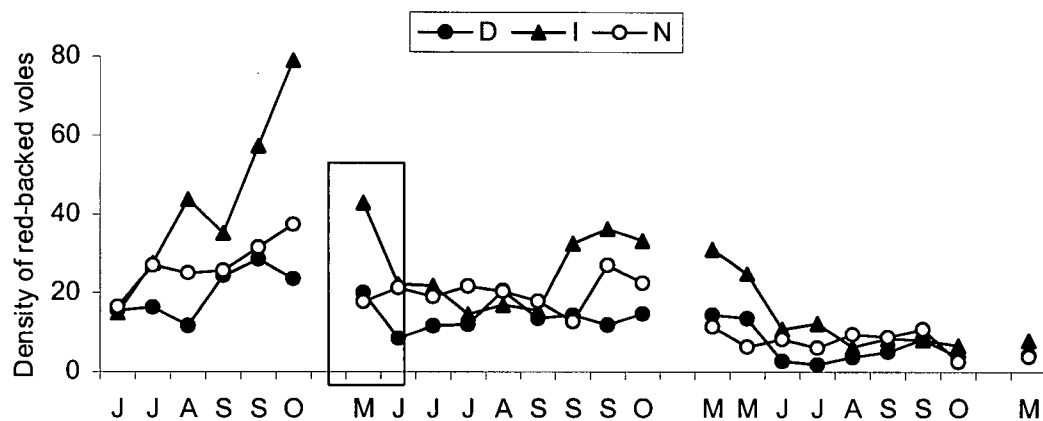
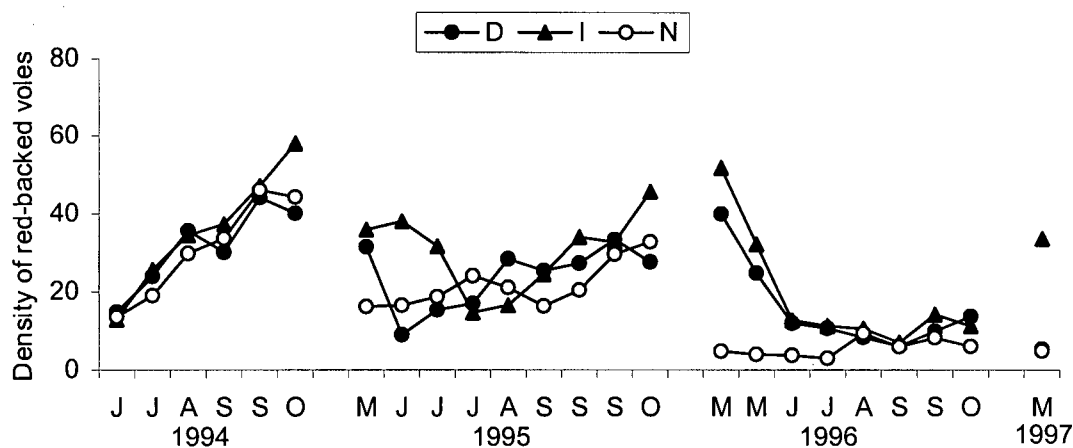
Appendix 2d. Estimated density of deer mice on forested sampling grids at Sicamous on a) *low* b) *medium* and c) *high* treatment areas for each replicate separately. Downed wood was manipulated in spring/summer 1996 (indicated by outlined area).

a) *Low*b) *Medium*c) *High*

Appendix 2e. Estimated density of meadow voles on clear-cut sampling grids at Opax on a) *low* b) *medium* and c) *high* treatment sites for each replicate separately. Downed wood was manipulated during harvesting in winter 1993-4, before trapping began on the site.

