POPULATION ECOLOGY OF SMALL MAMMALS IN CLEAR CUT AREAS OF WESTERN NEWFOUNDLAND AND THEIR SHORT-TERM RESPONSE TO PRESCRIBED BURNING

RINA KATHRYN NICHOLS

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BY

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ABSTRACT

A study of small mammals was conducted from May to September 1994 in a heavily logged area in western Newfoundland, Canada. This study consisted of two main projects: 1) an ecological study of a population of small mammals with emphasis on meadow voles, *Microtus pennsylvanicus*. 2) a study of the short-term response of small mammals to prescribe burning. Both populations were studied via live-trapping and telemetry.

The first project examined a population of small mammals on a 3.2 ha plot established in a 9-year-old clearcut. Three main habitat types were present in the plot: forest regeneration which comprised 89 percent of the area, and relatively small percentages of clearings and moist meadow patches. Three species were captured on the site during the study: meadow vole (*Microtus pennsylvanicus*), masked shrew (*Sorex cinereus*) and deer mouse (*Peromyscus maniculatus*). Only three *Peromycus* were captured over the four months of the study and *Sorex* were difficult to live-trap, therefore efforts were focused on meadow voles. Thirteen resident female *Microtus*, five adults and 8 eight juveniles, were radio-collared from June until late August 1994.

Survival, recruitment and density of meadow voles peaked in June and then decreased to very low numbers in the fall. Density of voles in western Newfoundland were lower than those reported for continental vole populations. Only six percent of juvenile voles showed signs of sexual maturity in the summer of their birth. Several juveniles were sixty to ninety days old and still were not reproductively active. *Microtus* exhibited strong preference for the moist meadow patches in the 9-year-old clearcut. Seven of the eight juveniles radio-collared had a portion of their home range in the meadow habitat. Four of the five adults were located in the meadow or moist patches during excursions away from the nest. Plant species highly palatable to voles, as revealed by a

food preference test, were most abundant in the small meadow areas. The highly palatable species could not be predicted by nitrogen concentration, phenol concentration or the ratio of nitrogen to phenols. The forage selection patterns of voles in western Newfoundland are still unknown.

Space use of female voles in this study tended to differ from other vole populations. Periphery home range size and interfix distance were larger than those reported in the literature for similar species. Core home range sizes were smaller for adult females than juveniles females in the study area. Female voles tended to travel longer distances in the late morning than early morning possibly due to increased predator activity at dawn.

The second project was an experimental manipulation study designed to examine the short-term response of small mammals to prescribed burning with an emphasis on the role of cover in this response. The design consisted of three treatments: prescribed burn, prescribed burn plus cover and control. Each treatment consisted of two 0.81 ha plots established in a two year-old clearcut. All treatment plots were placed at least 75 meters apart to ensure that animals did not move between plots. Plots were established in August 1994 and trapped for a week to ensure small mammals were present in the area. In September 1994, the burn and burn plus cover treatments were burned by Newfoundland Forest Service personnel. Following the burn, the burn plus cover plots were homogeneously covered with slash consisting of branches and tree tops with no living vegetation. The two remaining plots were left unburned to serve as controls.

Three small mammal species were captured on the study area: meadow vole (*Microtus pennsylvanicus*), masked shrew (*Sorex cinereus*) and deer mouse (*Peromyscus maniculatus*). All species were relatively low in abundance. Almost twice as many voles were captured on the burn plus cover treatment than the burn or control treatments, however there was high variation within treatments. The length of time a vole remained

on a plot did not vary between treatments. The catch per unit effort of *Sorex* was significantly higher on control plots than the burn or burn plus cover plots. Overall *Peromyscus* numbers were too low for comparisons between treatments.

The Braun-Blanquet method of vegetation surveying revealed that herbaceous cover and total number of plant species were significantly lower on the burn plots than the control plots. Palatable cover was lower on the control plots relative to the burn and burn plus cover plots. The only habitat variable which differed between burn and burn plus cover plots was slash cover thereby validating this study as testing for the effects of cover independantly of food. Nutrient analysis revealed that nitrogen concentration was significantly higher in plant species on the burn and burn plus cover plots than the control plots.

Four female voles were radio-collared for this second project. Females established home ranges on the control and burn plus cover sites, but not on the burn sites suggesting that cover is an important factor determining vole distribution. Three of four females established their home ranges in fairly close proximity to a small moist meadow similar to the spacing patterns exhibited by voles on the 9-year-old clearcut. Female *Microtus* on both study areas distributed themselves in relation to highly palatable plant species.

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CHAPTER ONE - GENERAL INTRODUCTION

1. 1. Background

1.1.1. Small mammals in Newfoundland

The island of Newfoundland has an impoverished terrestrial mammalian fauna consisting of 13 native and 13 introduced species (Dodds 1983). The small mammal component consists of a single native species, the meadow vole (*Microtus pennsylvanicus terraenovae*), and nine introduced species.

Red squirrels (*Tamiscurius hudsonicus*) were introduced in 1967 to insular Newfoundland (Payne 1976) and are presently well established throughout the province (Dodds 1983; Montevecchi *et al.* submitted). Eastern chipmunks (*Tamias striatus*) were introduced to three Provincial parks in the 1960s (Northcott *et al.* 1974). All three areas appear to have slowly expanding populations (J. Brazil pers. comm.). Masked shrews (*Sorex cinereus*) were introduced in 1958 as a means of controlling larch sawfly (Haines 1965). Since 1970 *Sorex cinereus* has been found in a variety of habitat types throughout Newfoundland (Folinsbee 1971). Three *Clethrionomys* species were introduced to offshore islands in Notre Dame Bay, but have not yet been reported on the main island of Newfoundland.

The Norway rat (*Rattus norvegicus*) and house mouse (*Mus musculus*) were accidental introductions reported on the island of Newfoundland as early as 1864 (Dodds 1983) and both are found primarily in areas with human activity. The deer mouse (*Peromyscus maniculatus*) was also an accidental introduction thought to have been brought to the island with imported bales of hay. The first specimen was caught in 1968 (Gould and Pruitt 1969), and numbers have been increasing ever since (Bateman 1983; Tucker *et al.* 1988). All sightings of this new *Peromyscus* population have been reported in western Newfoundland. Of the seven species of small mammals established on the island of Newfoundland only 3 three species *Microtus pennsylvanicus*, *Sorex cinereus*, and *Peromyscus maniculatus* were captured in the study area, and only *Microtus pennsylvanicus* were abundant enough to enable a detailed study of movement and space use.

1.1.2. General Biology

1.1.2.1. *Microtus pennsylvanicus*

The meadow vole has been extensively studied throughout North America. Meadow voles occur most commonly in open habitats such as moist grasslands and meadows (Eadie 1953; Thompson 1965; Zimmerman 1965; Grant 1969). They will also utilize old fields, prairies, and openings in wooded areas as long as herbaceous ground cover is available (Banfield 1974). Meadow voles have been shown to actively avoid forested areas which is the common habitat of the Red-backed vole (Grant 1969). Folinsbee *et al.* (1973) found that meadow voles on the island of Newfoundland were similar to their mainland counterparts in showing a strong preference for grassland areas. *Microtus* were also occasionally caught in barren and bog areas but rarely in disturbed or forested habitat. Cameron (1958) reported that the meadow voles of Newfoundland were not restricted to grassland areas. Additional trapping studies have revealed that Newfoundland *Microtus* utilize a variety of habitat types. Cameron (1965) caught 27 out of 43 *Microtus* in wooded areas. Voles have been caught in old-growth forest and mixed hardwood forest (Tucker 1988; K. Knox and J. Brazil pers. comm.). Dodds (1983) suggests that voles occur throughout all habitats of Newfoundland, except in barren tundra habitats.

M. pennsylvanicus exhibit three to five year cyclic population fluctuations characteristic of microtine rodents (Krebs and Myers 1974). Cameron (1958) indicates that vole densities on Newfoundland were high in 1948 and again in 1952. Dodds (1983) found high densities of *Microtus* in 1956 and 1960 noting that voles were ' almost too numerous to count'. A six year study revealed synchronous fluctuations between Labrador and Newfoundland *Microtus* populations (Pruitt 1972). Densities of Newfoundland *Microtus* appear to fluctuate, however not enough continuous data are available to determine if these fluctuations are cyclic in nature.

The food preferences of *Microtus* on the mainland of North America are quite variable. *Microtus* are primarily herbivorous, and most commonly graze on forbs, sedges and grasses (Zimmerman 1965). In winter, when the vegetative parts of plants are scarce, voles eat seeds, roots, bark and twigs (Riewe 1971; Banfield 1974). *Microtus* have also been shown to include insects and meat in their diet (Wellwood 1956; Riewe 1971). The food habits of Newfoundland voles appear to vary somewhat from voles on the mainland. Riewe (1971) found that voles on offshore islands of Newfoundland, like mainland voles, prefer herbaceous vegetation and will take advantage of this food resource when it is available. However, Newfoundland voles have been shown to also feed on plant species characteristic of forested areas (Riewe 1973). They also tended to feed upon almost as many shrubs as forbs (Riewe 1973). Mainland voles show low preference for shrubs and do not select plants characteristic of forested habitat (Zimmerman 1965; Norrie and Millar 1990).

1.1.2.2. *Sorex cinereus*

The masked shrew is a ubiquitous insectivore found in virtually all habitat types in North America. Humidity appears to be the main factor affecting their distribution (Getz 1961a). The population of shrews on Newfoundland appears to be similar in this respect. By 1970, 12 years after the introduction of 22 animals onto the island, shrews were present in all habitat types and had colonized nearly all of Newfoundland (Dodds 1983). Currently, *Sorex cinereus* is distributed over the entire island with the exception of dry barren habitat.

Folinsbee (1971) reported that the masked shrew have dispersed at a rate of 33 km/year since the introduction, and that topographical barriers did not seriously affect this rate. He collected shrews in most habitat types, but found numbers to be highest in areas of deciduous shrub and lowest in bogs and fens. Tucker (1988) found shrews utilizing old-growth forests and harvested sites of different ages, with clearcut sites over twelve years having the highest densities. K. Knox and J. Brazil (pers. comm.) captured shrews in a variety of habitats, including bogs, barrens and forests. A live-trapping study conducted by Folinsbee (1971) found that individual recaptures of shrews were uncommon and suggested that Newfoundland shrews may not set up home ranges. Conversely, mainland shrews are territorial and establish home ranges (Banfield 1974).

1.1.2.3. *Peromyscus maniculatus*

The deer mouse is found in a wide variety of habitat types in North America ranging from grasslands to heavily forested area . They are nocturnal and forage primarily on seeds, grains, vegetation and insects (Banfield 1974). *Peromyscus* are the most recent small mammal to inhabit the island of Newfoundland. Deer mice have been reported in old and young clearcuts and old-growth forest in western Newfoundland (Tucker 1988; J. Brazil pers. comm.), however, no specimens have been reported in central or eastern regions of the province. Very little is known about the population dynamics of these new residents, although the limited trapping studies suggest that densities are relatively low (Tucker 1988; K. Knox and J. Brazil pers. comm.).

1.2. Habitat Disturbance

1.2.1. Clearcutting

The changes brought about to the micro- and macro-habitats of newly clearcut sites are quite significant. Small mammals appear to respond to these changes in relation to their habitat preferences. A review by Kirkland (1990) found that small mammals show a general positive response to clearcutting of North American forests. Some studies have found that harvesting had a more profound effect on the species composition of a community rather than the overall abundance of small mammals (Martell and Radvanyi 1977; Martell 1983; Monthey and Soutiere 1985; Medin 1986). Probst and Rakstad (1987) reported a marked change in numbers of small mammals but not in community structure following forest clearcutting. Other studies suggest that both abundance and species diversity are enhanced in harvested sites (Kirkland 1977). Response to clearcutting by small mammals will vary among studies due to differences in forest type or different population levels before disturbance (Kirkland 1990). However, overall patterns are evident for each species and are dependent on species specific survival requirements.

Microtine rodents generally tend to show a negative response to newly cut sites. In other words, they tend to leave newly cut sites and not colonize the area for several years. Meadow voles will only recolonize an area once adequate herbaceous cover and moisture have been established (Martell and Radvanyi 1977). Medin (1986) noted that herbaceous cover in logged sites approached values found in unlogged areas within two years of harvest. This supports the findings by Martell and Radvanyi (1977) who found that voles appeared on the cutover site the second year after harvesting. Use of cutover sites by *Microtus* appears to be positively correlated with moist habitat and dense forb and/or grass cover (Swan *et al.* 1984; Monthey and Soutiere 1985; Morrison and Anthony 1989).

Sorex species exhibit different responses to clearcutting. Several studies have shown that *Sorex* densities are higher on clearcut sites than uncut sites (Krull 1970; Kirkland 1977; Martell and Radvanyi 1977; Martell 1983; Swan *et al.* 1984). The suggested reason for this exploitation of cutover sites is the increase in invertebrate food following harvesting (Lovejoy 1975). Studies have also shown that shrew numbers decrease following harvesting (Probst and Rakstad 1987; Clough 1987). The age of a harvested site also appears to have an effect on shrew numbers. Tucker (1988) found that shrew numbers on the island of Newfoundland were three to five times greater following harvesting of old-growth forest, but not until several years after logging. Monthey and Soutiere (1985) found that *Sorex* activity was higher in four to 15 year old clearcut sites than in one to three year old sites. The high moisture requirements of shrews (Getz 1961a) may make newly clearcut sites unattractive to *Sorex* species.

Peromyscus has been reported exhibiting a positive response to clearcutting within the first five years post-logging (Martell and Radvanyi 1977; Martell 1983; Monthey and Soutiere 1985). Ramirez and Hornocker (1981) found that densities of deer mice were significantly higher in five year-old clearcuts and noted a peak in abundance in years two to five post-logging. Swan *et al.* (1984) caught *Peromyscus* more frequently on three year-old harvested sites. Conversely, deer mice abundance has also been shown to be higher in older (10+ years) cutover sites (Scrivner and Smith 1984). A detailed study of the animal community in forested and clearcut sites revealed that young cutovers are dominated by young, highly active males, suggesting that clearcuts act as dispersal sinks for presaturation dispersers and/or subordinate individuals (Martell 1983).

1.2.2. Prescribed burning

The abundance and diversity of most small mammal communities decreases rapidly following a fire (Lawrence 1966; Martell 1984; Grooves and Steenhof 1988). Several studies have examined the effect of prescribed burning on small mammal populations (for review see Kaufman *et al.* 1990) and revealed that most species exhibit fire-negative responses.

In general, Microtine rodents respond negatively to prescribed burning. The secondary effect of micro-habitat disturbance appears to have a greater impact on voles than the actual fire, since fire induced mortality is very low for small mammals (Crowner and Barrett 1979; Erwin and Stasiak 1979; Geluso *et al.* 1986; Clark and Kaufman 1990). Harty *et al.* (1991) found that *Microtus pennsylvanicus* recolonize burned areas as quickly as four months following a fire. Other studies report that recolonization will not occur until at least one year post-fire (Sims and Buckner 1973; Vacanti and Geluso 1985). The reduced abundance of litter following a fire will affect species, such as *Microtus*, which need cover for runway and nest construction. Vacanti and Geluso (1985) found that the return of voles to previously burned areas coincided with vegetation reaching its maximum cover. Cook (1959) noted that *Microtus* densities were similar on burned and unburned areas once the herbaceous growth was re-established. Vegetative cover appears to be the restricting factor for *Microtus* species (Cook 1959).

Sorex cinereus also exhibit a fire-negative response. Shrew numbers have been shown to decline rapidly following fire (Sims and Buckner 1973; Martell 1984). The high humidity requirements of shrews is most likely the main factor influencing the slow recolonization of shrews onto burned areas. Harty *et al.* (1991) suggest that the return of shrews twelve to nineteen months after a fire could be due to the gradual re-establishment of vegetation and hence herbaceous invertebrates such as larvae, snails, slugs and millipedes. The return of vegetative cover could also facilitate an increase in micro-habitat humidity resulting in a more optimal habitat for shrews.

Peromyscus is one of only a few species which exhibit a fire-positive response. Several studies have reported an increase in *Peromyscus* abundance following prescribed burning (Ahlgren 1966; Clark *et al.* 1989; Kaufman *et al.* 1990). The recolonization of deer mice onto burned areas has been recorded as quickly as five days post-fire (Tevis 1956). Kaufman *et al.* (1988) noted that deer mice chose areas with a high portion of exposed soil and little or no litter and therefore the selection of recently burned areas over unburned areas by deer mice appears to be a function of habitat preference The increase in seed availability following litter removal may also explain why deer mice select recently burned areas (Cook 1959).

