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The Effects of Timber Harvest in the Boreal Forest on Deer Mice and Red-Backed Voles

by

Robin Lee Weaver ©

A thesis
submitted to the Faculty of Graduate Studies and Research in partial
fulfillment of the requirements for the degree of Master of Science.

Department of Zoology

Edmonton, Alberta
Spring 1996

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled The effects of timber harvest in the boreal forest on deer mice and red-backed voles submitted by Robin Lee Weaver in partial fulfillment of the requirements for the degree of Masters of Science.

Dr. S.A. Boutin

Dr. S.J. Hannon

Dr. R.S. Currah

Date April 19/96

I dedicate this thesis to David Tizzard

(Mousing's Done - Let's Ride)

ABSTRACT

The effects of timber harvest on deer mice and red-backed voles include: (1) First and second year clearcuts in mixed-wood aspen forests in northern Alberta were not acting as dispersal sinks for deer mice and red-backed voles. Instead deer mice had equal or larger densities and productivity in clearcuts. Whereas red-backed voles either did not live in clearcuts or had smaller similarly productive populations as the forest populations. (2) In summer 1994, red-backed voles lived in the clearcut portions surrounding residual patches in cutblocks, and not clearcuts lacking residual patches. The mechanism causing this difference is still unknown. (3) Higher densities of deer mice in the forest edge may be a function of individuals being drawn to the edge or overflow of individuals from higher density clearcuts. Red-backed voles showed varied trends, while survival rates showed no relationship with distance from edge.

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I am grateful for the support that my parents and my brother Chris have always given me; they have helped me open many doors in my life.

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INTRODUCTION

Recent technological advances have made trembling aspen (*Populus tremuloides*) an economically viable species for the production of pulp and paper. These advances have shifted the interests of forestry companies towards large stands of aspen found in the boreal forest of Canada. Currently, over three million hectares of aspen mixed-wood forests in northern Alberta are managed by forestry companies. The challenge for these companies is to manage these forests for both timber harvest and species conservation (Hansen et al. 1991). To conserve forest communities keystones species in the system may require special attention (Paine 1961). One group of organisms that interact with many other species, and may be keystones in the boreal forest, is small mammals such as deer mice (*Peromyscus maniculatus*) and red-backed voles (*Clethrionomys gapperi*; Thompson and Colgan 1987). There are three major interactions between these small mammals and other species that may be affected by forestry: first, small mammals are thought to affect plant regeneration and growth by spreading mycorrhizal fungi (Maser et al. 1978a and 1978b; Martell 1981), and eating and disseminating seeds (Sullivan 1979). Second, small mammals form an important prey base for secondary consumers such as furbearers (e.g., weasel, marten) and raptors (e.g., great horned owls, goshawks; Thompson and Colgan 1987; Boutin 1995; Jedrzejewski et al. 1995), and third, small mammals have been identified as important egg predators (Maxson and Oring 1978; Cotterill 1996). Thus, determining the effect of forestry on small mammals may lead to a greater understanding of the effect of forestry on other related species.

I have taken three approaches in my research to assess the effect of harvesting mixed-wood aspen forests in northern Alberta on deer mice and red-backed voles. The first approach was to compare the habitat quality of first and second year clearcuts with the habitat quality of the original forested stand for these small mammals. The assessment of habitat quality is a critical part of wildlife management, and is the basis of habitat suitability index models (HSI) created to understand and make decisions about species conservation (Bonar 1993). However, techniques used to assess habitat quality in many studies have been questioned (Noss 1990). In a landmark paper by Van Horne (1983), it was suggested that previous researchers who rely solely on density estimates may inaccurately assess habitat quality. In particular, "sink" habitats (low quality) may be confused with "source" habitats (high quality) if the researcher does not determine reproductive output and survival of individuals in the area. However, in most studies reproductive output is hard to measure, for it is difficult to differentiate between individuals born *in situ* and immigrants. Thus, although it has been suggested that many individuals may occur in "sink" habitats (Pulliam 1988; Howe et al. 1991), "source" and "sink" habitats have been rarely identified for most species (Dunning et al. 1992). In my research, I have used intensive trapping and radio-telemetry to mark juveniles born *in situ,* allowing me to determine reproductive output in clearcuts and forests. I have also calculated summer and over-winter survival and density estimates and have determined growth, recruitment and immigration rates. All of these features allowed me to assess habitat quality of clearcuts and forests for deer mice and red-backed voles and predict the effect of future forestry on the demographics of these two species of small mammals.

One method to alter habitat quality of clearcuts for small mammals is to vary the amount of residual material left after timber harvest. In summer 1994, unlike in the clearcuts (<2% residual material), there were viable red-backed vole populations in cutblocks that had about 12% residual material (Moses Pers. Comm.). Thus, to understand how residual material transforms clearcuts into areas where red-backed voles live the second approach in my research was to assess the effect of this residual material on lactating red-backed voles' nesting and foraging behaviour.