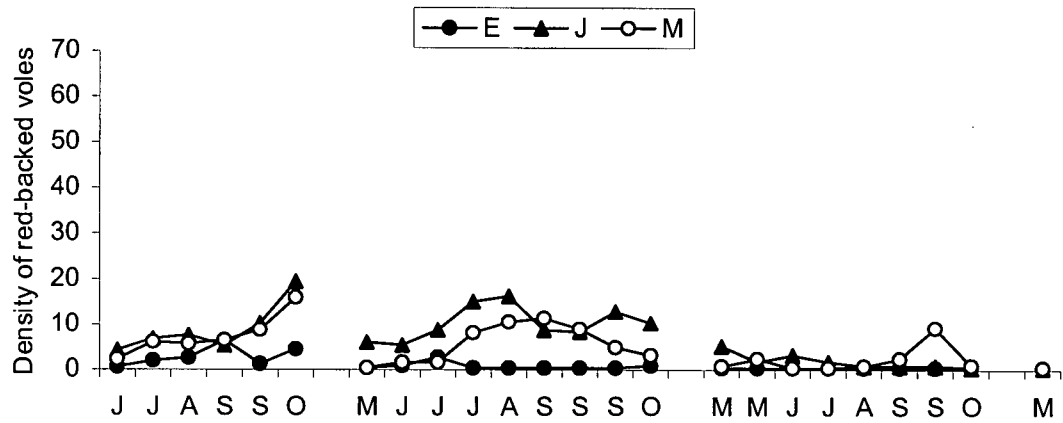
a) *Low*b) *Medium*c) *High*

Appendix 2f. Estimated density of long-tailed voles on clear-cut sampling grids at Sicamous on a) *low* b) *medium* and c) *high* treatment sites for each replicate separately. Downed wood was manipulated during harvesting in winter 1994-1995 and spring 1995 (indicated by outlined area).

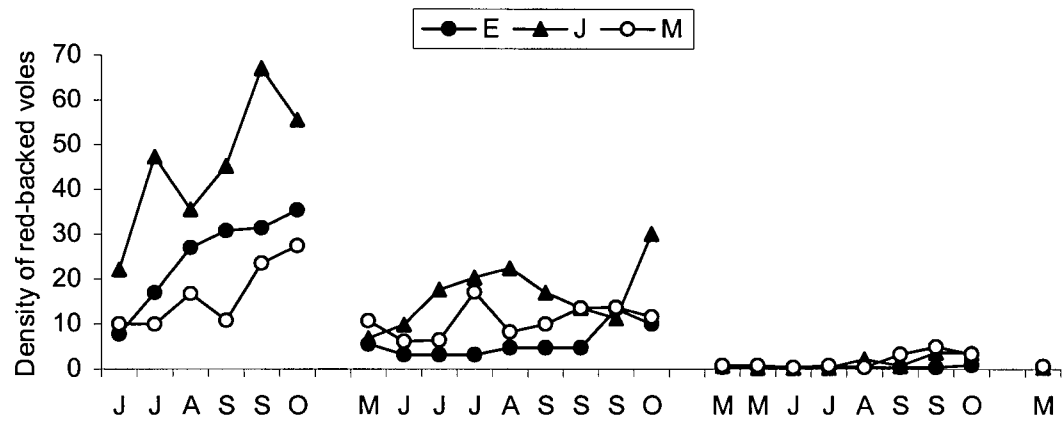
a) *Low*b) *Medium*c) *High*

Appendix 2g. Estimated density of red-backed voles on forested sampling grids at Opax on a) *low*, b) *medium*, and c) *high* treatment areas for each replicate (block D, I, N) separately. Downed wood manipulations occurred in summer 1995 (indicated by outlined area).