1.3. Objectives of Study

There were two main projects carried out during this study. The first project was a comprehensive study of a population of meadow voles. The objectives of this project were: 1) to examine population parameters of *Microtus* such as density, recruitment and survival from weekly live-trapping sessions, 2) to examine space use and habitat selection at the micro- habitat level by radio-collaring resident meadow voles, 3) to determine food preference of voles by offering captive animals different vegetative plant species present in the study area (also known as a cafeteria test).

The second project was an examination of the short-term response of small mammals to prescribed burning. This study focused on the influence of cover on small mammal colonization of burned areas (herein referred to as the Burn study). This was an experimental manipulation study conducted in a large two year-old clear cut. Six live-trapping plots were subject to three treatments: control, prescribed burn and prescribed burn plus cover. This study was undertaken with the following objectives in mind: 1) to determine an index of small mammal abundance on the experimental plots, 2) to estimate the time spent by *Microtus* foraging on treatment areas, 3) to describe the vegetation structure on all experimental plots to determine which habitat variables influence vole distribution and space use.

CHAPTER TWO - GENERAL METHODS

2.1. Study Area

This project was conducted from May through September 1994 near Glide Lake, approximately 22 km northeast of Pasadena, in the Western ecoregion of insular Newfoundland (Damman 1983). The natural vegetation of the area is classified as boreal forest (Rowe 1972) and is dominated by balsam fir (*Abies balsamea*) with some black spruce (*Picea mariana*), white spruce (*Picea glauca*) and white birch (*Betula papyrifera*). The area has been logged since the early 1900s and is dominated by different age clearcuts with small patches of second-growth forest scattered throughout. Soils of the ecoregion are more fertile and plant growth is more favorable than other parts of Newfoundland. The average growing season for this area is 170 days (Gordon 1983). Total precipitation from May to September ranges from 261-516 mm with a mean of 394 mm (Treidi 1978 cited in Banfield 1983). The average percentage of annual total precipitation falling as snow is 36%. Average monthly precipitation and air temperatures from June to September 1994 are reported in Appendix A.

2.2. Live-Trapping

From mid May until late September 1994 a capture-mark-release study of small mammals was conducted on the 9-year-old clearcut plot and the Burn study area. Plots were trapped two days a week for 16 consectutive weeks. Traps were checked at least twice a day. If female with young were present on the plot, traps were checked three times a day. One handmade wooden multi-capture trap was placed at each trap station on all plots. Although *Sorex* were sometimes able to escape, these traps were successful in trapping *Microtus* and *Peromyscus*. Traps were baited with rolled oats and peanut butter and cotton was provided for nesting material. All bait was removed between trapping sessions. Meadow voles and deer mice were individually marked by toe-nail clipping upon initial capture. This method of marking is similar to toe-clipping except that only a small amount of skin, and not a large portion of the toe, is removed with the nail. This prevents the nail from growing back and the observer can identify the animal individually by the lack of a toe-nail instead of the lack of a toe. Juvenile voles for this study were defined as animals which did not show signs of reproductive activity during the study period (generally <30 g). Adult voles were defined as animals which showed signs of reproductive activity during the study, but not necessarily at time of capture (generally >35 g). Female voles were considered reproductively active if they were lactating, pregnant, or if the vagina was perforated. Males were considered reproductively active if testes were scrotal. For all individual captures the identification number, date, station number and time of capture were recorded. Voles and mice were weighed to the nearest 0.1 gram using a Pesola handheld spring scale once per trapping session. *Sorex* were very difficult live-trap because of their high metabolism. Shrews captured in the traps were released immediately if still alive. Upon capture of a shrew, the time of day, date, trap station and status of the animal (alive or dead) were recorded.

2.3. Telemetry

Microtus with a mass of 20 grams or greater captured on the same plot for two consecutive weeks were outfitted with radio-collars mounted on plastic cable ties. Animals between 20 and 30 grams were fitted with two-stage, 1.5 g collars (Holohil, Woodlawn, Ontario). These collars had a battery life of approximately 12 to 17 days. Animals greater than 30 grams were fitted with 1-stage, 2.0 g collars (L.L. Electronics, Mahomet, Illinois). These collars had a battery life of approximately 25 to 30 days. Each collar transmitted at a different frequency (153.00-154.00 MHz). Once a collar was placed on an animal a two day acclimatization period was allotted. After that period, the animals were tracked eight times a day for four consecutive days with a handheld antennae and a Tr-4 receiver (Teltonics, Arizona). On the first day of tracking all collared animals were located once an hour from 0600 to 1300 h. The second day, all collared animals were located once an hour from 1400 to 2100 h. This was repeated for the third and fourth day. Collars were removed during the next trap session. The location of a vole was determined by triangulation of the hand held antennae. The location was then marked with flagging tape and distance and angle (0-180 compass degress) to the nearest trap station were recorded. Locations were later transformed into X and Y coordinates and then entered into the Calhome (1992) program to analyze space use data. This program computed home range size and interfix distances. The Adaptive Kernel Method was used to calculate home range size (Worton 1989). Home range size was computed using 50 percent and 95 percent utilization distributions (UD). Ninety-five percent utilization distributions were referred to as periphery home range size and 50 percent utilization distributions were referred to as core home range size. Interfix distance were the distances traveled by an animal between successive one hour locations. Large interfix distances represent greater movement, while small interfix distances represent little movement.

2.4. Vegetation Surveying and Plant Sampling

A detailed description of the vegetation on each site was conducted using the Braun-Blanquet method of vegetation surveying (cited in Shimwell 1971) to determine if small mammal space use and distribution were influenced by vegetation structure. Quadrats were established randomly within each plot. Quadrat size and number was chosen to ensure that at least seven percent of the area was sampled. Vegetation within the quadrats were recorded by species and percent cover in each of five stratification layers (see Appendix B). Percent cover was determined visually as the percent of an area covered by each species. In several cases plant species were present in more than one stratification layer. Dispersion patterns were also recorded for all plant species (Appendix B).

Plant samples were collected in July and August for nutrient analysis. Plants were collected from randomly selected areas throughout each plot. Bergeron and Jodoin (1987) define high quality food for *Microtus* as plants with high nitrogen concentrations and low phenol concentrations. In the present study, total nitrogen and phenol concentrations of different plant species were measured to determine if voles chose forage in relation to plant quality. Each sample consisted of at least five or six different individual specimens collected from different locations within the plot. Samples were then dried for forty-eight hours at 60°C, ground to a powder, and stored at 4°C. Nitrogen concentration (percent dry mass x 6.25) was analyzed by personnel at Canadian Forestry Service, Natural Resources Canada, at the regional laboratory in St. John's, Newfoundland. The procedure to determine total phenolic concentration (percent dry mass) followed the methods of Bergeron and Jodoin (1987) and Singleton and Rossi (1966). The ratio of nitrogen to phenols was obtained by dividing the nitrogen concentration by the phenol concentration.

2.5. Statistical Analysis

Detailed descriptions of statistical methods such as individual models and variables are reported in the appropriate chapters while general statistical procedures are described here. Data were analyzed using SAS and MINITAB statistical packages. Type three sums of squares was reported. When required, means were compared using Tukey's procedures (Sokal and Rohlf 1981). Before testing for treatment effects, replicates (plots) within treatment groups were tested for homogeneity. This was done by incorporating the nested factor into the full model. The nested factor was tested for significance, and removed from the model if found to be non-significant. An examination of the residuals and model was conducted in SAS using PROC UNIVARIATE and in MINITAB using histograms, rootograms and plots of residuals versus fits. Data sets with non-normal residuals were randomized in SAS (T. Bult pers. comm.) 2000 times to obtain a calculated p-value from an empirical F-distribution. A p-value of equal to or less than 0.05 was considered significant.

Auto correlation coefficients were obtained in MINITAB using ACF (lag1) and then averaged to obtain a single coefficient for interfix distances of all voles. Correlation coefficients were obtained in MINITAB. William's correction factor was used when calculating a G-statistic (Sokal and Rohlf 1981). Means are reported ± 1 standard error (S.E.) unless otherwise stated.

CHAPTER THREE - ECOLOGY OF A POPULATION OF MEADOW VOLES IN WESTERN NEWFOUNDLAND

3.1. Introduction

Microtus pennsylvanicus and *Sorex cinereus* are the only two small mammal species found on the island of Newfoundland in any abundance (Cameron 1958; Northcott 1974). In western Newfoundland, both *Microtus* and *Sorex* are present in relatively high numbers, whereas *Peromyscus maniculatus* are less abundant (Tucker 1988; J. Brazil pers. comm.). Red squirrels are also present in western Newfoundland, however densities are rarely high in harvested areas.

Microtus in Newfoundland are considered a distinct subspecies, *Microtus pennsylvanicus terraenovae* (Cameron 1958) based mainly on cranial and dental characteristics. Newfoundland voles have been reported to utilize forested area and exist at low densities relative to other populations (J. Brazil and K. Knox pers. comm.). All the information known about Newfoundland *Microtus* has been derived from annual short-term trapping studies designed to estimate density and habitat selection. Other detailed population characteristics have not yet been examined. The purpose of this project was to comprehensively examine a *Microtus* population in western Newfoundland. A 3.2 ha plot was established in a 9-year-old clearcut which was found to support relatively high vole densities. This population was studied from May to September of 1994. Population parameters such as density, survival and recruitment, as well as habitat selection, food preference, food quality and space use were examined. Comparisons of Newfoundland *Microtus* characteristics were made with mainland and offshore island vole populations.

3.2. Methods

3.2.1. Study Site

Several areas within the Glide Lake vicinity were live-trapped for five days in May 1994 to determine where small mammals were most abundant. A 9-year-old clearcut supported the highest number of small mammals, and therefore a permanent 3.2 ha grid was established within this area (49° 06' N latitude and 57° 22' W longitude) with traps placed 15 meters apart in a 8x15 grid.

Three main habitat types were found within the plot: forest regeneration, clearings and meadows. Forest regeneration sites consisted mainly of *Abies balsamea* and *Picea mariana* regeneration (1.5 - 3.5 m) with mosses and *Cornus canadensis* as the dominant ground cover. Forest regeneration comprised 89 percent of the plot. Clearings covered 6.8 percent of the study plot and consisted mainly of *Epilobium angustifolium*, *Rubus ideaus*, and *Anaphalis margaritacea.* Meadows covered 4.2 percent of the plot and were dominated by *Equisetum sylvaticum*, *Carex* species, *Athyrium filix-femina* and grasses. Meadows were higher in moisture and lower in cover relative to clearings and regeneration areas.

3.2.2. Habitat Preference

Habitat preference of meadow voles in western Newfoundland was studied at both the macro-habitat and micro-habitat level. From June through August 1994, four different habitat types were live-trapped to determine macro-habitat preferences of voles. Plots were established within a 25 year-old second growth forest, a 45 year-old second growth forest, a meadow habitat, and a cutover site less than one month old. One 2.6 ha plot was established in each habitat type with traps located 20 meters apart in an eight by eight grid. The meadow plot was 1.1 ha with traps placed every 15 meters in a seven by seven grid. Each plot was trapped three days a week for three consecutive weeks. Traps were set in the morning of the first day, and then checked at dusk and dawn for the next three days. Traps were closed at dusk of the third day. One Sherman single capture live trap (Sherman Trap Company, Tallahassee, USA) was placed at each station. Traps were baited with oats and peanut butter and cotton was provided for nesting material. Data were collected for each captured animal using the same techniques as stated in section 2.2.

To study micro-habitat use by voles and to determine if voles were occupying areas with highly palatable plant species (section 3.2.3), information was collected on plant species and habitat structure within a 1 m^2 area of all radio-locations for each collared vole. A brief description of the area was included to determine if other micro-habitat variables such as moisture or presence of slash or stumps were influencing space use. The number of locations in which highly palatable species were present in the 1 m^2 area was divided by the total number of locations taken for that animal to determine the percent of time each vole spent utilizing areas with preferred plant species.

3.2.3. Vegetation Surveying and Plant Sampling

Fifteen 9x9 m Braun-Blanquet quadrats (section 2.4) were randomly established within the 3.2 ha plot. All vegetation within the area was recorded by species and percent cover in each of five stratification layers (see Appendix B). Plants were collected from the plot in late July for nutrient analysis (section 2.4). The same 25 species used in the feeding trials (see below) were collected for nutrient analysis to determine if plant quality could predict plant preference.

3.2.4. Food Preference Trials

The 25 plant species chosen to test food preference were done so partially on the basis of plant species abundance within the plot and partially by reviewing the literature of vole feeding habits. Seven voles were kept in captivity for three days and offered 25 plant species (Appendix C). Voles were housed individually in plastic cages (60 cm x 30 cm x 20 cm) and soil, bark and cotton were provided for cover and nesting material. Water was provided *ad libitum*. Animals were kept in a cool shaded area for the duration of the study. Before the animals were offered any plant species they were given a one hour acclimatization period. During this time, lab chow and water were placed in the cages. After the acclimatization period, each vole was offered seven or eight plant species each day for three consecutive days. To avoid any biases, all trial lengths were eight hours and plant species were offered at the same time to all voles (0700 to 1500 h). The combination of plants offered within each trial was randomly selected. After each trial the plants were removed and each species was given a palatability score depending on the amount of plant consumed. This was determined visually as the percent of plant eaten (palability score of 0 = 0% eaten, palability score of 1= 1-30% eaten, palability score of 2= 31-60% eaten, palability score of 3= 61-100% eaten). Voles were released to the same area of capture after the trials were completed.

For each plant species, palatability scores were calculated by averaging the scores obtained for all seven voles. Highly palatable plant species were those with an average palatability score of 2.5 or higher (Appendix C). Plant species were grouped into 1) trees and shrubs, 2) forbs, 3) grasses and sedges, and 4) 'other' (Appendix C) to determine if palatability could be predicted by plant group. Plants were also catagorized by habitat type (Appendix C) to determine if palatability could be predicted by habitat. Some plant species were present in more than one habitat type. In this case, habitat type was designated as the habitat in which the plant species occurred more frequently as determined by the Braun-Blanquet vegetation data.

3.2.5. Statistical Analysis

Population estimates of meadow voles were derived by the use of the Jolly-Seber

Model of Population Estimation (Program JOLLY, Krebs 1989). Jolly-Seber estimates of densities, survival and recruitment of voles could not be separated by sex or reproductive status due to the small sample size. Equal catchability of voles was determined by the Leslie, Chitty and Chitty Test (Program LESLIE, Krebs 1989). Equal catchability refers to all animals having the same chance of being captured in a trap, thereby preventing biases in the data by capturing certain animals too often. A G-test and Bonferroni Z-statistic were used to test habitat use and preference. Core and periphery home range sizes were compared between adult and juvenile females using a one-way ANOVA model where reproductive status (adult or juvenile) was the predictor. Overlap of home ranges was calculated manually by plotting the ranges on graph paper and determining the area of overlap. A two-way ANOVA model was used to test for the effect of reproductive status and time of day (0600 through 2100) on interfix distance. A one-way ANOVA model tested for the effect of reproductive status on the percent of time an animal was located in an area with highly palatable plant species (section 3.2.4). Three separate one-way ANOVA models tested for the effects of plant species, plant group, and habitat affinity on plant palatability. A multiple regression tested for the effects of nitrogen concentration, phenol concentration, and the ratio of nitrogen to phenols on plant palatability.

3.3. Results

3.3.1. Demography

Live-trapping conducted from May 21 until September 17 of 1994 resulted in the capture of 143 small mammals on a 3.2 ha plot. Most of the small mammals captured were meadow voles, while the remaining captures were masked shrews and deer mice (Table 3.1). All voles were found to have equal catchability. Vole density was highest in late June but decreased to low numbers by late August (Table 3.2). Survival of voles peaked at 80% in mid July and slowly decreased to 19% in early September (Table 3.2). The

Table 3.1: Summary of small mammal captures and recaptures from May to September 1994 during live-trapping of the 3.2 ha plot in the 9-year-old clearcut.

Species	Total Captures	Recaptures	Total Number of animals
Microtus pennsylvanicus	159	74	85
Sorex cinereus	53	-	53
Peromyscus maniculatus	10	5	5
Total	222	79	143

Table 3.2: Jolly-Seber Estimates of density, survival, and recruitment of meadow voles on the 9-year-old clearcut. Ninety-five percent confidence limits (C.L.) are by method of Manly (1989 cited in Krebs 1989).