Another habitat created through timber harvest, other than clearcuts, is forest edge. The final approach in my research was to determine if either of the two hypothesis explaining high densities of animals in the forest edge relate to the patterns observed for deer mice and red-backed voles. The first hypothesis is that animals are packed into the remnant edge after the surrounding habitat has been changed to inhospitable land (Lovejoy et al. 1986). The second hypothesis is based on Gates and Gysel (1978)'s "Ecological Trap Hypothesis" where animals are drawn to the edge due to high levels of food, but are unable to cope with edge pressures (i.e., increased predation rates) which reduces the survival of these individuals in the edge. By trapping small mammals in the clearcut through the forest edge and into the forest interior I was able to determine if small mammals "packed" into the remnant forests, or if deer mice or red-backed voles were drawn to the forest edge. I also predicted whether the changes in density or survival of small mammals with distance to edge could translate into edge effects on other related species.

In summary, small mammals interact with many other species, and thus play important roles in the boreal forest. The information gained from my research leads to an understanding of how current cutting practices affects small mammals, and the methods or data generated in this study can be used by other researchers to determine if clearcuts are comparable to areas created by natural disturbances (i.e., fire).

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THE EFFECTS OF TIMBER HARVEST ON HABITAT QUALITY FOR DEER MICE AND RED-BACKED VOLES.

CHAPTER 1

INTRODUCTION

The challenge for forestry companies is to manage forests for both timber harvest and species conservation (Hansen et al. 1991). In terms of conservation, one must understand how cutting practices affect habitat quality for resident species. Habitats can be of three qualities: (1) High quality (Source), characterized by high densities, survival rates and reproductive rates which lead to a viable local population without immigration, (2) Low quality (Sink), characterized by low densities, survival rates and reproductive rates which lead to a population dependent on immigration, or (3) Inhospitable land where no individuals can survive or breed, and thus there is no local population (Lewin 1988; Pulliam 1988; Harrison 1991; Howe et al. 1991; Danielson 1992; Pulliam et al. 1992). Forestry can alter habitat quality of a landscape by producing new habitats (clearcuts) which differ in quality from the original habitat. If the new habitat created is of poor quality (sink or inhospitable land) the resident species may have reduced viability (Wilcox and Murphy 1985). Altering habitat quality may also cause stable populations to fluctuate or visa versa (Bondrup-Nielsen 1987). Thus, one step in determining the effect of forestry on a species is to compare the quality of the new habitat (clearcuts) with the quality of original habitat.

There are many studies that have focused on the effect of forestry on habitat quality for small mammals (i.e., Kirkland 1990). This interest is due to the belief that small mammals influence many other groups of species such as mycorrhizal fungi (Maser et al. 1978a and 1978b; Martell 1981), fur bearers (Thompson and Colgan 1987; Boutin 1995; Jedrzejewski et al. 1995), and neotropical migrants (Maxson and Oring 1978; Cotterill 1996). However, there is still controversy about the habitat quality of clearcuts for small mammals. There are probably two major sources for this controversy. First, studies have taken place in various forest types where clearcuts may vary in quality. For example, red-backed voles are known to be a forest dwelling species (Tallmon and Mills 1994; Zuleta and Galindo-Leal 1994), and thus most would predict that red-backed voles would not live in clearcuts due to a lack of cover or food (Martell 1981; Mills 1995). The lack of voles in clearcuts has been found in several studies, such as those conducted in harvested aspen forests (Probst and Rakstad 1987). However, high densities of red-backed voles have been found in clearcuts in deciduous landscapes composed mainly of sugar maple and northern red oak (Kirkland 1977). Since forest type may influence the quality of the clearcut, and because the boreal forest has been largely neglected in past forestry studies (Martell and Ravanyi 1977), there is a need to determine the relative quality of clearcuts for small mammals in northern boreal aspen-mixed wood forests.

The second source of the controversy stems from the methods used in past studies. These methods may have led to inaccurate assessment of habitat quality for small mammals. To assess habitat quality one needs several pieces of information: (1) density estimates of the species, (2) summer and over-winter survival rates, (3) reproductive output and (4) immigration patterns (Van Horne 1983). However, many studies concerning the effects of logging on small mammal populations have only obtained density estimates (Verme and Ozoga 1981; Monthey and Soutiere 1985; Probst and Rakstad 1987; Kirkland 1990). These studies have found higher densities of deer mice in the clearcut than the forest and have concluded that the clearcut represents a high quality habitat for deer mice. However, with intensive trapping, Sullivan (1979) found that although there were high densities of deer mice in the clearcuts their growth rates were significantly less than those in the forest. He suggested that the clearcuts in forests dominated by western hemlock, western red cedar, and Douglas fir may not be high quality, but may be acting as dispersal sinks for deer mice. A similar conclusion was drawn by Van Horne (1981) who found clearcuts in spruce-hemlock forests containing high densities of nonbreeding juveniles. To increase the accuracy of habitat quality assessment, some researchers have added estimates of survival and reproductive output (Petticrew and Sadleir 1974; Sullivan 1979; Martell 1983). However, estimates of reproductive output are often confounded by immigration; due to a difficulty in differentiating between immigrants and individuals born *in situ* (Mangel and Tier 1994). Thus, although many researchers are interested in measuring habitat quality (i.e., Hansson 1977; Whitham 1989; Bonar 1993), source and sink habitats have not been identified for most species (Dunning et al. 1992). To identify these habitats, measures of reproductive output are required.