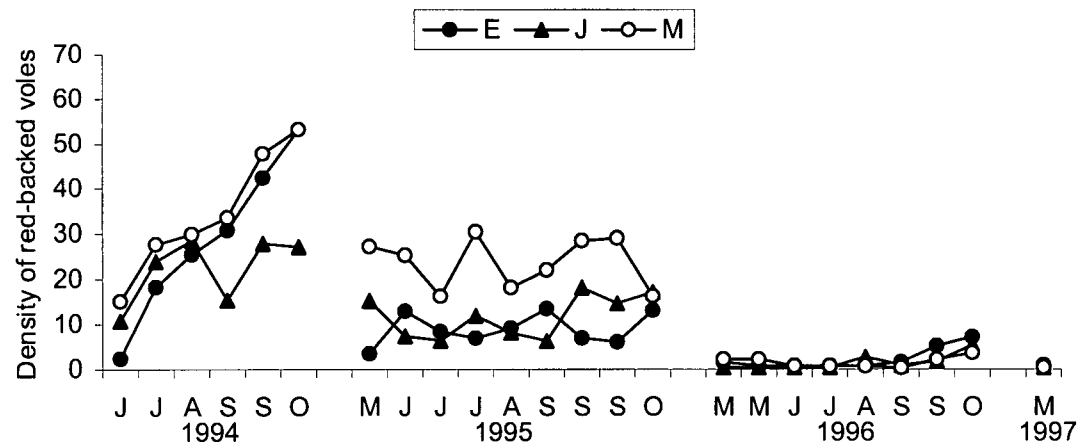
a) Low



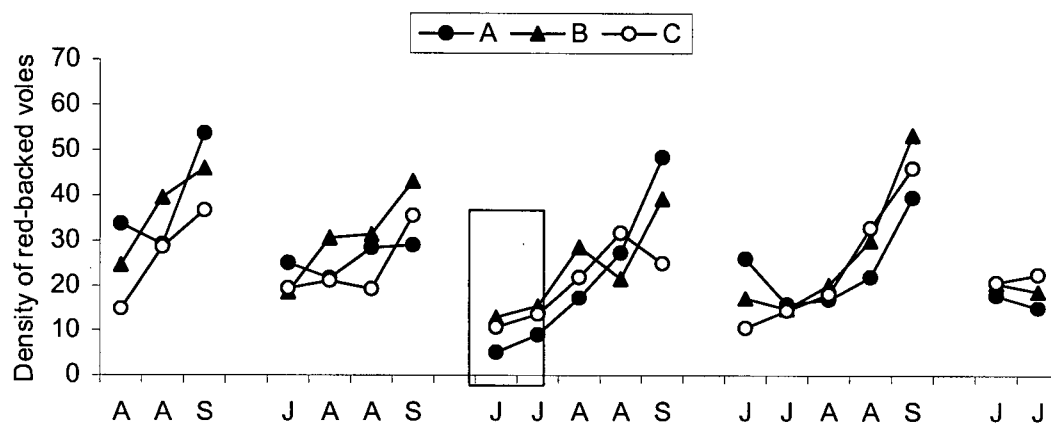
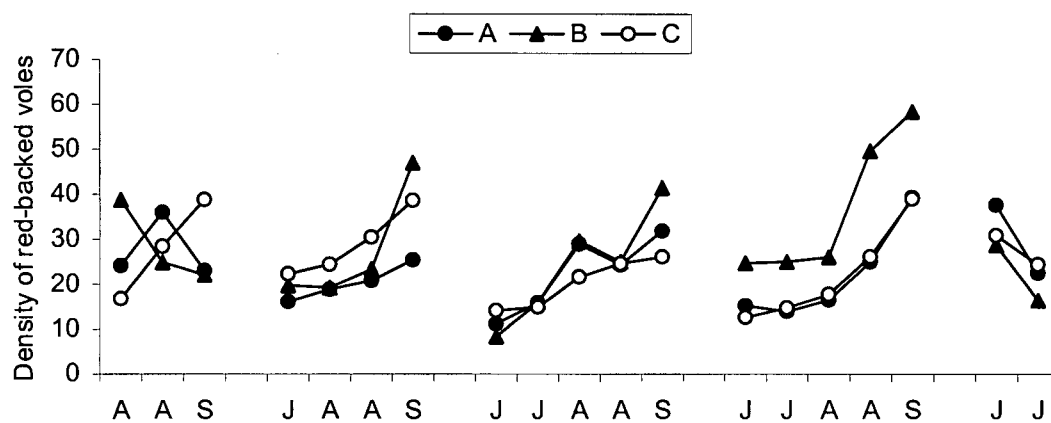
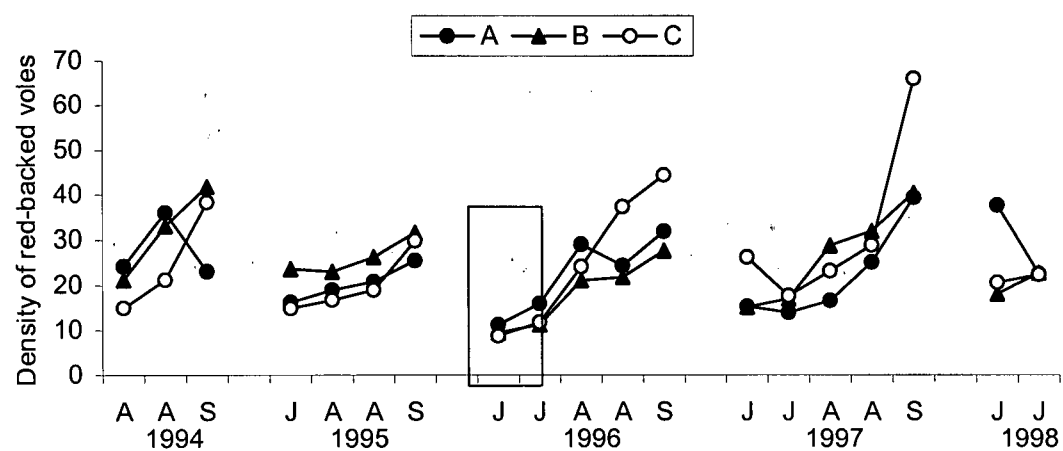
b) Medium