Trap session (week)	Number of voles (per 3.2 ha)	Number of voles with 95% C.L.	Probability of survival (±1S.E.)	Recruitment (±1S.E.)
1 (May 26)	-	-	-	-
2 (June 6)	3.2	2.2 - 6.0	0.57 (±0.37)	5.3 (±0)
3 (June 13)	7.3	5.7 - 16.3	0.82 (±0.27)	31.6(±14.1)
4 (June 19)	37.6	23.0 - 85.2	0.54 (±0.13)	15.8(±9.9)
5 (June 27)	36.1	24.8 - 53.8	0.70 (±0.12)	0.2 (±5.1)
6 (July 5)	25.5	21.7 - 31.9	0.54 (±0.11)	4.7 (±1.2)
7 (July 12)	18.4	17.2 - 21.9	0.81 (±0.11)	9.0 (±2.0)
8 (July 19)	23.9	20.6 - 29.8	0.79 (±0.14)	0.4 (±1.7)
9 (July 27)	19.3	15.3 - 23.6	0.65 (±0.17)	2.3 (±1.2)
10 (Aug. 3)	14.9	11.6 - 20.2	0.55 (±0.15)	0.3 (±0.7)
11 (Aug. 11)	8.0	7.3 - 13.2	0.25 (±0.15)	1.3 (±0)
12 (Aug. 20)	2.3	2.0 - 7.2	0.25 (±0.22)	0.7 (±0)
13 (Aug. 27)	1.3	1.0 - 4.9	0.20 (±0.14)	0.3 (±0)
14 (Sept. 3)	1.0	1.0 - 1.0	-	0
15 (Sept. 10)	1.0	1.0 - 1.0	-	0
16 (Sept. 15)	0.0	0	-	0

number of new animals entering the population (recruitment) peaked in mid June and was also relatively high in early July, then decreased to zero recruitment in September (Table 3.2). Voles could not be separated by sex and reproductive status due to the limitations of the Jolly-Seber population estimates program. Therefore, total numbers of voles captured per trap session was used as an index of density to examine trends in abundance of juveniles, adult males and adult females. The total number of juvenile *Microtus* increased substantially in the third week of June and remained fairly high until the beginning of August. Total number of adults peaked in the third week of June but decreased to low numbers within three weeks (Fig 3.1). Adult females were more numerous than adult males (Fig 3.2). Of the seventeen juveniles which survived on the study plot for at least three weeks, only one became reproductive.

3.3.2. Habitat Preference

In both the 25 and 45 year-old second-growth forest plots the only small mammals captured during the trapping sessions were *Sorex*. No small mammals were captured on the one month old cutover, whereas all three small mammal species were captured in the meadow plot (Table 3.3).

From late June until mid-September 15 female meadow voles were fitted with radio-transmitters to study habitat preference and space use. Of these 15 animals, 13 (five adults, eight juveniles) were located enough times to be used for the statistical analysis. An attempt was made to collar two male voles, however, both animals could not be located more than five times as they traveled out of the range of the reciever. Radio-collared juvenile females exhibited preference for certain habitats within the 9-year-old clearcut ($G_{2,241}$=215.58, $p<0.00$). Meadow habitat was utilized more than expected, forest regeneration was utilized less than expected, and clearings were used in proportion to their availability (Table 3.4) Juveniles also appeared to distribute themselves in relation to the

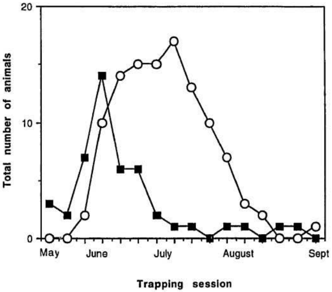

Figure 3.1: Total number of juvenile (circles) and adult (squares) *Microtus* captured per trap session from late May through September 1994 on the 3.2 ha 9-year-old clearcut study area.

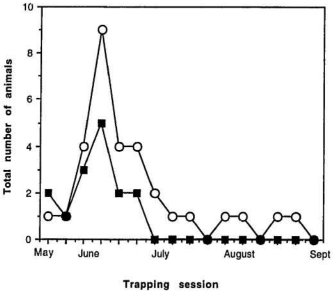

Figure 3.2: Total number of adult male (squares) and female (circles) *Microtus* captured per trap session from late May until September 1994 on the 3.2 ha 9-year-old clearcut.

Table 3.3: Number of small mammals captured three consecutive nights a week for three weeks on 2.6 ha plots in forest and clearcut habitat and on 1.1 ha plot in meadow habitat.

Habitat Type	*Microtus pennsylvanicus*	*Sorex cinerus*	*Peromyscus maniculatus*
25-year-old forest	0	2	0
45-year-old forest	0	4	0
Meadow	5	8	3
Recent cutover	0	0	0

Table 3.4: Occurrence of vole radio locations in meadows, clearings and forest regeneration of a 3.2 ha plot in a 9-year-old clearcut.

Habitat	Total area (ha)	Proportion[a] of total area (p_o)	Expected no.[b] of locations	Observed no. of locations	Proportion observed (p_i)	Confidence interval on proportion of occurrence (p_i)[c]	Habitat preference
Meadows	0.14	0.04	10	87	0.36	$0.28 < p_i < 0.43$	preferred
Clearings	0.22	0.07	17	15	0.06	$0.02 < p_i < 0.10$	expected
Forest	2.88	0.89	217	142	0.58	$0.51 < p_i < 0.66$	avoided
Total	3.24		n=244	244			

[a] proportion of total area represents expected number of radio locations as if voles utilized each habitat in exact proportion to the availability of each habitat type.

[b] calculated by multiplying proportion p_o x n; i.e. 0.89 x 244 = 217

[c] p_o represents theoretical proportion of occurrence and is compared to corresponding p_i to determine if hypothesis of proportional use is accepted or rejected, i.e. $p_o = p_i$.

small meadow patches within the clear cut (Fig. 3.3). All five radio-collared adult females had part of their home range outside the plot and therefore habitat preference could not be tested. However, when females were away their nests, 36±2% (n=5) of radio-collar locations were in meadow habitat or small wet patches. The adults with litters tended to establish nests along the edge of the plot in the forest regeneration area.

3.3.3. Space Use

Juvenile and adult female voles did not vary significantly with respect to periphery home range size ($F_{1,11}$=1.30, p=0.20) (Fig 3.4). However, core home range size was significantly larger for juvenile voles than for adult voles ($F_{1,11}$=7.07, p=0.03)(Fig 3.4). I was unable to calculate male home range size because they traveled beyond the one hundred meter range of the receiver. This may suggest that male voles in Newfoundland either have very large home ranges or are generally transient in nature. Overlap of periphery home ranges was more evident among juvenile females than adult females (Fig 3.3). Home range overlap in the juveniles averaged 36±9% (n=8), whereas only 2±1% (n=5) of the home ranges of adult females overlapped. During the radio-collaring sessions, both the juveniles and adults appeared to utilized three or four specific places which were usually located in either in meadow habitat or small moist patches.

Autocorrelation of interfix distances was found to be negligible (autocorrelation coefficient = 0.18) and therefore locations were considered independent. Results of a two-way ANOVA for the effect of reproductive status and time of day on interfix distance indicated that both reproductive status and time of day were significant predictors of interfix distance (Table 3.5). The interaction term was not significant and therefore removed from the model ($F_{15,372}$= 1.29, p=0.20). Average interfixed distance was 20±2 m/hr for juveniles and 14±2 m/hr for adults. Females traveled longer distances in the late morning (1000 and 1100 h) compared to early morning (0600 h) (Fig 3.5).

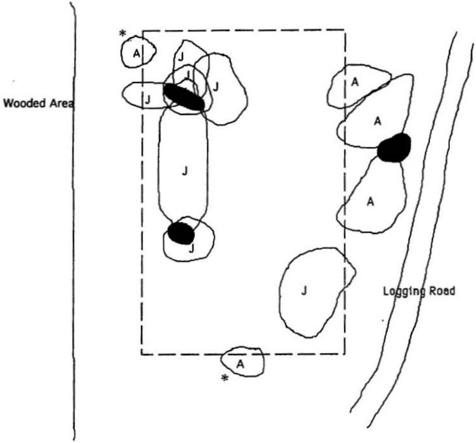

Figure 3.3: Pictorial representation of juvenile (J) and adult (A) periphery home ranges on the study plot (dotted line) in the 9-year-old clearcut. Gray shaded areas represent the meadow patches. An * denotes females with litters.

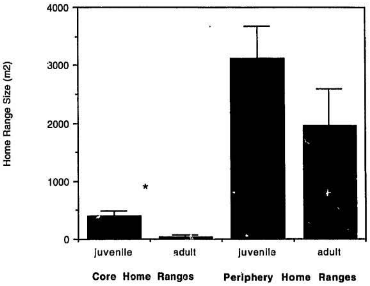

Figure 3.4: Core and periphery home range sizes (±1 S.E.) of the juvenile (n=8) and adult (n=5) female meadow voles on the study plot in the 9-year-old clearcut based on radio-telemetry. Core home ranges were significantly larger for juveniles, whereas, periphery home ranges did not differ significantly between juvenile and adults (see text).

Table 3.5: Reduced ANOVA model for the effect of reproductive status (RS) and time of day (TIME) on interfix distance. SS refers to sums of squares.

Source	DF	SS	F	P
RS	1	4476	22.0	0.0001
TIME	15	5988	2.0	0.02
Error	387	7884		

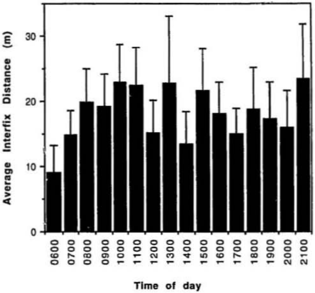

Figure 3.5: Average interfix distances (±2 S.E.) traveled by female voles during daylight hours. Distances traveled at 1000 and 1100 h were significantly longer than distances traveled at 0600 h (see text).

3.3.4. Food Preference and Plant Nutrients

Microtus exhibited preference for certain plant species (Table 3.6, Fig 3.6). Palatability of plant species could not be predicted by plant group, but could be predicted by the habitat in which it was most abundant (Table 3.6). Voles preferred plants found in the meadow habitat significantly more than plants found in the clearings or forested area (Fig. 3.7). Juveniles were located in areas with highly palatable species significantly more than adult voles ($F_{1,11}$ =45.84, p=0.0001)(Fig 3.8). Plant palatability could not be predicted by nitrogen concentration, phenolic concentration or the ratio of nitrogen to phenols (Table 3.7, Fig 3.9). All interaction terms were non-significant and therefore removed from the model (interaction between nitrogen and phenols: $F_{1,17}$=0.22, p=0.64; interaction between nitrogen and ratio of nitrogen to phenols: $F_{1,17}$=1.07, p=0.31; interaction between phenols and ratio of nitrogen to phenols: $F_{1,17}$=0.05, p=0.83; interaction between nitrogen, phenols and ratio of nitrogen to phenols: $F_{1,17}$=0.75, p=0.40).

3.3.5. Predation

Although predation was never directly measured in this study anecdotal evidence was recorded. During August and September, seven ermines (*Mustela erminea*) were captured in the study area, of which two were recaptures. Red fox (*Vulpes vulpes*) were also observed in the study area in August and September. Hawk owls (*Surnia ulula*) and Kestrels (*Falco sparverius*) were observed in the study area for most of the summer. A hawk owl was observed to prey on an adult vole on the study plot. A relatively high density of hawk owls occurred in western Newfoundland from May to August 1994 and many exploited clearcuts as hunting areas (J. Gosse and W. Montevecchi pers. comm.).

Table 3.6: ANOVA models for the effect of **a)** plant species, **b)** plant group and **c)** habitat on plant palatability. SS refers to sums of squares.

Source	DF	SS	F	P
a)Plant species	24	221601	29.36	0.0001
Error	150	47170		
b)Plant Group	3	7.199	2.55	0.10
Error	21	19.76		
c)Habitat	2	14.43	12.67	0.0002
Error	22	12.53		

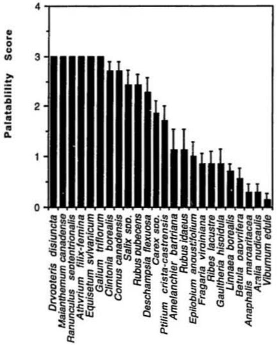

Figure 3.6: Palatability scores (±1S.E.) of plant species offered to captive *Microtus*. A palatability score of 3 denotes the highest plant preference.

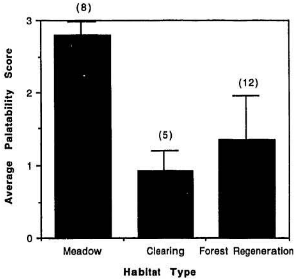

Figure 3.7: Average palatability score (±1 S.E.) of plant species found within three habitat types in the 9-year-old clearcut site. Sample sizes are in parentheses. Palatability scores of plant species in meadow habitat were significantly higher than those of plants in clearings or forest regeneration (see text).

Table 3.7: Reduced multiple regression model for the effects of nitrogen concentration, phenol concentration and the ratio of nitrogen to phenols on plant palatability. SS refers to sums of squares

Source	DF	SS	F	P
nitrogen concentration	1	0.438	0.35	0.55
phenol concentration	1	0.818	0.66	0.42
ratio of nitrogen to phenols	1	0.772	0.62	0.43
Error	21	26.10		

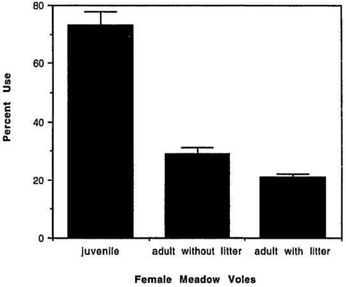

Figure 3.8: Female *Microtus* use of areas with highly palatable plant species on the 3.2 ha plot as determined by radio-telemetry. Juveniles were located in areas with highly palatable plants significantly more than adults with and without litters (see text).

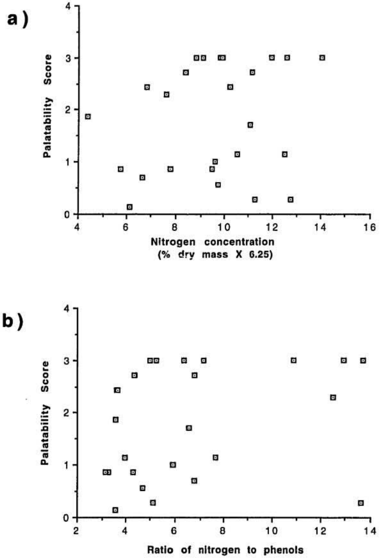

Figure 3.9: Relationship of two measures of plant quality **a)** nitrogen concentration **b)** ratio of nitrogen to phenols to plant preference (palatability score) in 25 plant species. Palatability of plant species to *Microtus* could not be predicted by either nitrogen concentration or nitrogen to phenol ratio (see text).

3.4. Discussion

3.4.1. Demography

The results from this study are consistent with past findings that small mammal densities in western Newfoundland are relatively low (Folinsbee *et al.* 1973; J. Brazil and K. Knox pers. comm.). Densities of meadow voles in late May were one individual/ha, peaked at 11.8 individuals/ha in June and declined to 0.3 individual/ha in late August and early September. Comparatively, on the mainland in Massachusetts, Ostfeld *et al.* (1988) observed a population increase from a low of 28 voles/ha in May, to a high of 85 voles/hectare in July, followed by a slow decline to 33 voles/ha by December. Seventeen years of data on *M. pennsylvanicus* populations throughout North America revealed that at the onset of breeding in the spring, densities average 57 individuals/ha and at the end of breeding in the fall, densities average 172 individuals/ha (Taitt and Krebs 1985). Due to cyclic nature of *Microtus* species, it may be argued that the low densities of voles found in this study are simply a crash in the population cycle. However, spring and fall densities reported in past studies of voles on insular Newfoundland have always been considerably lower than continental averages. The highest vole densities reported in the literature for Newfoundland is 25 voles/ha (Tucker 1988), whereas desities of voles on the mainland have been reported in the hundreds, and average 172 voles/ha in the fall. Furthermore, Brazil and Knox (pers. comm.) have reported low numbers of voles in western Newfoundland for eight consectutive years.

Survival of *Microtus* was highest in early summer and lower in the fall. Conversely, Mihok (1984) found survival of *Microtus* in southeastern Manitoba to be poor in midsummer and high in late season. Juvenile meadow vole abundance remained high from late June until mid-August and then declined rapidly until only one juvenile animal was captured in early September. Meadow vole numbers in general were very low in the fall of 1994. W. Adair (pers. comm.) captured only two voles in 7200 trap nights during the fall of 1994. J. Brazil and K. Knox (pers. comm.) have observed low fall densities of *Microtus* in western Newfoundland since 1988. Vole numbers in the present study did not increase through summer, but decreased starting in July until there was no recruitment of new individuals in September. In other vole populations densities are relatively high at the end of the breeding season (Taitt and Krebs 1985). Hasler (1975) noted that individuals of the genus *Microtus* can attain sexual maturity at approximately 30 days of age. However, this age can vary with density, season, and time of birth. In a detailed 10 year study of the life history profiles of boreal meadow voles, Mihok (1984) found that most young of the year captured early in the breeding season (May to July) matured in the year of their birth. In the present study seventeen juveniles were first captured in June and July, however, only one animal matured by late September. The one juvenile to become reproductively active showed signs of maturity at 60 days of age. Several other juveniles were 70 to 90 days of age and still showed no signs of sexual maturity. Voles born in low density years are more likely to mature than in years of high density (Mihok 1984). In southwestern Manitoba, even in peak densities of 100 voles/ha as high as 38% of juveniles attained maturity in the year of their birth. In the present study, only 6% of juveniles matured during the summer when densities were 11 voles/ha. This delayed reproduction observed in juveniles must have played an important role in the low densities observed on the study plot, specifically at the end of the study period (for further discussion see section 3.4.5). It is not known whether this low reproductive rate is typical of Newfoundland voles since reproductive rate can vary quite substantially between years.