In this study, with intensive trapping and radio-telemetry, I measured density, summer and over-winter survival rates, and reproductive output for deer mice and red-backed voles in clearcuts and original habitat. I also measured immigration of deer mice into clearcut and forest areas. These measures permitted me to determine the effect of harvesting medium aged (≈ 60-70 years old) aspen in boreal forest on the habitat quality for these two species of small mammal.

METHODS

Study Location and Trapping Protocol

This study took place during summers 1994 and 1995 about 50 km north of Lac La Biche, Alberta (Township 69 in Range 13, ≈ 55° N, 111° 54' W). During summer 1994, I had four study sites. Two of the sites were located in ≈ 60-70 years old mixed-wood aspen forests (forest^1 and forest^2), and the other two sites were located in clearcuts that were logged during the winter of 1993/94 (clearcut^1 and clearcut^2). Logging in these areas included the removal >98% of trees and leaving slash (tree branches, etc.) on the ground. The trapping grids were typically 350m by 175m, (6 ha.) with a minimum of 50m between grid edge and forest edge. Trap lines on the grids were 25m apart. In summer 1994, Longworth live traps were placed at 50m intervals along each grid line. However, in July, due to high densities of small mammals, traps were placed at 25m intervals in the two forest grids. Only during the final trapping session were densities of deer mice high enough to warrant placing traps at 25m intervals in the clearcuts.

During summer 1995, I continued to trap small mammals at the original grids and I also added 2 more ≈ 60-70 years old mixed-wood aspen forest grids (forest^3 to forest^4) and 4 more clearcut grids (clearcut^3 to clearcut^6) that were logged during the summer of 1994. The trapping grids on each new study site were 3 ha. in size, and were 225m by 125m. Longworth live traps were located 25m apart on all grids.

Traps were pre-baited with sunflower seeds and oats for 5 days at the beginning of each trapping season. Cotton bedding was provided for insulation in the traps. Traps were set for three consecutive nights every two weeks from April 20 to August 31, 1994 and 1995. These trapping seasons were followed one trapping session at the beginning of October 1994 and 1995 on forest$^{1\&2}$ and clearcut$^{1\&2}$. Any small mammals captured were identified (deer mice or red-backed voles), tagged with a numbered eartag at initial capture, sexed, and weighed. Reproductive status was also recorded and included the following categories: Breeding males - distended testes, Non-breeding males - abdominal testes, Breeding females - pregnant or lactating, Non-breeding females - not pregnant or lactating.

Density Estimates

Closed population models used by the program CAPTURE (Otis et al. 1978) provided a density estimate for each species, for each trapping session, on all grids for summers 1994 and 1995. The best fit model was always chosen for the density estimate. The number of trapping occasions (3 nights), the number of individuals captured, and the total number of captures over the three nights are used by the CAPTURE to generate these density estimates.

Survival Estimates

Summer survival rates of deer mice and red-backed voles could not be directly measured. Instead program POLLOCK (Pollock et al. 1989) was used to calculate persistence of individuals on a grid, and this persistence was used as an indication of survival. Individuals were grouped into four categories based on species (deer mice or red-backed vole) and age (young of the year (<18 grams at initial capture) or over-wintered adults (>18 grams at initial capture)). Young of the year will now be referred to as juveniles. Individuals had to be captured for more than one session to be included in the model. The fate of an individual was determined by trapping. For each individual there was an initial capture date, subsequent captures (every two weeks) which were used as an indication of survival, and the final date that the animal was trapped was used as an indication of disappearance.

Over-winter survival rates of deer mice and red-backed voles were determined by comparing the number of residents (trapped more than one session) caught during the last session in October 1994 with the number remaining until the first session in April 1995. This calculation provided the minimum number of individuals that survived winter.

Reproductive output

During summer 1994, trapping every two weeks allowed me to determine the number of breeding females and the number of juveniles in the clearcut and forested areas. However, I could not conclusively determine if breeding females were successful (weaned at least one young) or how many of juveniles caught on the grid were produced *in situ*. To determine these elements (reproductive output), I also trapped for one day between the three day trapping sessions on forest^1 and clearcut^1. This extra trapping permitted me to closely track the reproductive status of female deer mice and red-backed voles, and I could also more accurately estimate their date of parturition. After a female had been lactating for two weeks I sedated her with Metofine and placed a radio-collar on her. After locating the female at least three times in her nest, nest characteristics were recorded and traps within 50 meters of the nest were set. When the female was trapped I removed her radio-collar. After she was lactating for 2 1/2 weeks I placed 8 Longworth traps and 2 pitfall traps at her nest. Traps were set every second night until there had been at least two consecutive trap nights where no juveniles were caught. Newly captured individuals were sexed, weighed, and marked with a numbered ear tag. Trapping these individuals allowed me to determine the number of females in forest^1 and clearcut^1 that weaned young, and the number of weaned individuals emerging from a nest.