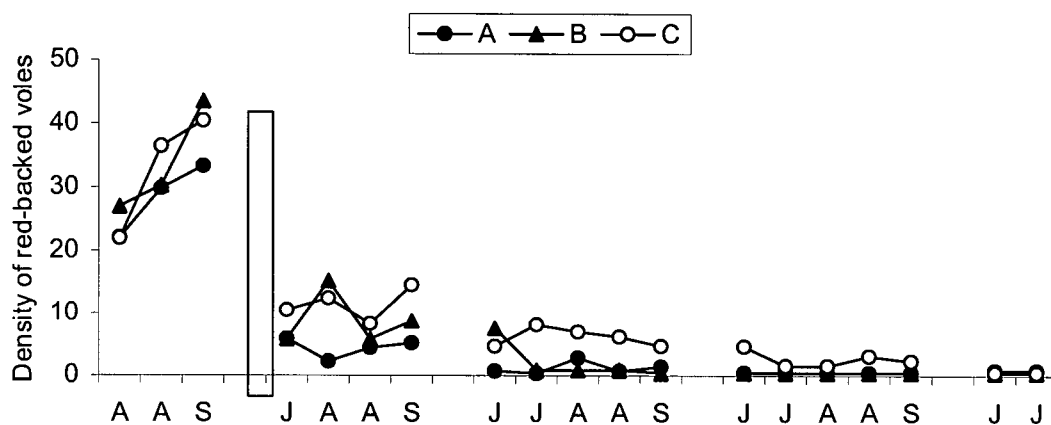
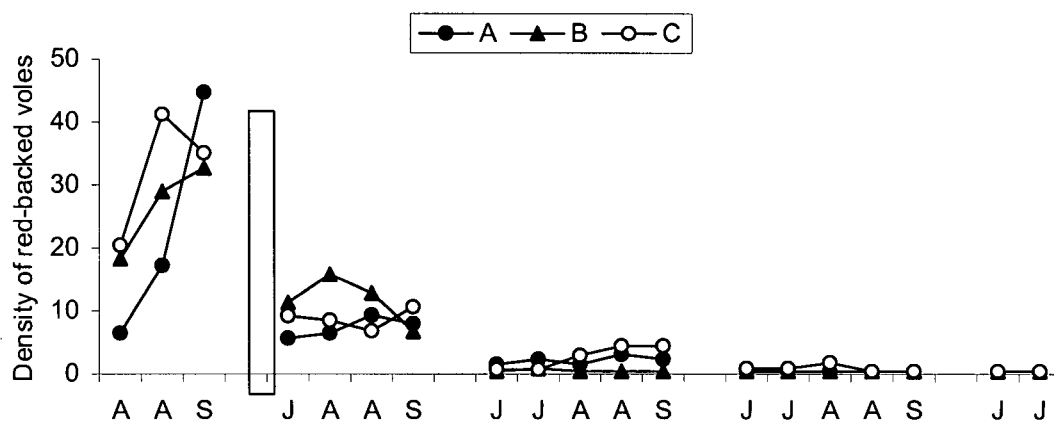
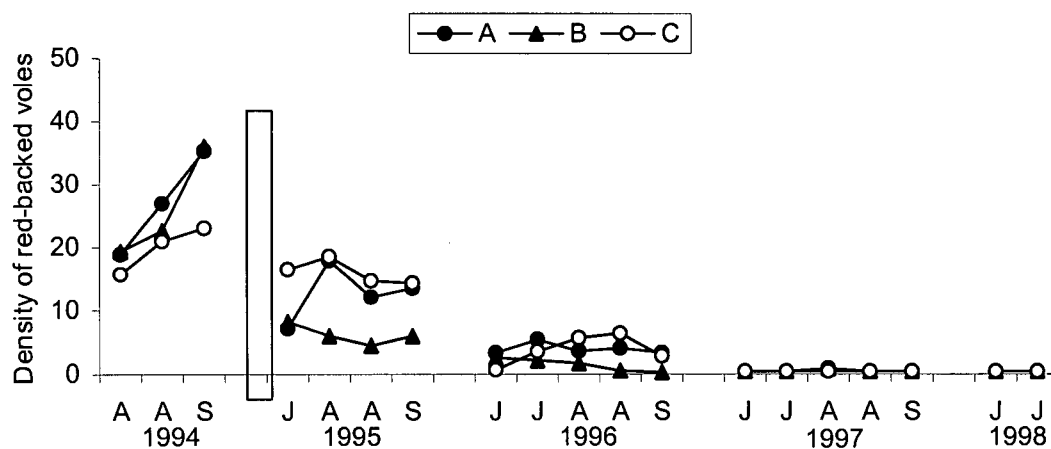
c) High