Sorex cinereus densities appear to vary between habitat types on the island of Newfoundland. Tucker (1988) reported *Sorex* densities of 75 individuals/ha in a 13 year-old cutover and 10 individuals/ha in a one year-old cutover during the same trapping session. J. Brazil and K. Knox (pers. comm.) report difficulty in determining a general density for shrews because of the fluctuation in shrew numbers among habitat types and years. Studies of *Sorex cinereus* on continental North America have reported densities ranging from 1-23 individuals/ha (for a review see Churchfield 1990). Over the four months of this study 53 shrews were captured on the 3.2 ha plot. Unfortunately, density estimates could not be made because shrews were observed escaping from the handmade wooden live-traps. Also, during trap checks, shrews were released immediately from the traps if still alive and therefore removal estimates of density could not be used. However, since trapping techniques were standardized across plots, this study revealed that shrew numbers were highest in the meadow habitat.

Density estimates have not been determined for *Peromyscus* in Newfoundland. Tucker (1988) captured a total of 44 deer mice in old-growth forest and clearcut areas totaling 60 hectares from spring 1986 to fall 1987. K. Knox and J. Brazil (pers. comm.) have also reported very low numbers of *Peromyscus* in old growth forest. In the present study, only five deer mice were captured on the 3.2 ha plot in a four month period, and three were captured in a 1.1 ha meadow plot over a three week period. These limited trapping studies suggest that *Peromyscus maniculatus* occur at low densities in western Newfoundland.

3.4.2. Habitat Preference

In western Newfoundland, meadow voles appear to exhibit preference for moist meadows or habitats in close proximity to small moist areas. Seven of the eight juvenile females which were radio-collared had a portion of their home range within meadow habitat. Furthermore, during times away from the nest the mothers were observed in meadow habitat and/or small moist clearings. J. Brazil and K. Knox (pers. comm.) also noted that voles were captured at higher densities in grassy areas or if moist openings or meadow habitat were close to the trap line. Other studies (Cameron 1958; Tucker 1988) have shown that Newfoundland voles occurred at relatively high densities in forested areas. Cameron (1958) reported that voles were located in forested areas as far as 20 miles from any clearings *of appreciable size* (italics mine). The present study, however, found that meadows or moist clearings utilized by voles can be quite small in size (less than 1 m^2). A description of the micro-habitat may have revealed small moist patches in the wooded areas trapped by Cameron (1958). Furthermore, the high densities of voles in the forested area found by Tucker (1988) may have been a rare occurrence. Since 1988, small mammal live-trapping studies conducted in forest sites of the same study area as Tucker (1988) have resulted in considerably lower vole densities (J. Brazil and W. Adair pers. comm.). The higher densities of voles observed in the present study may have been due to the presence of small moist areas and meadows within the 9-year-old clearcut.

Newfoundland is covered mostly by coniferous and mixed forests, barrens and bogs whereas meadow and grassy areas are uncommon. D. Wells (pers. comm.) suggests that moist meadow areas occupy less than five percent of the landscape of western Newfoundland. Meadow voles appear to colonize these meadow areas first (Folinsbee *et al.* 1973), but at high densities will utilize the less preferred habitats such as forests and bogs (Dodds 1983). This may help explain the conflicting trapping evidence in the literature. The fluctuation of vole numbers in Newfoundland (Pruitt 1972) can make year to year comparisons of population densities quite difficult. Tucker (1988) reported a 'crash' of the meadow vole population in which vole densities declined within the same trapping grid of an old-growth forest from 25 individuals/ha in 1986 to 0 individual/ha in 1987. Fluctuation peaks when densities are high, may result in voles being present in forested areas and fluctuation crashes when densities are low, may result in voles being absent from forested areas. Similarly, Grant (1971a) reported that the movement of *Microtus* from a grassland to woodland area only occurred at high densities. In general, it appears that Newfoundland voles prefer moist meadow habitat but will colonize other less preferred habitats during years of relatively high density.

Meadow voles on insular Newfoundland appear to exhibit similar preferences for meadows as do continental populations, although forest dwelling rodents such as Red-backed voles are not present in forests of Newfoundland as they are on the continent of North America. It has been hypothesized that competitive interaction between meadow voles and Red-backed voles restricts each species to its preferred habitat (for review see Grant 1971). Several studies conducted on off-shore islands found that in the absence of any typical woodland species, grassland species will utilize the forest area as well as their preferred habitat (Webb 1965). *M. pennsylvanicus* may not utilize forested areas even in the absence of red-backed voles (Morse 1973) suggesting that the absence of a competitor species, by itself, is not a sufficient reason for the use of wooded area by *Microtus*. Meadow voles in Newfoundland may use forest area when densities are high and competitors are few.

On offshore islands of Newfoundland, introduced *Clethrionomys gapperi* and native *M. pennsylvanicus* were found to co-exist (Payne 1974). Since *C. gapperi* have not yet been reported on the mainland of Newfoundland, Payne (1974) suggests this may have more to do with differential dispersal and establishment abilities between *M. pennsylvanicus* and *C. gapperi* rather than with competitive exclusion. Crowell (1973) found that *Clethrionomys* was a poor colonizer and unable to maintain sufficient numbers even when introduced. Kirkland (1988) suggests that long-distance dispersal in meadow voles may be an adaptation to the type of habitat present in North America before Western colonization, when continuous forested areas were dominant and small herbaceous patches were scattered widely throughout the landscape. By means of long-distance dispersal, *Microtus pennsylvanicus terraenovae* may be able to reach and exploit patchy meadow habitat throughout the island of Newfoundland. Furthermore, Payne (1974) indicates that *M. pennsylvanicus* appears to be better able to establish and maintain a population on island situations than *C. gapperi*. These two characteristics may help explain why *Microtus pennsylvanicus* is the only vole species established on the island of Newfoundland.

Cover also appears to affect habitat use of female meadow voles with litters. Female with young were found to occupy home ranges in forest regeneration habitat which are areas of relatively high cover. Feeding activity, however, was observed in meadow habitat or small moist patches where cover was relatively lower. Cover is important for protection from predators and has been shown to increase survival, immigration and reproduction of small mammals (Taitt *et al.* 1981; Taitt and Krebs 1983). Similarly, Getz (1970) noted that small mammal densities and survival rates were higher in a marsh area with a litter layer as compared to one without a litter layer. Furthermore, Heteromyid rodents were shown to move to areas of good cover when predators were present (Brown *et al.* 1988). In the present study, female with young may have established home ranges in areas of increased cover to protect their young from predators. During times away from the nest, four of the five adult female voles were located in the meadow habitat or small moist patches which were areas of relatively lower cover. This suggests that the benefits of feeding in meadows may outweigh the increased risk of predation.

Shrews were found in several habitats during the present study except a one month-old cutover site. The lack of moisture in this newly altered habitat is the most likely reason for this finding, as moisture appears to be the main factor affecting shrew distribution (Getz 1961a). As with the meadow voles, shrew numbers were greatest in the meadow habitat. Shrews have been found in a variety of habitat types in western Newfoundland with densities highest in deciduous shrub and lowest in bogs and barrens (Folinsbee 1971). Tucker (1988) found the highest shrew densities in 13 year-old clearcut sites whereas Roscoe and Ouelette (1980) reported high densities of shrews in black spruce/balsam fir forests with moss and litter as the dominant ground cover. J. Brazil and K. Knox (pers. comm.) captured shrews in all habitat types from bogs and barrens to mixed hardwood forest. Shrews appear to be present in a variety of habitats dependant on moisture and a small amount of ground cover.

Peromyscus were captured in both 9-year-old and two year-old (section 2.4.1) clearcut sites. Other studies of *Peromyscus* in Newfoundland have reported deer mice in young and old cutovers and old growth forest (Tucker 1988; K. Knox and J. Brazil pers. comm.). The present study found that deer mice also occur in meadow habitat in western Newfoundland. On the mainland, *Peromyscus* are found in a large variety of habitat types (Banfield 1974) suggesting that deer mice have the ability to adapt to many different environments. *Peromyscus* have only been reported in western Newfoundland, although only a few small scale trapping studies have been conducted in eastern and central Newfoundland since the early 1980's (L. Duquette pers. comm.). The rate of dispersal and distribution of *P. maniculatus* are uncertain at present. With the ability of this mouse to exploit new environments it is highly likely that most habitats within Newfoundland will eventually be colonized by this species.

3.4.3. Space Use

The size of female meadow vole home ranges in western Newfoundland appears to be larger than those reported for similar voles elsewhere in North America. In the present study, 9 out of 13 home ranges established were over 2500 m^2 with only four voles establishing home ranges under 2000 m^2. In Michigan, Getz (1961b) found female ranges averaged from just over 100 m^2 to almost 500 m^2 whereas Reich (1981) reported home range size in female *M. pennsylvanicus* to range from 160 m^2 to 3115 m^2. It is important to note that between study comparisons of home ranges may be difficult to interpret. Methodology is not standardized for home range estimates and will vary between studies due to different techniques used (Getz 1961b). In the present study, home ranges were estimated from radio-collared females, whereas Getz (1961b) estimated home range size from live-trapped populations. Home range size estimates are substantially larger in the present study than by Getz (1961b) and are similar to the largest home range size observed by Reich (1981) suggesting that, even with variation, voles in western Newfoundland may establish comparatively large home ranges.

Large home ranges can be the result of low densities (Getz 1961b; Taitt *et al.* 1981; Wolff 1984), low resource availability (Jones 1984; Ims 1987), low food quality (Jones 1990) and/or inferior micro-habitat (Sheridan and Tamarin 1988). As stated earlier, densities of meadow voles are low and preferred habitats are rare and scattered throughout Newfoundland. These factors may play a part in the home range dynamics of Newfoundland voles. Bergeron *et al.* (1990) concluded that crowding conditions and availability of high quality food concurrently influenced space use by female meadow voles. Predation has been shown to reduce small mammal movement and home range size (Desy *et al.* 1990). Predation may be affecting home range distribution of voles in Newfoundland as all adult females with litters established nests in areas of relatively high cover.

Reproductive status does not appear to affect periphery home range size. Conversely, Ostfeld *et al.* (1988) reported smaller home ranges in females which had successfully reared young. Core home range size was significantly smaller for reproductive females than non-reproductive females which is consistent with the findings of Sheridan and Tamarin (1988) who found female with young to be more site tenacious. Due to the scattered food resources on the study site, female voles may have established large home ranges to allow access to food. The use of space within the home range may have been reduced for adults because of the care required by a litter. Several authors have conducted multifactorial experiments and found that a number of factors act simultaneously in determining space management of voles (Taitt and Krebs 1983; Desy and Batzli 1989; Desy *et al.* 1990). In the present study, low densities, scattered food supplies, reproductive status and predation may all have played a role in the home range size and distribution of meadow voles on Newfoundland.

The very small amount of overlap of adult females found in this study suggests that adult female voles in Newfoundland are territorial. This is similar to the findings of several authors (Madison 1980; Ostfeld *et al.* 1988) who have observed little or no overlap of adult female *Microtus* home ranges. Juvenile voles, however, exhibited up to 75 percent overlap of home ranges. Similarly, Ostfeld *et al.* (1988) found that females without litters had home ranges which overlapped to a greater extent than those with litters. In the present study, most home range overlap between the juveniles occurred in the meadow habitat. Since meadow habitats are rare and highly preferred, defending this type of habitat would require much time and energy. Sharing the resources may result in the maximum fitness benefit for juvenile voles.

Home ranges of male voles in Newfoundland could not be determined due to the long distances they traveled out of the range of the reciever. This suggests that males in western Newfoundland are either transients or establish very large home ranges. Male *M. pennsylvanicus* have been reported to establish home ranges which can vary in size from 405m^2 to 3480m^2 (Reich 1981). Males set up home ranges which overlap and allow access to several reproductive females (Ostfeld 1986). In situations where defensibility of a key resource (i.e. females) is not beneficial in terms of reproductive success then animals will not establish home ranges (Lott 1984). In other words, males would rove in search of estrous females. Similarly, Storey *et al* (1995) argues that at low population densities searching, rather than mate guarding, may be the best male meadow vole strategy. This may explain why males did not persist on the study area. In western Newfoundland, vole densities were low and females have large home ranges, therefore defending females may not be energetically beneficial and males may have to search for receptive females. Populations in which males rove and females are territorial are indicative of promiscuous mating systems (Madison 1980) in which males will mate with more than one female, and females will mate with more than one male (Clutton-Brock 1989). Promiscuous mating systems are fairly common for *Microtus pennsylvanicus* (Madison 1980a; Madison 1980b; Boonstra *et al* 1993).

Microtus pennsylvanicus were active all day from dusk until dawn, although distance traveled varied with time of day and reproductive status. In the present study, female voles moved significantly longer distances in late morning compared to early morning. Webster and Brooks (1981), however, found no difference between crepuscular and diurnal activity. Traveling shorter distances during early hours may decrease the risk of predation as raptors in western Newfoundland tend to be active in the early morning (J. Gosse pers. comm.). Juveniles traveled longer distances then adult females. Since increased activity increases risk of predation (Kaufman 1974) females with litters may benefit by traveling shorter distances. Similarly, Getz (1961b) suggests that maternal care of the young limits the range of activity of female meadow voles with litters. However, Webster and Brooks (1981) noted that reproductive *Microtus* females tended to move further distances in summer and autumn than non-reproductive voles. Although the reason for these conflicting results is unknown at present, Sherman (1984) reported that after the first week of lactation female meadow voles begin to spend less time at the nest. Therefore, reproductive females may travel longer distances as the litter becomes older and requires less maternal care.

Newfoundland voles traveled from 9 to 23 meters between successive one hour locations. These distances are considerably longer than those reported in the literature for other meadow vole populations. Ambrose (1973) found that voles traveled between 1.9 m/hr and 6.3 m/hr. In Ontario, non-reproductive females traveled, on average, 3.8 m/hr and reproductive females traveled, on average, 4.4 m/hr (Webster and Brooks 1981). Home ranges established by Newfoundland voles tend to be larger, therefore distances moved would most likely be further. The scattered distribution of food resources may also result in longer distances traveled by Newfoundland voles. Studies have shown that meadow voles are also nocturnally active (Osterberg 1962). In fact, Webster and Brooks (1981) observed no difference between frequency of movement in reproductive females during night and daytime. It is not known whether Newfoundland voles are nocturnal, although a few sightings of voles after dusk (pers. observ.) suggest that they are active to some degree during darkness.

3.4.4. Food Preference

Newfoundland voles appear to differ in feeding habits from mainland voles. Ferns, horsetail and certain forb species were highly preferred by all voles tested in western Newfoundland, whereas *M. pennsylvanicus* on the mainland in Quebec, Alaska and Illinois have been shown to prefer grasses and sedges (Bergeron and Juillet 1979; Bangs 1984) and forbs (Neal *et al.* 1973; Lindroth and Batzli 1984). Norrie and Millar (1990) found that voles in Alberta prefered grasses and sedges more than other plant species. Forbs were the second most palatable group, followed by 'other' species (ferns, moss, horsetail and lichen). Ferns, horsetail, *Salix* species, and bunchberry were all highly palatable to voles in the study conducted by Norrie and Millar (1990) and voles in the present study. However, several species differed in their palatability between the two vole populations. *Carex* species, grasses and mosses had higher palatability scores, whereas *Rubus* species had lower palatability scores by voles in Alberta than voles in Newfoundland.

In Newfoundland, plant palatability appears to be related to habitat preferences rather than plant groupings. Plants found in the highly preferred meadow habitat were highly palatable. Low palatability was observed in plant species found in the less used habitats, forest regeneration sites and clearings. Norrie and Millar (1990) tested plants within the voles preferred habitat and therefore did not examine plant palatability in relation to habitat preference. Riewe (1973) conducted a similar feeding trial and reported that voles occupying islands in Notre Dame Bay, Newfoundland foraged on plant species dominant in typical meadow habitat. Riewe (1973) also found that species characteristic of forested areas were accepted by the voles year round indicating that feeding habits may have become adjusted to habitat use since voles were observed utilizing forested area on offshore islands. In the present study it was also observed that some plant species typical of forests such as *Salix* species, *Cornus canadensis*, and *Clintonia borealis* were highly palatable to the meadow voles. This suggests that Newfoundland voles could subsist on plant species in forested areas. Although some studies have reported that small mammals forage generally in relation to plant availability and not preference (Dyke 1971; Sharp 1965 cited in Dyke 1971; Zimmerman 1965), voles on insular Newfoundland appear to have adapted a feeding strategy which seems to parallel plant preferences, and not plant availability. Similarly, Batzli (1988; Batzli and Lesieutre 1991) found that voles densities could be predicted by preferred forage species abundance.