Recruitment was defined as the capture of any juveniles (<18 grams at initial capture), later in the summer, in breeding condition (males - scrotal; females - pregnant). These breeding females were also monitored intensively, allowing me to determine their reproductive output. Growth rates were calculated for all juveniles until they were 17 grams when their growth rates leveled off or females became pregnant.

In summer 1995, I defined juveniles as being born in *situ* if they were captured weighing <12 grams. This decision was based on my finding in summer 1994 where 95% of the juveniles caught on the grid and weighing <12 grams were previously marked near a nest (*in situ* reproduction). Individuals >12 grams caught on the grid were a mixture of juveniles born *in situ* and immigrants.

Immigration Patterns

Since I marked all deer mouse juveniles produced *in situ* and resident deer mouse adults living on clearcut^1 and forest^1 during summer

1994, I assumed that all unmarked deer mice trapped elsewhere on the grid during the summer were immigrants. The number and fate of these clearcut and forest immigrants were compared. I could not mark all the vole juveniles produced *in situ*, and thus could not measure immigration for voles.

RESULTS

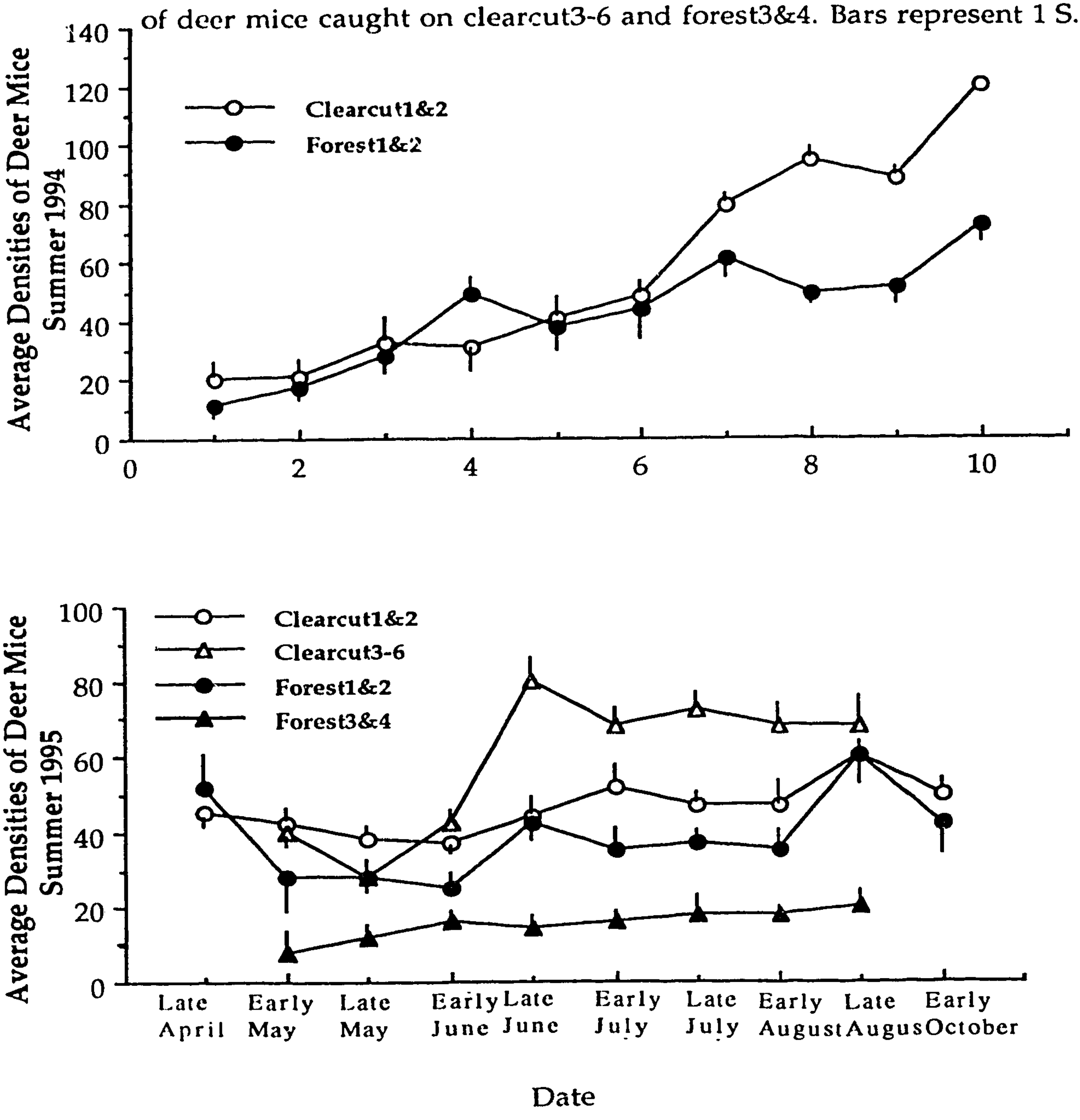
Density estimates for Deer Mice:

The standard errors of the density estimates generated by program CAPTURE were similar in all grids ranging from 0.06% - 10.4% of the estimated density. In summer 1994, during the first year of vegetative growth on clearcut$^{1\&2}$, average densities of deer mice increased 6 fold from 20 individuals captured in late April to 120 individuals captured in early October (Fig. 1-1). Over the same time the average densities in forest$^{1\&2}$ increased 5 fold from 15 individuals to 75 individuals. The higher densities of deer mice in the clearcuts were apparent by late July, and by early October there were almost 1.6 times more deer mice in the clearcut than forest grids.