Appendix 2h. Estimated density of red-backed voles on clear-cut sampling grids at Opax on a) *low*, b) *medium* and c) *high* treatment areas. Downed wood was manipulated in winter of 1993-1994.

a) *Low*b) *Medium*c) *High*

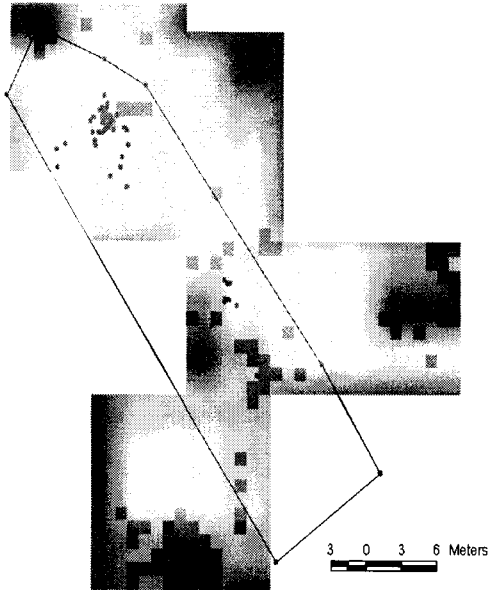
Appendix 2i. Estimated density of red-backed voles on forested sampling grids at Sicamous on a) *low*, b) *medium*, and c) *high* treatment areas for each replicate separately (Blocks A-C). Downed wood manipulations occurred during summer 1996 (indicated by outlined area).