The present study found no relationship between plant preference and nitrogen and/or phenolic concentration, whereas several studies have found that meadow voles prefer plant species with high protein content and low digestive inhibitors (Jung and Batzli 1981; Bergeron and Jodoin 1987; Bucyanayandi and Bergeron 1990). Huntly and Inouye (1987) reported that small mammal density and diversity were limited by nitrogen of plant species. These conflicting findings may be the result of differential allocation of plant resources to chemical defense. Lindroth (1984) noted that at high vole population densities, plant grazing by meadow voles induced the production of phenols. In Newfoundland small mammal densities are constantly low and during vole crash years when densities are extremely low, large portions of habitat are probably unutilized. The low densities of voles in western Newfoundland may result in very low allocation of plant resources to chemical defense. In the present study, plant phenol concentrations were low relative to other studies (Bergeron and Jodoin 1987). Although secondary compounds have been shown to have deleterious effects on *Microtus* (Jung and Batzli 1981; Lindroth *et al.* 1986), plants in Newfoundland may have such low phenolic concentrations that vole fitness is not affected.

Bergeron and Jodoin (1987) consider high quality food resources for voles to be plants which are high in nitrogen and low in phenols. Since the ratio of nitrogen to phenols did not effect preference of plant species to *Microtus* in western Newfoundland it appears that food selection patterns are different for voles in this study. Batzli (1988) measured quality of plant species by its direct effect on juvenile growth rate and found plant quality to be highly correlated to plant palatability. Batzli and Lesieutre (1991) noted that only the highly palatable species maintained or supported growth in young voles suggesting that highly palatable species were the highest in quality. Voles which forage on high quality foods show increased reproductive success (Batzli 1986; Desy and Batzli 1989) and can contribute to population growth even when negative effects such as predation are constant. Areas with higher quality food support higher densities of voles (Batzli 1976; Cole and Batzli 1979; Batzli and Lesieutre 1991).

3.4.5. Predation

Meadow voles and shrews are the dominant small mammals throughout Newfoundland and therefore are likely to be a highly utilized food resource. The small size of the *Sorex* may make them a less energetically beneficial forage item to predators than *Microtus*. On islands off Newfoundland, Riewe (1971) found that ermine and rough-legged hawks (*Buteo lagopus*) preyed heavily on *Microtus*. J. Gosse (pers.

comm.) reported that hawk owl and rough-legged hawk pellets collected in western Newfoundland in 1993 and 1994 contained over 85% small mammal remains, all of which were *Microtus*. Tucker (1988) found that *Microtus* were an important prey item for pine marten (*Martes americana*) in western Newfoundland. Predation may have been a factor causing adult females to establish home ranges in forest regeneration since small mammals tend to utilize areas of higher cover if predators are present (Brown *et al.* 1988).

Predation on *Microtus* may be contributing to the constant low densities of this species throughout Newfoundland. The low diversity of alternate small mammal prey species in Newfoundland could result in continual predation on meadow voles. Hansson (1984) found that extended periods of low density in microtine cycles can be attributed to continual predation. Continual predation can cause extended low densities by suppressing reproduction, as shown by Ylonen (1989), or by delaying maturation of young (Heikkila *et al.* 1993). During the present study only six percent of the young captured became reproductive over the four month period of the study suggesting that some factor suppressed reproduction in young voles. The presence of adult females have been shown to inhibit maturation of young (Rodd and Boonstra 1988). This only occurs at high densities and therefore may not be applicable in Newfoundland. Riewe (1971) reported that only five of the 334 juveniles examined during his study were sexually active. Other studies of insular microtines have also reported low reproductive rates (Jewell 1966 cited in Riewe 1971). Past studies have shown that ermine scent can delay maturation in juveniles (Heikkila *et al.* 1993) and several captures and sightings of ermine on the study area suggest that their abundance may have been quite high.

CHAPTER FOUR - THE SHORT-TERM RESPONSE OF SMALL MAMMALS TO PRESCRIBED BURNING IN WESTERN NEWFOUNDLAND

4.1. Introduction

Conventional clearcutting leaves an accumulation of bark, branches, coniferous tree tops and other debris on harvested sites. This debris is called slash and makes planting of new trees difficult and can prevent seeds from reaching fertile soil (Tevis 1956). Prescribed burning is a forestry method used to prepare cutover sites for planting or direct seeding by the removal of this slash. In Newfoundland, 8-10 clearcut sites have been prescribed burned in the past fifteen years (D. Wells pers. comm.). No studies have been conducted to document the effects of burning on any of these sites even though the possible ecological and/or environmental consequences are still poorly understood.

Several studies have examined the effect of prescribed burning on small mammal populations (Tevis 1956; Cook 1959; Tester 1965; Lawrence 1966; Sims and Buckner 1973; Krefting and Ahlgren 1974; Sullivan 1980; Martell 1984; Vacanti and Geluso 1985; Grooves and Steenhof 1988; Kaufman *et al.* 1990). Small mammal response to fire is species specific and seems to be related to habitat preference (reviewed in Kaufman *et al.* 1990). Herbivorous small mammals, such as *Microtus*, appear to recolonize burned sites at slow rates. Seed-eating rodents, such as *Peromyscus*, appear to colonize burned areas rapidly relative to herbivores. Several hypotheses have been put forth to explain why herbivorous rodents colonize burn areas slowly: lack of vegetative cover (Cook 1959), lack of food (Sims and Buckner 1973), increased desiccation (Kirkland 1990) and interspecific competition (Sullivan 1980). For granivores, the main reason suggested for their rapid colonization of burned areas is the increased availability of exposed seeds (Cook 1959).

The effects of prescribed burning on small mammal populations could have major implications for boreal forest ecology in Newfoundland since diversity and density of small mammals is low. Small mammals are a very important food source on the island, providing prey for a number of animals such as owls, hawks, eagles, fox, marten, ermine, and lynx (J. Brazil pers. comm.). Any changes in small mammal dynamics such as reduced abundance could have substantial effects on higher trophic levels, especially for animals which rely almost exclusively on small mammals for food.

The purpose of this study was to examine the short-term response of small mammals to prescribed burning with emphasis on the role of cover in this response. The design consisted of three treatments: prescribed burn, prescribed burn plus cover and control. Each treatment consisted of two 0.81 ha plots established in a two year-old clearcut. All treatment plots were placed at least 75 meters apart to ensure that animals did not move between plots. In September 1994, the burn and burn plus cover treatments were burned by Newfoundland Forest Service personnel. Following the burn, the burn plus cover plots were homogeneously covered with slash consisting of branches and tree tops with no living vegetation. The two remaining plots were left unburned to serve as controls.

This study was designed to discern the interactive roles of food and cover on burn areas. Although the gradual re-establishment of vegetation on burned areas has been shown to coincide with small mammal recolonization (Vacanti and Geluso 1985), it is not certain whether slow recolonization by voles is due to a gradual increase in food supply or an increase in cover since vegetative regrowth can be utilized as both. Studies have shown that both food and cover are important factors affecting vole distribution and abundance (Eadie 1953; Birney *et al.* 1976; Desy and Thompson 1983). Taitt and Krebs (1981) found that voles on experimental plots with added cover increased reproduction and started breeding earlier relative to voles on experimental plots with added food. This suggests that additional cover may be more beneficial to voles in terms of reproduction than additional food. Clark (1989), however, found that breeding populations of small mammals were higher in areas of higher food availability rather than in areas of higher cover. The present study was designed to determine the importance of cover to *Microtus* independent of food. To control for cover effects, a non-vegetative slash was applied to the appropriate experimental sites. This approach allowed me to study the effects of cover independently of food since slash is not a food source for herbivorous small mammals.

Since prescribed burning will presumably decrease vegetation and hence food for herbivorous rodents, and cover will aid in protecting animals from predators by providing shelter for their nests and runways, I predict that densities of voles on covered burn sites will be high relative to the uncovered burn sites. Control plots will support the highest densities. I also predict that voles on control and covered burn treatments will be more active relative to the uncovered burn treatment. Voles on control and covered burn plots will have increased protection from predation and, in turn, be able to increase foraging time. Voles on the uncovered burn sites will have no protection from predation and therefore have less opportunity to forage. The high moisture requirements of shrews will make burn and burn plus cover sites suboptimal habitat relative to control sites. However, cover may increase microhabitat humidity, and therefore I predict that control sites will support the highest densities of shrews, followed by covered burn sites. Burn sites will support the lowest densities of shrews. I predict that *Peromyscus* will exhibit a fire-positive response, and abundance will be higher on the burn and burn plus cover sites and lower on the control sites. The addition of cover on covered burn sites may increase protection from predation and therefore abundance will be higher on covered burn sites relative to burn sites.

4.2. Methods

4.2.1 Experimental Design

In early August of 1993, six experimental plots were established in a large two year-old clearcut near Glide Lake Newfoundland (49° 05' N latitude and 57° 24' W longitude). Plots were 90x90 meters (0.81 hectares) and trapping grids within each plot were established in seven by seven grids with traps 10 meters apart. Traps were placed 10 m inward from the edge of the plot so as to trap animals residing on the plot and not from adjacent habitats. Plots were established at least 75 meters apart to minimize animals traveling between plots. Small mammals were trapped on each plot to obtain an estimate of population density. Each plot was trapped for six consecutive days and checked three times a day. Plots A through D were trapped from August 16 to 21; plots E and F were trapped from August 22 to 27. Trapping techniques are reported in section 2.2.

In September of 1993, Plots A through D were burned by Newfoundland Forest Service personnel according to standard forestry practices. In October, all plots were trapped for five consecutive days to remove resident animals so that spring densities could be compared among treatments. Victor snap traps were baited with peanut butter and placed at trap stations. Traps were checked twice daily. Immediately following removal trapping, Plots B and D were homogeneously covered with slash from a nearby large clearcut site. The slash consisted of dead branches and tree tops, and did not contain any needles or living vegetation. The slash added to the cover sites was similar to the slash on the control plots.

The experimental design of this study is summarized in Table 4.1.

From late May through mid September of 1994 plots A through F were live-trapped (section 2.2) to study the response of small mammals to prescribed burning. Catch per unit effort (CPUE) was calculated as the number of individuals captured per 8 hour trap check. The length of time a vole remained on a plot (herein referred to as duration) was calculated as the first capture minus the last capture. Four female *Microtus* were radio-collared in July and August to study space use (section 2.3).

4.2.3 Vegetation Surveying and Plant Sampling

Eight 5x5 m Braun-Blanquet quadrats (section 2.4) were randomly established in all six plots in July of 1994 to study habitat structure. To compare floristic characteristics among treatments, the following seven habitat variables were described: slash cover, total number of plant species, herbaceous cover, total number of palatable species, palatable cover, vertical structure and plant diversity. Slash was measured visually as the percent of the quadrat covered by slash. Herbaceous cover was also measured visually as the percent of the quadrat covered by herbaceous vegetation. Palatable species was determined as the number of species on the plot which received a palatability score of 2.5 or higher (see Appendix C). Palatable cover was calculated by adding up the herbaceous cover percents of all palatable species within the quadrat. Vertical structure was recorded as the stratification layer with the highest amount of herbaceous cover. The Shannon Index (Smith 1990) was used to calculate plant diversity.

Seven plant species were collected from each plot in late June and late July to determine if plant nutrients (section 2.4) differed among treatments. Plants were sampled at two different times, July and August, to ensure that treatment differences were detected. The species collected from each plot were: Plume Moss (*Ptilium crista-castrensis*), Yellow Clintonia (*Clintonia borealis)*, Bunchberry (*Cornus canadensis*), Twin flower (*Linnaea borealis*), Gold Thread (*Coptis groenlandica*), Blueberry (*Vaccinium angustifolium*) and Chuckley-Pear (*Amelanchier bartramiana*). The plant species chosen were those present on all six plots.

4.2.4 Statistical Analysis

One-way ANOVA models were used to test for the effect of treatment on total number of animals, CPUE and duration of *Microtus* and *Sorex*. The effect of treatment on habitat variables was tested separately for each variable in a one-way ANOVA. A three-way ANOVA tested for effects of treatment, species and time on nitrogen concentration, phenol concentration and ratio of nitrogen to phenols.

4.3. Results

4.3.1. Live-trapping

Capture-mark-release trapping captured 54 small mammals in the Burn study area (Table 4.2). Total number of *Microtus*, *Sorex*, and *Peromyscus* captured over the four month period was relatively low for all treatments (Fig. 4.1). Total number of *Microtus* captured was not significantly different among treatments (Table 4.3). Although the total number of *Sorex* captured on the control plots was three times higher than the cover or burn plots, the difference was not significant (Table 4.3). Catch per unit effort (CPUE) of *Microtus* did not different significantly among treatments but CPUE was significantly higher for *Sorex* on burn and cover plots (Table 4.4). The length of time *Microtus* remained on a plot averaged 8.5±2.5 days and did not vary among treatments ($F_{2,28}$=1.30, p=0.30).

4.3.2. Space Use

Due to the low density of voles on the study area only four female voles were collared during the study. Periphery home range size of the four female voles averaged 2115±675m^2. Core home range size was 179±96m^2. Overlap of home ranges did not occur. Three of the four females established home ranges within fairly close proximity to

Table 4.1: The number of small mammals captured during the pre-burn survey in August of 1993 and a summary of the treatments applied to the plots.

	August 1993			Experimental Treatments*
Plot	*Microtus*	*Sorex*	*Peromyscus*	
A	4	2	0	BURN
C	1	1	4	BURN
B	2	2	0	COVER
D	3	0	1	COVER
E	1	0	2	CONTROL
F	2	2	0	CONTROL

*Experimental Treatments:

BURN - study plots in the 2-year-old clearcut were prescribed burned;

COVER - study plots in the 2-year-old clearcut were prescribed burned and then recovered with slash;

CONTROL -study plots in the 2 year-old clearcut remained unburned

(section 4.2.1)

Table 4.2: Total number of small mammals captured on burn, cover and control plots from May to September 1994. Recaptures were minimal and therefore not included in the table.

Plot (Treatment)	*Microtus*	*Sorex*	*Peromyscus*
A (Burn)	5	2	1
B (Cover)	5	2	2
C (Burn)	3	0	0
D (Cover)	12	0	1
E (Control)	5	5	0
F (Control)	4	7	0
Total	34	16	4

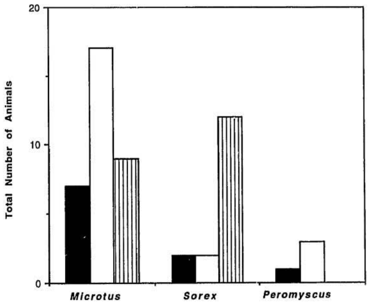

Figure 4.1: Total number of *Microtus*, *Sorex* and *Peromyscus* captured on the Burn study area during live-trapping sessions on burn (solid bars), cover (open bars) and control (lined bars) plots from May to September 1994.

Table 4.3: Reduced ANOVA models for the effect of prescribed burning on total number of *Microtus* and *Sorex*. SS refers to sums of squares.

Variable	Source	DF	SS	F	P
Microtus	Treatment	2	34.33	1.56	0.15
	Error	3	33.33		
Sorex	Treatment	2	33.33	8.33	0.10
	Error	3	6.00		

Table 4.4: Reduced ANOVA models for the effect of prescribed burning on catch per unit effort of *Microtus* and *Sorex*. SS refers to sums of squares.

Variable	Source	DF	SS	F	P
Microtus	Treatment	2	1.206	1.89	0.15
	Error	294	93.7		
Sorex	Treatment	2	0.666	6.82	0.0013
	Error	294	14.36		

a small moist patch of meadow. The following description of female vole space use is summarized in Fig 4.2. Female 1 established a home range partially on control plot F, but predominantly in the meadow. This female was located in the moist meadow habitat 83% of the time and on the control plot under the slash piles 17% of the time. Average distance traveled by Female 1 was 22.1±2.8 m/hr. This was the only non reproductive vole collared in the Burn study area. Female 2 was reproductively active but did not have a young litter during radio-collaring. She establised her home range in the cutover between a burn and a burn plus cover treatment (plots A and B). She was located within meadow habitat 3% of the time and in the cutover the remaining time and traveled 15.7±3.4 m/hr. Female 3 was the only female to have a litter during radio-collaring. She established her home range in the cutover and was never located in a meadow. She was captured on the burn treatment (plot A) several times during live trapping sessions and traveled 5.9±1.1 m/hr. Female 4 was reproductively active but did not have a litter at the time of radio-collaring. She utilized the cover plot D the majority of the time, but was also located in the meadow area 25% of the time. Average interfix distance of female 4 was 21.0±9.0 m/hr. Autocorrelation of interfix distances was negligible (autocorrelation coefficient = 0.31) and therefore each location was considered independent. Time of day was not a significant predictor of distance traveled ($F_{15,87} = 0.87$, $p=0.53$).