Over winter 1994/1995 the densities of deer mice declined by 63% in the clearcuts$^{1\&2}$ (from 120 individuals to 45 individuals) compared to 31% in the forests$^{1\&2}$ (from 75 individuals to 52 individuals). Winter was followed by a spring decline in densities (from late April to late June) on both clearcut$^{1\&2}$ and forest$^{1\&2}$. This decline was a more dramatic in the forest grids that had a 50% drop in deer mouse density (52 individuals to 25 individuals). Unlike, summer 1994, densities did not steadily increase over summer 1995 and there was no significant difference in densities between clearcut$^{1\&2}$ and forest$^{1\&2}$ (Fig. 1-1).

Clearcut$^{3-6}$ also displayed a spring decline in deer mouse densities (Fig. 1-1). However, unlike clearcut$^{1\&2}$ and forest$^{1\&2}$ the decline was short- lived and from late June to late August there was almost a 2 fold increase in density on clearcut$^{3-6}$ and forest$^{3\&4}$. In clearcut$^{3-6}$ the average density increased from 40 individuals in early May to 70 individuals in late August. These densities were slightly higher than those obtained in clearcut$^{1\&2}$ and forest$^{1\&2}$ during summer 1995. In comparison, the average densities in forest$^{3\&4}$ were 3.5 to 5 times lower than clearcut$^{3-6}$ and ranged from 8 individuals to 20 individuals over the same time. These densities in forest$^{3\&4}$ are also lower than the densities obtained in clearcut$^{1\&2}$ and forest$^{1\&2}$.

Fig. 1-1. Summer 1994 and 1995 average densities of deer mice caught in clearcut1&2 and forest1&2 and (2X) the summer 1995 average densities of deer mice caught on clearcut3-6 and forest3&4. Bars represent 1 S.E.