a) *Low*b) *Medium*c) *High*

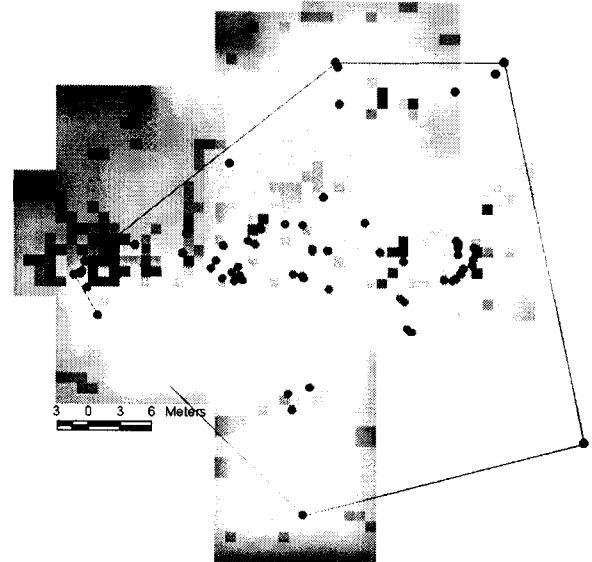
Appendix 2j. Estimated density of red-backed voles on clear-cut sampling grids at Sicamous on a) *low*, b) *medium*, and c) *high* treatment areas for each replicate separately. Harvest and downed wood manipulations occurred in winter 1994/5 to spring 1995 (indicated by outlined area).

Appendix III

Maps of 10 red-backed vole home ranges described in Chapter 6. Each base map illustrates the placement of large pieces of downed wood (>20cm) in the vole home range, the locations of voles (black dots), and the 95% MCP home range. Multiple pieces of downed wood are indicated by darker colours.