4.3.3. Habitat Structure

The results of the Braun-Blanquet survey are reported in Appendix D. Four of the seven habitat variables measured were significantly different among treatments (Table 4.5). Herbaceous cover and total number of species were significantly lower on the burn than the control treatments (Table 4.6). Slash cover was significantly lower on the burn than the control or cover treatments and palatable cover was significantly lower on the control than the burn or cover plots. (Table 4.6). Treatment areas did not differ with

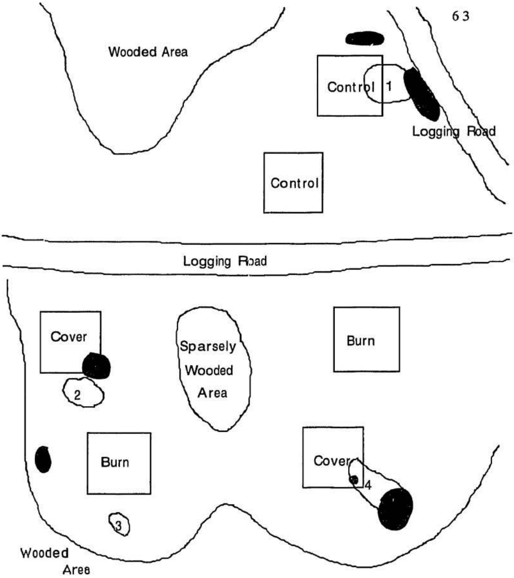

Figure 4.2: A pictorial representation of periphery home ranges (1-4) of females within the Burn study area in 1994. Gray shaded areas represent meadow habitat. Home range numbers correspond to female numbers reported in the text. i.e. Female 1 in text would correspond to home range 1.

Table 4.5: Reduced ANOVA models testing for the effect of treatment on slash cover, total number of species, herbaceous cover, palatable cover, palatable species, vertical structure and plant species diversity. SS refers to sums of squares.

Habitat Variable	Source	DF	SS	F	P
Slash cover	Treatment	2	1065	17.1	0.0001
	Error	45	13996		
Total Number of Species	Treatment	2	364.6	7.60	0.0072
	Error	45	1488		
Herbaceous Cover	Treatment	2	31924	3.20	0.03
	Error	45	22460		
Palatable Cover	Treatment	2	2284	3.86	0.03
	Error	45	13322		
Palatable Species	Treatment	2	8.000	2.15	0.13
	Error	45	83.81		
Vertical Structure	Treatment	2	0.161	2.49	0.11
	Error	45	1.456		
Diversity	Treatment	2	0.696	1.29	0.29
	Error	45	12.18		

Table 4.6: Habitat variables measured on the burn, cover and control treatments in August 1994. Numbers with the same letter are significantly different. Vertical structure, diversity and palatable species and were not significantly different among treatments (see Table 4.5) and therefore not included in this table. Means ±1 S.E. are reported.

	Treatment		
Habitat Variable	Burn	Cover	Control
Herbaceous cover (%)	101.8 ± 12.3^{a}	145.0 ± 17.7	163.3 ± 22.4^{a}
Slash cover (%)	1.3 ± 0.72^{bc}	37.2 ± 6.6^{b}	24.7 ± 3.8^{c}
Total Number of Species	9.3 ± 0.10^{d}	12.6 ± 1.3	16.1 ± 1.9^{d}
Palatable Cover (%)	10.7 ± 2.9	20.6 ± 6.7^{e}	6.9 ± 1.5^{e}

respect to number of palatable species, vertical structure or diversity.

4.3.4. Vegetation Analysis

Nitrogen concentration of plant species was significantly different among treatments, although the effects of time and species on nitrogen concentration could not be determined due to a significant time-species interaction (Table 4.7). Non-signifiicant interactions were removed from the model (interaction between treatment and species: $F_{12,42}=1.05, p=0.42$; interaction between treatment and time:$F_{2,42}=0.38, p=0.68$; interaction between treatment, time and species:$F_{12,42}=0.60, p=0.82$). Nitrogen concentration was higher on the burn and cover treatments than the control treatment (Table 4.8). Time did not affect phenol concentration. Treatment and species effects on phenol concentration could not be interpreted due to a significant treatment-species interaction (Table 4.7). All non-significant interactions were removed from the model (interaction between species and time:$F_{6,42}=0.20$, $p=0.97$; interaction between treatment and time: $F_{2,42}=0.03, p=0.97$; interaction between treatment, time and species:$F_{12,42}=0.20$, $p=0.99$). Nitrogen to phenol ratio was significantly different between July and August although treatment and species effects could not be determined due to a significant treatment-species interaction (Table 4.7). Non-significant intertactions were removed from the model (interaction between species and time: $F_{6,42}=0.43, p=0.85$;interaction between treatment and time: $F_{2,42}=0.32$, $p=0.73$; interaction between treatment, time and species: $F_{12,42}=0.39, p=0.96$). Nitrogen to phenol ratio was higher in July than in August (Table 4.8).

For all significant interactions stated above, post hoc tests as in Winer (1991) were not possible due to low number of replicates. Therefore, to determine the nature of the interactions data were graphed and visually interpreted. For the significant interaction between time and species for nitrogen concentration, *Clintonia borealis*, *Coptis* *groenlandica* do not appear to differ over a months period, whereas *Amelanchier bartramiana* and *Ptilium crista-castrensis* decreased in nitrogen concentration from July to August (Fig. 4.3). For the significant interaction between treatment and species for phenol concentration, *Vaccinium angustifolium*, *Clintonia borealis* and *Amelanchier bartramiana* appear to have the lowest phenol concentration on cover plots, whereas phenol concentration of *Linnaea borealis* and *Cornus canadensis* are highest on cover plots (Fig. 4.4). For the significant interaction between treatment and species for nitrogen to phenol ratio, *Ptilium crista-castrensis*, *Coptis groenlandica*, *Linnaea borealis* and *Amelanchier bartramiana* appear to have high ratios on cover plots, whereas *Clintonia borealis*, *Cornus canadensis* and *Vaccinium angustifolium* have low nitrogen to phenol ratios on cover plots (Fig. 4.5).

Table 4.7: Reduced ANOVA model for effects of treatment, species and time on nitrogen concentration, phenol concentration and ratio of nitrogen to phenols.SS refers to sums of squares.

Variable	Source	DF	SS	F	P
Nitrogen	Treatment	2	19.72	10.48	0.0004
	Species	6	409.5	66.8	0.0001
	Time	1	44.14	43.21	0.0001
	Species*Time	6	21.70	3.85	0.0023
	Error	68	63.96		
Phenols	Treatment	2	0.817	1.26	0.29
	Species	6	28.10	14.48	0.0001
	Time	1	0.011	0.04	0.85
	Treatment*Species	12	10.56	2.72	0.0051
	Error	62	20.06		
Nitrogen to phenol	Treatment	2	1.430	0.31	0.73
	Species	6	55.32	3.96	0.0021
	Time	1	18.00	7.72	0.0072
	Treatment*Species	12	112.9	4.04	0.0001
	Error	62	144.5		

Table 4.8: Nitrogen concentration, phenol concentration, and ratio of nitrogen to phenols of plant species (n=14) on burn, cover and control treatments in July and August. Nitrogen concentration was significantly higher on burn and cover plots. Ratio of nitrogen to phenols was significantly higher in July than August (see text). Means ±1 S.E. are reported.

	Treatment					
Variable	Burn		Cover		Control	
	July	August	July	August	July	August
Nitrogen concentration (% dry mass X 6.25)	10.7±0.69	9.0±0.64	10.6±0.76	9.2±0.69	9.5±0.50	8.3±0.62
Phenol concentration (% dry mass)	2.0±0.23	1.9±0.19	1.8±0.25	1.7±0.25	1.7±0.24	1.7±0.21
Ratio of nitrogen to phenols	6.2±0.67	5.0±0.42	6.2±0.50	5.7±0.53	6.4±0.50	5.3±0.43

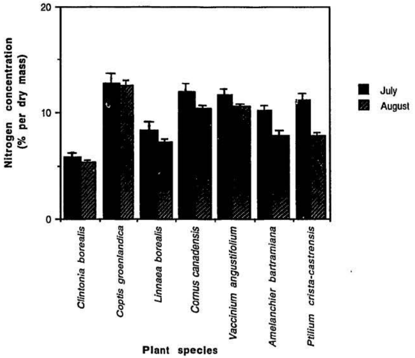

Figure 4.3: Nitrogen concentration of plant species in July and August on the burn study area.

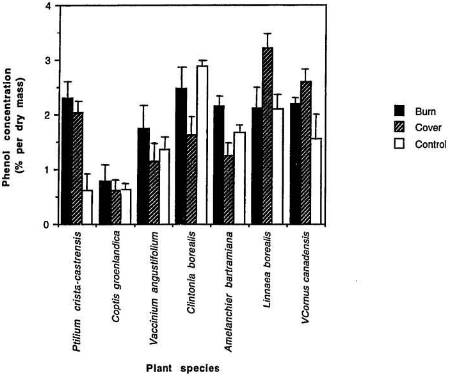

Fig 4.4: Phenol concentration of plant species on burn, cover and control plots in the Burn study area.

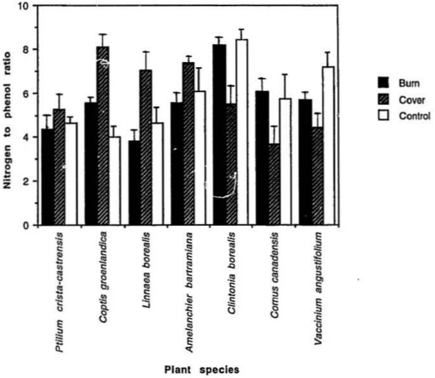

Fig. 4.5: Nitrogen to phenol ratio of plant species on burn, cover and control plots in the burn study area

4.4. Discussion

4.4.1. Small mammal response to prescribed burning

The present study found no significant difference between burned and unburned areas for vole abundance, catch per unit effort or duration of *Microtus*. These results are not consistent with past studies which found that *Microtus* generally exhibit a fire-negative response (Sims and Buckner 1973; Vacanti and Geluso 1985; Kaufman *et al.* 1990). The reason for these conflicting findings may be due to several factors. The type of habitat in which the study was conducted may be an important factor affecting *Microtus* response to prescribed burning. The present study was conducted on a two year-old clear cut, whereas Cook (1959), Vacanti and Geluso (1985) and Kaufman *et al* (1990) conducted their studies in prairie grassland. In prairie grassland the habitat is homogeneous and in the event of a fie *Microtus* may disperse to surrounding grassland habitat. In western Newfoundland the habitat is heterogeneous and preferred meadow habitat are scattered and rare. Small patches of meadow habitat were left within experimental areas after the burn. During radio-collaring sessions voles were located in these meadow patches near and within the burned areas. This may explain why *Microtus* were live-trapped on burn plots and appeared to exhibit a fire-positive response. The voles captured on the burn areas were actually utilizing the moist meadow patches and not the burned habitat. Also, the composition of populations may also be an important factor in small mammal colonization of burned areas. In the present study only three species were captured in the study area: *Microtus*, *Sorex* and *Peromyscus*. Furthermore, only three individual *Peromyscus* were captured over the four months period. In other studies which examine small mammal response to burning (as stated in the introduction) generally more than seven small mammal species were present during the study, including fire-positive species. These fire-positive species, such as *Peromyscus*, may make colonization of burned areas difficult for *Microtus* due to increased interspecific competition (Sullivan 1980). In the present study, *Peromyscus* were very rarely captured within the study area. This lack of competition by other small mammal species in western Newfoundland, especially fire-positive ones may help explain why *Microtus* were captured on burned areas in the present study and not in the past studies. Lastly, methodological factors may have also affected these conflicting findings. The length of time a vole remained on a plot, measured as duration, may not have been an appropriate measure of vole space use because an animal may not have remained within the plot boundries from the first to last capture. In one instance an adult female was radio-collared on a burn plot as she had been live-trapped within the plot for several consectutive weeks, however, radio-tracking revealed that she had established a home range on the adjacent clearcut. During four consecutive days of tracking she was never located on the burn plot suggesting that her use of burn habitat was minimal, whereas the live-trapping data suggested she utilized the burn area quite frequently. Also, since vole densities in western Newfoundland are generally low (section 3.3.1) and home ranges are relatively large (section 3.4.3) the plots established in the Burn study area may have been too small to obtain an adequate sample size, since 1 ha is equal to about four female home ranges. A larger plot size may have yielded more conclusive results.

The lack of long-term resident *Microtus* on any plots and the presence of only a few short-term residents suggests that all treatments were not optimal habitat for voles. The cover treatment supported more *Microtus* than the burn or control treatments. However, interpretation of treatment effects is difficult since the number of voles differed between the two cover plots (see Table 4.2) and was marginally non-significant ($p=0.15$). Control and burn plots were both low in either abundance of food or cover, whereas cover plots were high in both cover and abundance of palatable plant species. This suggests that vole abundance may be related to a combination of cover and food abundance. Vacanti and Geluso (1985) also found that a number of factors which were directly related to vegetation growth and litter accumulation influence recolonization of meadow voles on burned areas. Brooks and Struger (1986) reported that, in an orchard environment, when given the choice between good cover and higher quality food, meadow voles choose cover. Getz (1970) noted that the main factor influencing distribution of meadow voles was a litter layer, however, this was a unifactorial study testing only between presence and absence of litter. On the other hand, Clark (1989) found breeding populations of small mammals to be higher in areas of higher food availability rather than in areas of higher cover. Past studies suggest that both food and cover are important factors affecting vole distribution and abundance. However, there may be a 'minimum threshold affect' for both factors. If an adequate or 'minimum threshold' amount of cover is available, areas with higher quality and abundance of food may influence vole dynamics. In an environment with an adequate or 'minimum threshold' amount of food, cover may be the determining factor. Voles may select habitat which supports a specific combination of both food and cover.

Shrews were most abundant on control plots and only occasionally captured on burn and cover plots. This confirms past findings that *Sorex* generally exhibit a negative response to prescribed burning (see Kaufman *et al.* 1990). This may be attributed to the high metabolic rate of shrews and a subsequent loss of body water which limits them to moist areas. Harty *et al.* (1991) suggests that gradual re-establishment of vegetation and hence herbaceous invertebrates may influence colonization rates onto burn areas. The return of vegetative cover may also facilitate an increase in micro-habitat humidity resulting in a more suitable habitat for *Sorex*. A study of the invertebrate populations on all study plots revealed that diversity and volume of invertebrates was highest on the burn and cover sites (C. Bassler pers. comm.). If food abundance was the influencing factor in shrew distribution then numbers would be highest on burn and cover plots. This was not the case as shrew numbers were highest on control plots. This suggests that factors besides food are affecting shrew distribution. The lack of moisture in recently burned sites may partially explain the absence of shrews from these areas. The distribution of *Sorex* is likely the result of a combination of several factors important to shrew survival. The present study does reveal that food abundance alone will not affect *Sorex* distribution.

Contrary to other studies (for review see Kaufman *et al.* 1990), *Peromyscus* did not colonize burned areas. Interpretation of these results is difficult since *Peromyscus* numbers were extremely low on all treatments suggesting that factors other than prescribed burning were affecting deer mouse abundance. Predation may have influenced population levels as several raptors and ermine were observed in the study area. *Peromyscus* numbers were also low on the 9-year-old clearcut (section 3.3.1) suggesting that low deer mice abundance was not unique to the Burn study area. In 1993, seven deer mice were captured in five consecutive days of preliminary trapping of the Burn study plots. In 1994, only four mice were captured over a four month period on the same study plots. This suggests that *Peromyscus* populations in western Newfoundland may exhibit temporal fluctuations. Although *Peromyscus* populations are generally stable in nature (Terman 1965), it has been shown that densities of island populations fluctuate in apparent three to four year cycles (Drost and Fellers 1991). Competition by *Microtus* also may have played a role in the low densities of deer mice found in on the study area. Grant (1971b) found that *Microtus* had a small deterring effect on *Peromyscus* and can exclude them from grassland habitat. Similarly, Bowker and Pearson (1975) found that *Peromyscus* shift habitat to a more sparsely vegetated area and increase escape rates when *Microtus* numbers are increased.