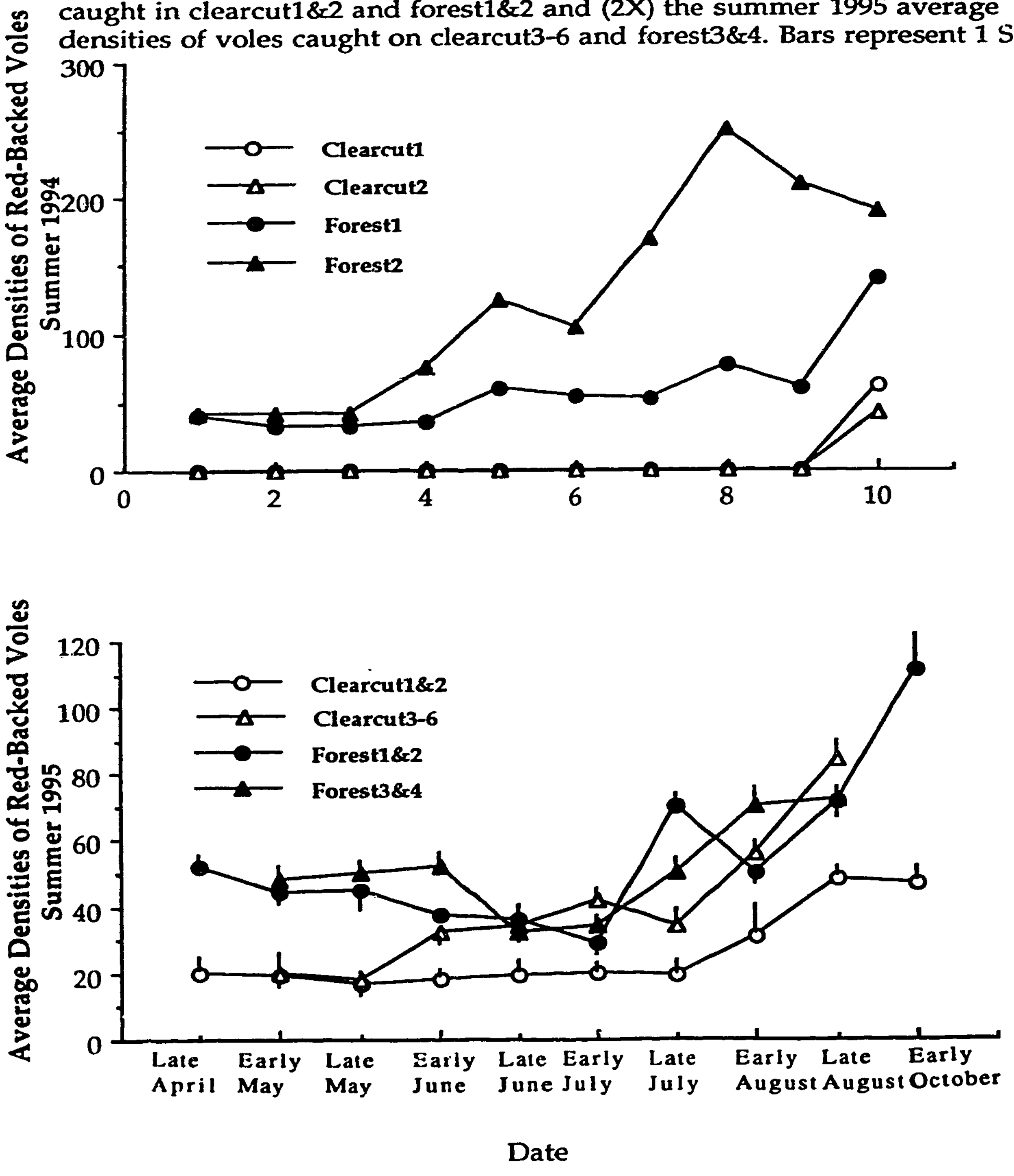


Density of Red-backed Voles:

The standard errors of the density estimates for red-backed voles generated by program CAPTURE were higher than those generated for deer mice, but were similar in all grids ranging from 1.6 - 16.8% of the estimated density; except for August 1995 samplings in forest^{1} and October 1995 samplings in forest$^{1\&2}$ where the standard errors ranged from 55-129% of the estimated density. Red-backed vole densities increased throughout summer 1994 in forest$^{1\&2}$ (Fig. 1.2). However, densities of voles were higher in forest^{2} than forest^{1}, and by early August the density of voles in forest^{2} was 3 times higher than the density in forest^{1}. Red-backed voles were only present on clearcut$^{1\&2}$ in early October.

Over winter 1994/1995 the densities of red-backed voles declined by 71% in forest$^{1\&2}$ (from 173 individuals to 50). Similar to deer mice, red-backed voles in forest$^{1\&2}$ also experienced a spring decline in densities from late April to early July. Density of voles increased 2.3 fold thereafter and reached a final density of 115 individuals by late October. Unlike summer 1994, during summer 1995 red-backed voles lived in clearcuts$^{1\&2}$ and clearcut$^{3-6}$. The densities of red-backed voles were 1.5 to 3 times lower in the clearcut$^{1\&2}$ than the forest grids. In clearcut$^{1\&2}$ densities of red-backed vole remained constant until late July and then increased 2.4 fold and reached a final density of 48 individuals by early October. In contrast, although in early May, clearcut$^{3-6}$ began at a similar density (20 individuals) as clearcut$^{1\&2}$, by late August clearcut$^{3-6}$ had increased 4 fold making the density of red-backed voles slightly higher on clearcut$^{3-6}$ than the forest grids (80 individuals compared to 70 individuals).

Fig. 1-2. Summer 1994 and 1995 average densities of red-backed voles caught in clearcut1&2 and forest1&2 and (2X) the summer 1995 average densities of voles caught on clearcut3-6 and forest3&4. Bars represent 1 S.E.



Summer Survival Estimates for Deer Mice:

Two week survival rates for deer mice were high for all clearcut and forest grids in summers 1994 and 1995 (Tables 1-01). Overlapping confidence limits indicates that there were no significant differences in survival rates for deer mice in the clearcuts compared to the forest grids.

Table 1-01. Two week survival rates calculated by program POLLOCK for adults and juvenile deer mice in clearcut$^{1\&2}$ and forest$^{1\&2}$ during summers 1994 and 1995 and in clearcut$^{3\text{-}6}$ and forest$^{3\&4}$ during summer 1995. Numbers in brackets indicate confidence limits and "n" represents number of mice included in the analysis.

Summer 1994	Clearcut^{1}	Clearcut^{2}	Forest^{1}	Forest^{2}
Adult	0.91 (0.04)	0.87 (0.06)	0.95 (0.04)	0.86 (0.06)
	n=32	n=23	n=24	n=26
Juvenile	0.87 (0.06)	0.95 (0.05)	0.91 (0.05)	0.91 (0.03)
	n=91	n=78	n=62	n=59

Summer 1995	Clearcut^{1}	Clearcut^{2}	Forest^{1}	Forest^{2}
Adult	0.86 (0.06)	0.89 (0.04)	0.83 (0.05)	0.84 (0.06)
	n=44	n=43	n=29	n=58
Juvenile	0.95 (0.04)	0.94 (0.03)	0.93 (0.06)	0.91 (0.04)
	n=26	n=43	n=18	n=39