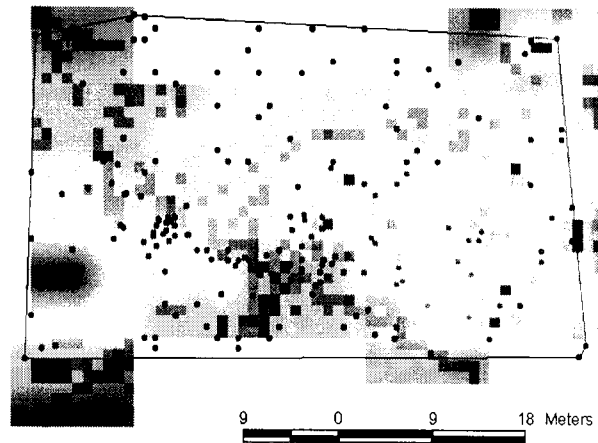
a) Vole 31



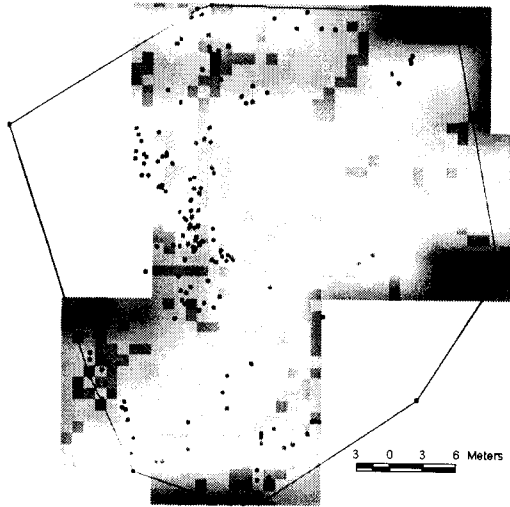
b) Vole 57



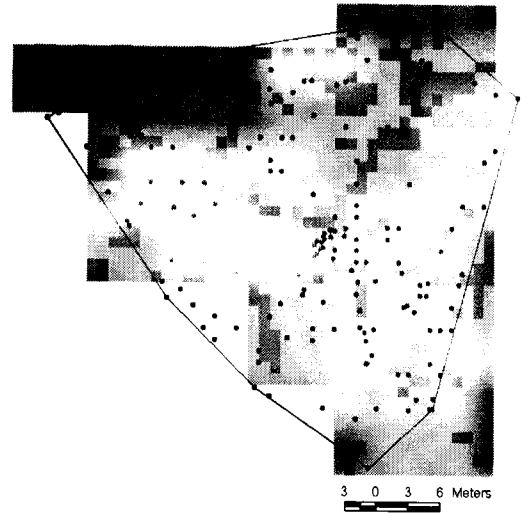
c) Vole 73



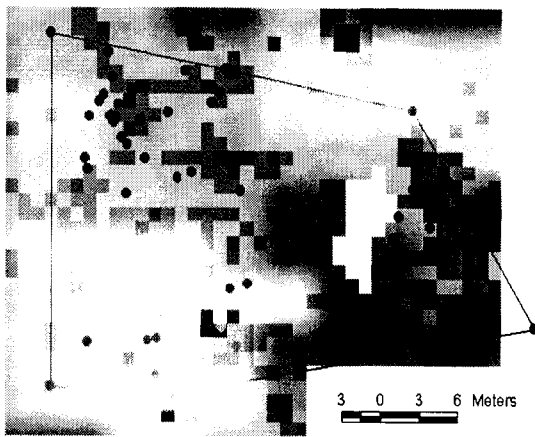
d) Vole 21



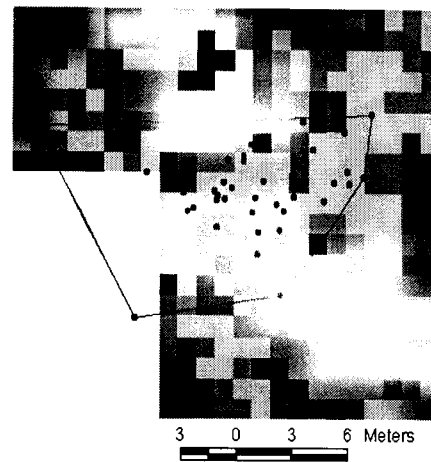
e) Vole 23



f) Vole 49



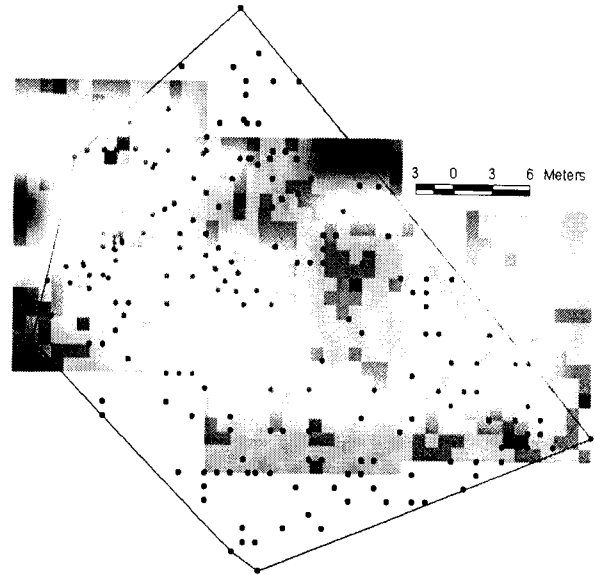
h) Vole 51



I) Vole 55



i) Vole 84



j) Vole 90