4.4.2 <u>*Microtus* use of Burn study area</u>

Three of the four radio-collared voles established their home range in close proximity to a small moist meadow. This is similar to findings on the 9-year-old clearcut where females showed strong preference for moist meadow habitat (section 3.3). The occurrence of highly palatable forage species in the meadows (section 3.3.3) suggests that Newfoundland voles distribute themselves in relation to food. Several studies have shown that female voles space themselves in relation to food resources (Ostfeld 1985; Ims 1988). The use of meadow habitat on the Burn study area varied substantially from zero to seventy percent. This may be due in part to reproductive condition of female voles. On the 9-year-old clearcut, females with litters utilized the meadow habitat less frequently than juveniles (section 3.3.2). On the Burn study site, the only female not found in the meadow was a female with three young. She established her nest in a dead tree stump under a slash pile suggesting that cover may also play an important role in determining space use of females with litters on the Burn area. The juvenile was the only vole to heavily utilize the meadow habitat which is consistent with the findings from the 9-year-old clearcut.

Female voles established their home ranges in a variety of habitats. Although all females had at least a portion of their home range on the clearcut, one female established her range predominantly on the cover site while another utilized the control plot. No females established ranges on burn plots. Furthermore, during radio-collaring sessions no voles were located on the burn plots. The few animals captured on the burn plots during live-trapping sessions were captured in traps near the edges of the plot suggesting that these voles were utilizing the adjacent clearcut and only rarely venturing onto the burn. Since the only difference in measured variables between burn and cover plots was the amount of cover it appears that a minimum amount of cover is necessary to support vole activity. These results also suggest that prescribed burned areas may be habitable if an adequate amount of cover is available.

The average interfix distance was similar for voles on the control and cover plots and the adjacent clearcut. Female 3 traveled considerably shorter distances. This was probably due to reproductive condition more than any other factor since females with young are generally more site tenacious (Sheridan and Tamarin 1988). Time of day did not affect the distance traveled by female voles on the Burn study area. This supports the findings of Webster and Brook (1981) who found no difference between diurnal or crepuscular activity exhibited by female voles. Conversely, females on the 9-year-old clearcut site traveled longer distances in late morning than early morning (section 3.3.2). It is not known why these two populations have different temporal patterns but it may be related to predation pressures. Predator sightings and captures were noticeably higher on the 9-year-old clearcut site relative to the Burn site. The lower predation pressure may have allowed voles on the Burn study area to remain active throughout early and late morning.

4.4.3. *Microtus* space use of clear cut areas

Both the 9-year-old clearcut site and Burn study area were located within a heavily logged area in western Newfoundland with scattered patches of small and large forest which did not support any *Microtus* populations during the study (section 3.3.4). If voles in western Newfoundland are generally found in forested areas during years of high density then 1994 was most likely a year of relatively low vole density.

The present study found that vole abundance was lower on the 2-year-old clearcut than the 9-year-old clearcut site. Over the four months of the study, five voles/ha were captured on the unburned 2-year-old clearcut compared to 26 voles/ha captured on the 9-year-old clearcut. This is consistent with other studies which found that older clearcuts supported higher vole densities (Monthey and Soutiere 1985; Medin 1986). Several authors report that *Microtus* use of clearcut sites increases approximately five years post-harvest (Martell and Radvanyi 1977; Monthey and Soutiere 1985). The increased number of moist meadow patches on the older cut may explain the difference in vole abundance since meadows supported the preferred plant species for voles (section 3.3.3). Similarly, Martell and Radvanyi (1977) found vole density to be higher on wetter grassier sites, and Swan *et al.* 1984) also reported relatively high *M. pennsylvanicus* abundance in clear cuts with wet habitat.

Sorex were also present in higher numbers on the older cut (17 shrews captured in four months/ha) compared with the younger cut (seven shrew captured in four months/ha). Moisture is an important factor affecting the distribution of shrews (Getz 1961a) and an older cut may be the more suitable habitat and able to support higher *Sorex* numbers. Kirkland (1977) and Monthey and Soutiere (1985) also found older cutovers to support higher densities of *S. cinereus*.

Moisture is a key factor in vole and shrew distribution (Swan *et al.* 1984; Getz 1961a). Older cuts may be more apt to be wetter because of increased cover and micro-habitat humidity. However, topography may also play an important role in site moisture. For the present study, moist meadows were present in the 9-year-old clearcut, the unburned 2-year-old clearcut, and even in the cover sites. The voles utilizing these different habitats showed strong preference for moist meadows suggesting that habitat type at the macro scale may not be as important to voles as micro-habitat. Voles may utilize several different macro-habitats as long as moist meadow patches are present or in close proximity to the habitat.

CHAPTER FIVE - SUMMARY, CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE RESEARCH

5.1 Summary

5.1.1 Project 1: 9-year-old Clearcut Study Area

Several of the population characteristics examined in this study differed from those reported for other *Microtus* populations. Survival of meadow voles in western Newfoundland was highest in June and lowest in the fall, whereas Mihok (1984) reported lowest survival of juvenile meadow voles in mid-summer and highest survival in fall. Recruitment of meadow voles also showed the same trend. The number of new voles entering the population was highest in June and very low in fall. Densities of *Microtus* in western Newfoundland were low relative to those reported for continental *Microtus* populations, especially in spring and fall. Densities of vole populations are typically higher in the fall (Taitt and Krebs 1985), whereas in the present study densities were lower in the fall. Only six percent of juveniles attained sexual maturity in the year of theri birth. Several voles in this study were 60 to 90 days old and still showed no signs of reproductive activity.

The preferred habitat of meadow voles in the study area was the moist meadow patches. Even though the meadow was only 4.2% of the available habitat, juveniles utilized these areas almost forty percent of the time. Four of the five adults radio-collared were located in these small moist patches during times away from the nest. The meadow patches were areas of lower cover relative to the areas in which the females with litters established their nests suggesting that the benefits of these excursions into the meadow outweigh the increased risk of predation. A food preference test revealed that the moist meadow patches supported plant species with the highest palatability. It appears that female voles are distributing themselves in relation to food resources.

Spacing patterns exhibited by voles in western Newfoundland tend to be exaggerated compared with documented vole populations in other areas of mainland North America. Periphery home ranges were larger and interfix distances were longer than those reported in the literature. Female voles tended to move further distances in late morning than in early morning possibly because of increased raptor activity at dawn.

Hawk owls were sighted in the study area from June to September and five ermine were captured in the study area in August and September. The scent of the ermine in the study area may have been sufficient enough to suppress juvenile vole maturation.

5.1.2 Project 2: Burn Study Area

No significant differences were found among burn, cover or control treatments for total number of *Microtus*, catch per unit effort or duration. This was not consistent with past studies which found voles to exhibit a fire-negative response. This inconsistency could to due to several factors. Habitat type may have influenced vole response to prescribed burning. In the present study several patches of moist meadow habitat were left within the burned areas after the prescribed burn. Animals were found to use these preferred areas within the burn plots but not use the actual burn habitat. Therefore lie-trapping data would suggest Microtus were exhibiting a fire-positive response when actually they were keying in on moist microhabitat. Also, in the present study only three species were captured on the experimental plots. Past studies conducted on small mammal response to burning generally captured more than seven small mammal species in the study area. This lack of competition by other small mammals, including fire-positive ones, may have influenced *Microtus* space use. In the absence of interspecific competition meadow voles may utilize patchy burn habitat. Lastly, duration may not have been a good measure of vole space use as radio-collaring evidence suggested that animals captured on burn plots established home ranges in adjacent clearcuts. Also, since small mammal densities were so low the study plots were too small to obtain an adequate sample size. Although one cover plot did have higher vole numbers, the cover plots did support more voles than burn or control plots. Cover plots were both high in cover and palatable plant species suggesting that voles may select habitat which supports a specific combination of food and cover.

One common pattern exhibited by three of the four radio-collared females was their establishment of a home range in close proximity to a small moist meadow. The occurrence of highly palatable species in the meadows suggests that voles are distributing themselves in relation to food. Although all females had a portion of their home range on the clearcut, one female established her range predominantly on a cover plot while another utilized a control plot. No females established home ranges on burn plots suggesting that cover is important in spacing systems and that prescribed burned areas may be habitable if an adequate amount of cover is available.

Catch per unit effort (CPUE) of *Sorex* was significantly higher on control than burn or cover plots. This is consistent with past studies which found shrews to exhibit a fire-negative response. A study of the invertebrate populations on the Burn study area revealed that diversity and volume of invertebrates was highest on burn and cover plots (Bassler pers. comm.). Since *Sorex* numbers were highest on control plots it appears that other factors besides food were affecting shrew distribution. The lack of moisture on burned areas may partially explain low shrew numbers on burn and cover plots.

The very low numbers of *Peromyscus* observed on all treatments suggests that factors other than prescribed burning were affecting deer mouse abundance. Predation may have influenced population levels as several raptors and ermine were observed in the study area. Competition by *Microtus* may also have played a role in the low densities of deer mice as other studies have found that *Microtus* can exclude or deter deer mice from grassy areas.

5.2 Conclusions

A detailed study of space use revealed that female *Microtus* tended to establish home ranges within or in close proximity to meadow habitat. This pattern of space use was found on both the 9-year-old clearcut study area and the Burn study area as females utilizing these different habitats were located in meadows or moist patches during radio-collaring sessions. These results suggest that voles in western Newfoundland may utilize several different macro-habitats as long as small meadow patches are present within the overall habitat type. Also, the presence of highly palatable species in these meadow areas suggests that *Microtus* are distributing themselves in relation to food.

This study has shed some light as to why meadow vole densities are generally low on the island of Newfoundland. Several factors appear to be acting simultaneously to suppress vole numbers. First, the low reproductive rate of juvenile voles may be an important factor contributing to low fall densities. It is still unknown at present what caused the delayed maturation of juveniles. Past studies have shown that ermine scent can inhibit reproduction in young voles and several captures and sightings suggest ermine abundance was quite high in the study area. Second, terrestrial and avian predation may be directly suppressing vole numbers as predation on *Microtus* appears to be continual due to the lack of alternate small mammal prey species. Lastly, moist meadow areas which support the highly palatable forage species are rare and scattered in western Newfoundland, possibly as rare as less than five percent of the landscape, therefore the quantity of forage for voles is limited. All these factors may play an important role in population dynamics of voles in western Newfoundland.

5.3 Recommendations for Future Research

One important recommendation for future research on *Microtus* in Newfoundland is that plots established for trapping studies should be quite large in size. Meadow voles in Newfoundland are low in density and establish large home ranges relative to continental populations. Plot sizes should reflect these dynamics and be at least three or four hectares instead of the usual one hectare. Large plots should be established in areas with small moist patches or meadows to obtain an adequate sample size.

Two aspects of meadow vole dynamics observed during this study should be examined more thoroughly in the long term. Due to the short duration of this study, it could not be determined whether low reproduction rate of juvenile voles in Newfoundland is a usual occurence. A long term study of several vole populations across the island could determine whether juveniles exhibit low reproductive rates annually and locally. An integrated study could also include an experimental manipulation designed to examine the effects of ermine scent on juvenile reproduction to determine whether or not ermines were contributing to the delayed maturation of young voles. Learning more about juvenile reproduction could prove useful in explaining why voles occur at such low densities in Newfoundland. I also recommend a comprehensive study of male vole demography and space use since little is known about male *Microtus* in Newfoundland. Areas to focus on should include home range size, mating systems, reproductive success and space use. For all long-term studies of voles conducted on the island of Newfoundland, density or abundance indices should be recorded every year to determine whether or not vole population fluctuations are cyclic in nature. It is important to standardize the methods used from study to study so that year to year comparisons of abundance estimates are possible.

Further research of small mammals on the island of Newfoundland could also include a detailed study of *Peromyscus*. Systematic trapping grids established across the province could determine how far the deer mouse has dispersed across the island and the rate of dispersal. The presence of this new species on the island could have adverse affects on space use by *Microtus*. Diversity and therefore competition among small mammals on the island was historically quite low. This unique opportunity to study a newly introduced small mammal could further our understanding of mammalian population dynamics.

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APPENDIX A

Table A.1. Monthly averages of precipitaion and air and soil temperatures (in degrees Celcius) recorded in the Glide Lake study area from June to September 1994.

MONTH	Precipitation (mm)	Temperature Air 20 cm above surface	Temperature Soil 2 cm below surface
June (23-30)	10	10.7	13.0
July	147	16.6	14.6
August	59	12.6	14.8
September	110	7.0	10.0

APPENDIX B

Table B.1. Categories of the Braun-Blanquet method of plant surveying.

Category	
Stratification layer	T (tree layer) = plants > 1.5 meters
	S1 (shrub layer) = plants 1 - 1.5 meters
	S2 (lower shrub layer) = plants 40 cm to 1 meter
	H (herb layer) = plants 10 - 40 cm
	M (moss layer) = plants < 10 cm
Cover	5 = species covers >75% of quadrat
	4 = 50 to 75% of quadrat
	3 = 25 to 50% of quadrat
	2 = 5 to 25% of quadrat
	1 = numerous but < 5% of quadrat, or scattered and < 5%
	+ = few individuals, little cover
	r = solitary, no cover
Dispersion pattern	5 = plants in carpets without breaks
	4 = plants in carpets with breaks
	3 = many plants in patches
	2 = few plants in scattered clumps
	1 = solitary

APPENDIX C

Table C.1. Plant group, habitat affinity and palatability scores of plant species to *Microtus*.

Common Name	Scientific Name	Palatability Score	Plant Group*	Habitat**
Balsam Fir	*Abies balsamea*	0.14	T	F
Chuckley Pear	*Amelanchier bartramiana*	1.71	T	F
Pearly Everlasting	*Anaphalis margaritaceae*	0.57	F	C
Sarsparilla	*Aralia nudicaulis*	0.29	F	F
Lady Fern	*Athyrium filix-femina*	3.00	O	M
White Birch	*Betula papyrifera*	0.86	T	F
Sedges	*Carex* spp.	2.29	G	M
Yellow Clintonia	*Clintonia borealis*	3.00	F	F
Bunchberry	*Cornus canadensis*	2.71	F	F
Hair Grass	*Deschampsia flexuosa*	2.43	G	M
Oak Fern	*Dryopteris disjuncta*	3.00	O	M
Fireweed	*Epilobium angustifolium*	1.14	F	C
Horsetail	*Equisetum sylvaticum*	3.00	O	M
Strawberry	*Fragaria virginiana*	0.86	F	C
Bedstraw	*Galium triflorum*	3.00	F	M
Snowberry	*Gaultheria hispidula*	0.86	F	F
Twinflower	*Linnaea borealis*	0.71	F	F
Lily of the Valley	*Mianthemum canadense*	3.00	F	M
Plume Moss	*Ptilium crista-castrensis*	1.86	O	F
Swamp Buttercup	*Ranunculus septintrienalis*	3.00	F	M
Black Current	*Ribes lacustre*	1.00	T	F
Raspberry	*Rubus idaeus*	1.14	T	C
Dewberry	*Rubus pubescens*	2.43	F	M
Willow	*Salix* spp.	2.71	T	F
Squashberry	*Viburnum edule*	0.29	T	F

*Plant groups: T- trees and shrubs, F- forbs, O- other, G- grasses and sedges.

**Habitats: M- meadow, C- clearing, F- forest regeneration.

APPENDIX D

Braun-Blanquet Tables

Tables are set up by species and stratification. The 'Strata' column within the tables refers to the stratification layer (see Appendix B). The first number within the table refers to cover and the second number refers to dispersion pattern. For example, 2/4 means cover=2 and dispersion=4 (see Appendix B)

Table D.1. Braun-Blanquet data collected on the 9-year-old study site in July 1994. The qudrats were established in all three habitat types. (F refers to data collected within the forest regeneration habitat type, C refers to clearings and M refers to meadow habitat.)