S. 1995	Clearcut^{3}	Clearcut^{4}	Clearcut^{5}	Clearcut^{6}	Forest^{3}	Forest^{4}
Adult	0.86 (0.04)	0.88 (0.05)	0.81 (0.06)	0.84 (0.07)	0.88 (0.07)	0.86 (0.1)
	n=23	n=23	n=19	n=14	n=7	n=3
Juvenile	0.93 (0.03)	0.95 (0.04)	0.91 (0.05)	0.90 (0.06)	0.86 (0.09)	0.95 (0.05)
	n=32	n=23	n=18	n=18	n=9	n=5

Winter Survival of Deer Mice:

Of the 91 and 89 resident deer mice caught on clearcut$^{1\&2}$ in fall 1994 only 24% and 23% remained until spring 1995. Using contingency analysis it was found that a significantly higher percentage (46% and 59%) of the 60 and

72 resident deer mice caught on forest$^{1\&2}$ in fall 1994 remained until spring 1995 ($X^2=8.27$, $P<0.005$, df=1).

Summer Survival Estimates for Red-Backed Voles:

Summer survival rates of adult red-backed voles were slightly lower than the range displayed by deer mice and juvenile red-backed voles (Table 1-02). Overlapping confidence limits indicate that in summer 1995 there were no significant differences in survival rates for adult or juvenile red-backed voles in the clearcut compared to the forest grids.

Table 1-02. Two week survival rates calculated by program POLLOCK for adults and juvenile red-backed voles in forest$^{1\&2}$ during summer 1994 and in clearcut$^{1\&2}$, forest$^{1\&2}$, clearcut$^{3-6}$,and forest$^{3\&4}$ during summer 1995. Numbers in brackets indicates confidence limits and "n" represents number of mice included in the analysis.

Summer 1994	Forest^{1}	Forest^{2}
Adult	0.73 (0.04) n=49	0.80 (0.04) n=93
Juvenile	0.88 (0.05) n=41	0.93 (0.02) n=55

Summer 1995	Clearcut^{1}	Clearcut^{2}	Forest^{1}	Forest^{2}
Adult	0.74 (0.06) n=21	0.81 (0.08) n=19	0.75 (0.05) n=52	0.73 (0.04) n=71
Juvenile	1.00 (0.00) n=10	0.87 (0.09) n=9	0.87 (0.08) n=14	0.98 (0.02) n=23

S. 1995	Clearcut^{3}	Clearcut^{4}	Clearcut^{5}	Clearcut^{6}	Forest^{3}	Forest^{4}
Adult	0.79 (0.04) n=23	0.81 (0.06) n=16	0.76 (0.06) n=14	0.78 (0.07) n=13	0.76 (0.07) n=31	0.72 (0.06) n=29
Juvenile	0.92 (0.04) n=15	0.96 (0.04) n=10	0.92 (0.05) n=19	0.89 (0.06) n=14	0.87 (0.06) n=18	0.87 (0.05) n=16

Winter Survival of Red-Backed Voles:

There were no resident red-backed voles in clearcuts[1&2] in fall 1994. Thus, I could only compare the number of resident forest voles in fall 1994 with the number that survived until spring 1996. Over-winter survival rates were very low with only 19% of the 76 resident red-backed voles in fall 1994 remained in spring 1995 in forest[1] and only 8% of the 110 residents in forest[2].

Reproductive Output of Deer Mice:

In summer 1994, intensive trapping around nests and radio-telemetry provided detailed productivity information for deer mice living in clearcut[1] and forest[1]. There were more breeding female deer mice in clearcut[1] than in forest[1] and there was on average one more juvenile weaned per nest in clearcut[1] than in forest[1] (Table 1-03). Thus, the production in clearcut[1] was double that of forest[1] (99 weaned juveniles in clearcut[1] compared to 45 juveniles in forest[1]). There was a slight female bias in the sex ratio in the clearcut (59 out of 99) and an equal sex ratio in the forest. Recruitment and growth rates of the young were similar in the two habitats. I am confident that few juveniles were missed when trapping around nests because: (1) traps around nests would remain empty until several juveniles were captured at the same time, and these juveniles continued to be captured until I stopped trapping around the nest, and (2) greater than 95% of the <12gm juveniles caught on the grid were previously marked around a nest.

Table 1-03. Reproductive output obtained from radio-collaring and trapping around deer mouse nests in clearcut[1] and forest[1] during summer 1994. Numbers in brackets represent (S.E.).

	CLEARCUT[1]	FOREST[1]
# Breeding Females	24	16
# Breeding attempts	45	27
% Successful females	71%	60%
#Litters/succ. females	1.60 (0.21)	1.66 (0.29)
% Litters failed	38%	38%
#Juveniles/succ. litter	4.13 (0.38)	3.0 (0.34)
%Recruitment	14%	13%
Growth of Young	0.20 (0.01) g/days	0.20 (0.04) g/days

Similar trends in reproductive output of deer mice were generated from trapping "only" every two weeks on clearcut$^{1\&2}$ and forest$^{1\&2}$ (Table 1-04). Although there were similar numbers of breeding female deer mice in clearcut and forest grids, with a two sample *t* test it was determined that there were higher numbers of <12 gram juveniles caught on clearcut grids than forest grids (an average of 35 juveniles compared to 25 juveniles; T=19, P=0.03, df=1).