Species	Strata	F	F	F	F	F	F	F	F	F	C	C	C	M	M	M
Abies balsamea	T	4/3	2/4	1/2	2/2	2/2	r/1	2/3	1/1		2/1		+/2			
	S1	3/3	4/4	2/3	2/2	4/4				3/3	4/1	2/2	+/1			
	S2			1/2	2/3	1/2	1/2			1/1	2/1		+/1		r/1	
	H					1/2				+/1						
Acer rubrum	H				r/1							r/1			r/1	
Anaphalis margaritacea	S2	+/2			1/2		+/2			+/1	2/2	2/2	2/2	1/1		
	H		+/2		+/2	+/2		+/1					1/2	1/3		1/1
	M				+/1											
Aralia nudicaulis	S1				1/2											
	S2											+/1				
	H	1/3	1/2		1/2	1/2	2/2	1/2	2/1	1/1	1/1					
	M		1/2	1/2	1/2		+/1	1/2		1/1						
Aster puniceus	S2						1/2	+/1			1/1	2/2	1/2			
	H							1/2			1/1	1/1	1/2			
Athyrium filix-femina	H					+/2				1/2				1/2	2/2	1/2
	M										1/2	2/2				
Betula papyrifera	T	3/3	2/3	+/1	1/2	r/1	r/1	2/3	r/1		2/1	+/2	r/1	+/1	r/1	r/1
	S1	3/3	2/3	4/3	3/2	2/3	r/1	3/3	2/1	2/1	2/1			+/1	r/1	+/1
	S2		1/2	2/3	+/2	+/1	4/4	1/1	2/1	2/1			+/1	+/1	+/1	
	H			+/1	+/1		+/1									
Carex spp.	H												1/3	2/4	3/4	2/4
	M														4/4	2/4
Cinna spp.	H													+/2		1/2
Circaea alpina	M												r/1	+/1		
Cladonia spp.	M									+/1						
Clintonia borealis	H			1/2		+/2					1/2					
	M			1/2			1/2		1/2	+/1					+/1	
Cornus canadensis	H	3/4	3/4	3/3	3/3	3/4	2/2	3/3	2/3	2/3	3/4	1/3	2/2	2/3		
	M	4/4	4/4	3/3	3/3	3/4	3/3	3/3	2/3	3/4	3/4	1/3	2/2	2/3	1/2	1/4
Deschampia spp.	H											+/2		+/2	2/1	1/2
Dryopteris disjuncta	H				1/2				1/2					+/1		2/1
	M			1/2			1/2	1/2							1/1	1/1

Table D.1. continued

Species	Strata	F	F	F	F	F	F	F	F	F	C	C	C	M	M	M
Dryopteris spinulosa	S2					2/2		2/3	1/2	1/2			1/2		+/2	
	H	1/2	1/2		1/2		1/2				+/1			2/2	1/2	2/2
	M									1/2				2/2	1/2	2/2
Epilobium adenocaulon	H											1/1	+/1			
	M											r/1		1/2		
Epilobium angustifolium	S1	+/2	+/1		2/2		+/1		+/1	2/2	1/2		2/2	2/2	2/2	3/3
	S2	1/2	1/2	+/1	2/2	+/1	3/3	2/3		2/2	2/1	1/2	3/3	+/1	2/2	4/2
Equisetum sylvaticum	H						+/2							+/3		5/4
	M						1/2							2/3	3/3	4/4
	H			2/2		2/3	2/3		1/2	1/1		+/3		+/1		
Galium triflorum	H							+/1								
Gaultheria hispidula	M	1/2		1/2		1/2		1/2								
Geum rivale	H											1/3				
Glyceria spp.	S2														1/1	
Hieracium pratense	S1			+/1			r/1								+/2	+/1
	H				+/1				1/1				1/2			
Juncus effusus	H											+/3		+/3	2/3	1/2
Linnaea borealis	M	2/3	1/2	2/2	2/2	1/2	1/2	1/2	1/2	+/2		2/3		1/2	1/2	+/4
Mianthemum canadense	M					+/1				1/2				+/1	1/1	1/1
Mitella nuda	M													1/2	4/3	
Moss spp.	M	5/4	4/4	3/4	4/4	5/4	2/3	4/4	3/4	4/4	2/4	2/4	2/4	2/4	1/4	2/4
Osmunda cinnamomea	S2															+/1
Picea mariana	T	+/1			r/1			+/1				r/1				
	S1				+/1	r/1										
	H				+/1											
Prunus pennsylvanicus	S1			+/1					r/1	r/1						
Ranunculus septentrionalis	H													1/2		1/2
	M													1/2		
Ribes lacustre	H							+/1	+/1							

Table D.1. continued

Species	Strata	F	F	F	F	F	F	F	F	F	C	C	C	M	M	M
Rubus ideaus	S1						2/3	4/4	1/2			3/3				
	S2	2/3	2/3	2/3	2/3	+/2	3/4	2/3		1/2	3/3	5/4	3/3	1/2	1/3	2/2
	H	2/3	2/3	3/3	2/3	1/2	3/4	3/3	1/2	2/2	3/3	3/2	4/4	1/3	1/2	
	M	1/2	2/3	2/3	2/3	+/2	3/3	2/3			1/1					
Rubus pubescens	M	+/2					+/2						1/3	1/2		+/2
Rumex aceteosella	M				+/1		+/1									
Salix spp.	S2				r/1	r/1		r/1		r/1			r/1		+/1	
Sambucus pubens	S1	+/1	+/1	+/1	+/1		r/1	r/1				r/1				
	S2			r/1	r/1	+/1	+/1				r/1					
	H			+/1												
Scirpus atrovirens	S1															1/3
	S2															1/3
Solidago macrophylla	H		+/2			1/2					+/1		1/2			
	M							1/2								
Solidago rugosa	S2														1/2	1/3
Sorbus americana	T			+/1	+/1			+/1								
	S1			+/1			+/1	+/1				r/1				
Taraxacum officinale	H										+/1					
Trientalis borealis	M				+/1				+/1							
Tussilago farfara	H										1/2	2/2				
Viburnum edule	S2									r/1						
	H									r/1						

Table D.2. Braun-Blanquet data collected on burn plots in the Burn study area in July 1994. Quadrats 1 through 8 were sampled on plot A. Quadrats 9 through 16 were sampled on plot C.

Species	Strata	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Abies balsamea	H					+/1		+/1				+/1		+/1			
	M					+/1		+/1									
Acer rubrum	H						r/1		r/1								
Amelanchier bartramiana	H		+/1								+/1						
Betula papyrifera	H			+/1		r/2			r/1				r/1	r/1	r/1	r/1	
Carex spp.	M				r/2												
Cladonia spp.	M			+/1	+/1										+/1		
Clintonia borealis	H	+/1	2/1	+/1		2/1		2/2		2/2		1/2		2/2	2/2	1/1	
	H	+/2	+/1								2/2		1/2	1/1	1/2		
	M	+/2	+/1	+/1	+/2						1/2		1/2				
Cornus canadensis	H						2/3	+/2	1/2	3/4	2/2	+/1	2/2	1/2			
	M	+/2	1/2	1/2		+/2		2/3	1/2	3/2	1/2	2/2	2/2	1/2	2/2	2/2	1/4
Coptis greonlandica	M	+/2	+/2	1/2		1/2		1/2	1/2	1/2	1/2	1/2	1/2	1/2	+/2		
Dryopteris disjuncta	H						+/2										
	M						1/2						1/1				
Epigea repens	M						+/3							+/2			
Epilobium adenocaulon	S2					r/1		r/1			+/1		+/1	+/1			1/1
	M				+/1					+/1	+/1						
Epilobium angustifolium	H						+/1		+/1					+/1	+/1	+/1	
	M					+/1											
Equisetum sylvaticum	M						+/1										
Gaultheria hispidula	M				+/4		2/4		1/4			1/2	1/2				
Linnaea borealis	M					1/4			1/2		r/1	1/2	1/2	1/2	1/2	+/1	
Mianthemum canadense	M																
Moss spp.	M	1/4	5/5	4/4	5/4	5/4	4/4	5/5	4/4	5/5	5/5	5/5	5/5	4/5	4/5	5/5	4/4
Nemopanthus mucronata	H	r/1								+/1			+/1				
	M	+/1															
Picea mariana	H					+/1				+/1			r/1				
	M						+/1										
Prunus pennsylvanicus	H			+/1		r/1	r/1						r/1				
Rubus idaeus	H					1/2	r/1		+/1								
	M			1/2		+/1	+/1		+/1	+/2	1/2			+/1	r/1		
Trientalis borealis	M					+/1	+/1										1/1
Sorbus americana	H								r/1								
Vaccinium angustifolium	H		2/2	1/2			+/2			1/2	2/2	2/2	1/1	2/2			1/3
	M	+/2	2/2	+/2				+/2				1/2	2/2	1/2	1/2	1/3	
Viburnum cassinoides	M		+/1														

Table D.3. Braun-Blanquet data collected on the cover plots in Burn study area in July 1994. Quadrats 1 through 8 were sampled on plot B. Quadrats 9 through 16 were sampled on plot D.

Species	Strata	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Abies balsamea	H				r/1	r/1							r/1				
Acer rubrum	H				r/1												
Amelanchier bartramiana	H					r/1	+/1										
Aralia nudicaulis	H					+/1											
	M					+/1											
Aster puniceus	S2					+/2		+/2									
Athyrium filix-femina	S2				+/2				1/2								
	H							+/2						+/2			
Betula papyrifera	S2									+/1				r/1			
	H		r/1				r/1	r/1	+/2			+/1	+/1		+/1		
Carex spp.	M					2/4		r/2	4/4		+/2						2/4
Cladonia spp.	M					r/1											
Clintonia borealis	H	+/1	1/2		2/3	+/1			1/1			2/3	2/3	1/1	2/3	+/1	2/2
	M	+/1	1/2		+/1	+/1	2/2		1/1	1/2		1/2	1/3	1/1	1/2	+/1	2/2
Coptis groenlandica	M	+/2	1/2		1/2	1/2	1/2	+/2		+/2		1/2	1/3	1/2	1/2		1/2
Cornus canadensis	H	2/3			2/2	2/3		3/4	1/2	1/3	2/3	2/2	3/4	1/2	3/3	1/2	3/4
	M	2/2	2/2	r/1	1/2	1/2	2/2		1/2	2/3	1/2	2/3	2/3	2/2	2/3	1/1	3/3
Deschampia spp.	S2									1/3							
	H												1/3				
Dryopteris disjuncta	H				1/2		1/1		1/1							1/2	
	M				+/1	1/1		2/1			+/1		+/2				
Dryopteris spinulosa	H				+/1			+/2			1/2						+/2
Epilobuim adenocaulon	H	+/1	+/1	+/1	1/2	2/2			+/1	1/1			+/1				
	M				+/1					1/2					+/1		
Epilobium angustifolium	H	r/1	+/1							+/1	+/1	1/2	+/1	+/1			
	M			+/1	+/1		+/1		+/1	+/1	+/1		+/1	+/1	+/1		
Epigea repens	M				1/2	+/2		+/1				+/1		+/1			
Equisetum sylvaticum	H				+/1	+/1		2/1			+/1						
Gaultheria hispidula	M	+/2			+/2	+/1		1/4	1/2		+/2			+/1	+/2		
Hieracium pratense	H					1/2				1/2							
Kalmia angustifolia	H			+/2			2/2		+/2			1/2		1/2			
	M		1/2			2/2				+/2			+/1				
Linnaea borealis	M		1/2		1/2	1/2	1/3		1/4	1/2	1/2	2/3			1/2		1/2
Lycopodium annotinum	M						+/1										
Mianthemum canadense	M	+/1		+/1													
Moss spp.	M	5/4	5/4	5/5	5/5	5/4	3/4	4/4	2/4	5/5	5/5	5/4	5/4	5/5	5/4	5/4	5/4
Nemopanthus mucronata	M		+/1														

Table D.3. continued

Species	Strata	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Osmunda claytonia	S2				3/3												
	H				3/3			2/2			+/2						2/2
Picea mariana	H		r/1														
Prunus pennsylvanicus	H					+/1	+/2	+/1		+/1		r/1					
	M		r/1					r/1	r/1	+/1						+/1	r/1
Ribes lacustre	M				+/2												
Rubus idaeus	H	+/1				+/2	+/2	+/1				+/1					+/2
	M	+/1		+/1	+/1		r/1		1/2	1/2	1/2	1/2	+/1	1/1	+/2		
Rubus pubens	H						1/2										
	M														1/2		
Rununculus septietrientalis	H					1/3							1/2				
	M			+/1													
Sorbus americana	S2					r/1											
Taxus canadensis	H						+/1			r/1							
Trientalis borealis	M				r/1	+/1	+/1		r/1	+/2	1/2	1/2		+/2		1/2	
Vaccinium angustifolium	H	1/2	2/2			2/2		1/2	1/2			1/2	1/2	2/2	1/2		2/2
	M	1/2	1/2			+/2	1/2	1/2					1/2		1/2	+/1	2/2
Vaccinium vitis-idea	M			+/2			+/2							+/2			
Viburnum cassinoides	H			r/1	+/1						+/1		+/1		+/1		r/1

Table D.4 Braun-Blanquet data collected on the control plots on the Burn study area. Quadrats 1 through 8 were sampled on plot E. Quadrats 9 through 16 were sampled on plot F.

Species	Strata	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Abies balsamea	S2									+/1							
	H	+/1	1/1	1/1	2/1	1/1	+/1	1/1	+/1	+/1	+/1	+/1		+/1	+/1		+/1
	M	+/1				+/1			+/1								+/1
Acer rubrum	H							+/1			+/1	+/1	+/1		+/1		+/1
	M										+/1						
Amelanchier bartramiana	S2														+/1		r/1
	H			r/1	+/1		r/1	+/1		+/1	+/1	+/1	+/1	+/1		+/1	+/1
Anaphalis mararitacea	H									+/2							
Aster puncieus	H								r/1		+/2			1/2			
Athyrium filix-femina	H																+/1
Betula papyrifera	S2		r/1	+/1	+/1	r/1		r/1									
	H	+/1		+/1	+/1	+/1	r/1	r/1	r/1	+/1		r/1		r/1	+/1	+/1	
	M			+/1	r/1			r/1						+/1			
Carex spp.	H												1/2				
Cladonia spp.	M														r/1		
Clintonia borealis	H		+/1				1/1	1/1									
	M							1/1		1/1	1/1	1/1	1/1	1/1	1/1		+/1
Coptis groenlandica	M		+/1		+/1		r/1			+/1	+/2	1/2	1/2	1/2	+/2		+/2
Cornus canadensis	H	2/3	4/4				4/3	4/4	1/3			3/4	4/4	2/3		2/4	
	M		4/4			1/3	4/3	4/4	1/3	4/4	4/4	4/4	3/4		2/4	3/4	3/4
Cornus stolonifera	H									+/1	+/1						
Deschampsia spp.	H		+/2							+/1					+/1		
Dryopteris disjuncta	H				+/2										+/2		
Dryopteris spinulosa	H			+/2			+/2	+/1		+/1	1/1			+/2			
	M							+/1		+/1	1/4						+/2
Epilobium adenocaulon	S2												r/1				
Epilobium angustifolium	H						1/2	1/2		1/1		+/1		+/2			+/2
Epigea rupens	M	+/2	+/2	+/2		+/2	+/2		+/2		1/3	1/2	1/2	1/3	2/4	2/3	
Galium triflorum	H									+/2							
	M									+/2							
Gaultheria hispidula	M	3/4	1/4	2/4	2/4	+/3	1/3	1/4	+/3	+/3	3/4	2/4	2/4		1/2	1/3	+/2
Geum rivale	H									1/3							
Kalmia angustifolia	H					1/2	1/2					3/1					
Ledum groenlandica	H	+/2				+/2				1/1				+/1	+/2		
Linnaea borealis	M		1/4			1/1		1/1	1/3	+/1	+/3	+/2	1/2	1/3			+/2
Lycopodium spp.	M								r/2							r/2	
Mianthemum canadense	M					r/1						r/1		+/1	r/1		
Moss spp.	M	5/4	4/4	3/4	5/4	3/4	5/4	4/4	5/4	3/4	3/4	5/4	5/4	4/4	4/4	5/4	4/4

Table D.4. continued

Species	Strata	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Nemopanthus mucronata	H						r/1					+/1	+/1		r/1		
Osmunda claytonia	H												+/1				
Picea mariana	S2									1/2					+/1	+/1	+/1
	H	r/1	+/1	+/1	+/1	r/1	+/1		+/1	+/1	+/1	+/1	+/1	+/1	1/2	+/1	
Prunus pennsylvanicus	H		r/1	+/1			+/1					+/1			+/1	r/1	
	M						+/1	+/1									
Pyrola secunda	M		1/2														
Ranunculus septintientalis	H										1/2						
Rhododendron canadense	H	+/1					+/1					+/1					
Ribes iacustre	H									r/1	r/1	+/1				+/1	
Rubus ideaus	H		r/1	+/1	+/1			+/1	+/1		1/3				+/1		+/1
	M				+/1			+/1			1/3			+/1			+/1
Rubus pubens	H										2/4	2/4		1/2		2/3	
	M									3/4	2/4				2/3		r/2
Sanguisorba canadensis	H														+/2		+/2
Solidago rugosa	S2								1/2		r/1						
Sorbus americana	H				r/1		r/1										
Vaccinium angustifolium	H		2/3	+/2			1/2			2/3	2/4	2/3	2/3	2/3	2/2	2/3	2/3
	M			2/3			1/2			1/1	2/4	1/3	2/3	2/3	2/2	2/3	2/3
Vaccinium vitis-idea	M						r/2			+/2				+/2	1/3		1/2
Viburnum cassinoides	H			+/1		+/1		+/1		+/1	+/1	+/1	+/1	/1		+/1	+/1