Table 1-04. Reproductive output data obtained from trapping deer mice every two weeks in clearcut$^{1\&2}$ and forest$^{1\&2}$ during summer 1994. Two sample *t* test used. (S. E.)

	CLEARCUT$^{1\&2}$	FOREST$^{1\&2}$	STATISTICS
#Breed Females	17.5 (4.5)	20.5 (2.5)	T=0.43 P=0.74 df=1
#Lact/breeding F	1.23 (0)	0.95 (0.16)	T=1.73 P=0.33 df=1
#Juv/breeding F	2.12 (0.50)	1.23 (0.16)	T=1.22 P=0.44 df=1

However, in summer 1995, deer mice living in clearcut$^{1\&2}$ (second year of vegetative growth) had a similar reproductive output to the deer mice living in forest$^{1\&2}$ (Table 1-05). There were equal numbers of breeding females who entered into lactation at similar rates. There were also similar numbers of <12 gram juveniles on clearcut and forest grids (an average of 36 juveniles compared to 40 juveniles).

Table 1-05. Reproductive output data obtained from trapping deer mice every two weeks in clearcut$^{1\&2}$ and forest$^{1\&2}$ during summer 1995. Two sample *t* test used. (S. E.)

	CLEARCUT$^{1\&2}$	FOREST$^{1\&2}$	STATISTICS
#Breed Females	21.5 (0.5)	23 (2.99)	T=0.42 P=0.74 df=1
#Lact/breeding F	0.86 (0.15)	0.82 (0.08)	T=0.66 P=0.63 df=1
#Juv/breeding F	1.66 (0.08)	1.74 (0.03)	T=3.66 P=0.17 df=1

When comparing the reproductive output of deer mice in clearcut$^{3-6}$ (first year of vegetative growth) with forest$^{3\&4}$ similar patterns to summer 1994 were found (Table 1-06). There were higher numbers of breeding deer mice and <12 gram juveniles caught in the clearcut than the forest grids (an average of 20 juveniles compared to 2 juveniles - Two sample *t* test use; T=4.03, P=0.01, df=3).

Table 1-06. Reproductive output data obtained from trapping deer mice every two weeks in clearcut$^{3-6}$, forest$^{3\&4}$ during summer 1995. Two sample *t* test used. (S. E.)

	CLEARCUT$^{3-6}$	FOREST$^{3\&4}$	STATISTICS
#Breed Females	11.3 (4.6)	1.3 (2.1)	T=2.46 P=0.07 df=3
#Lact/breeding F	0.85 (0.25)	0.31(0.53)	T=0.76 P=0.49 df=3
#Juv/breeding F	1.74 (0.31)	1.70 (1.7)	T=0.05 P=0.96 df=3

Reproductive Output of Red-Backed Voles:

In summer 1994, no breeding red-backed voles were found in the clearcuts; thus I intensively monitored the breeding success of 14 female voles in forest^1 with the use of radio-telemetry and trapping around nests (Table 1-07). These 14 females had a low success rate and I never trapped any young from 80% of the nests. The average number of weaned individuals from a successful nest was similar to the deer mice at 3.8 ± 0.8 juveniles/nest. A total of 19 juveniles were caught, of which 11 were males. Recruitment and growth rate of the young were twice as high for voles than deer mice.

Table 1-07. Reproductive output data obtained from radio-telemetry and trapping around red-backed vole nests in forest^1 during summer 1994. (S. E.)

	FOREST^1
#Breeding Females	14
# Breeding attempts	28
% Successful females	36%
#Litters/successful females	1
% Failed litters	80%
# Juveniles/succ. litters	3.8 (0.8)
Recruitment	26%
Growth of juveniles	0.4 (0.1) g/day

Data from trapping every two weeks "only" in summer 1994 indicated that the reproductive output of red-backed voles in forest^{2} was higher than in forest^{1} (Table 1-08). Forest^{2} had more breeding females that frequently entered into lactation and had higher numbers of <12 gram juveniles (29 juveniles compared to 13 juveniles).

Table 1-08. Reproductive output data obtained from trapping red-backed voles every two weeks in forest$^{1\&2}$ during summer 1994.

	FOREST^{1}	FOREST^{2}
#Breeding Females	33	54
#Lactations/breeding F	1.18	1.37
#Juveniles/breeding F	0.39	0.54

In contrast, in summer 1995, red-backed voles were able to breed not only in clearcuts$^{1\&2}$ (second year of vegetative growth) but also clearcut$^{3-6}$ (first year of vegetative growth). Except for clearcut^{1}, there were fewer breeding red-backed voles in the clearcuts compared to the forest grids. However, the clearcut voles entered into lactation as often as forest voles and there were no significant difference in the number of <12 grams juveniles per breeding female in the clearcuts and the forest grids (Table 1.09 &1.10).

Table 1-09. Reproductive output data obtained from trapping voles every two weeks in clearcut$^{1\&2}$ and forest$^{1\&2}$ during summer 1995. Two sample *t* test used. (S. E.)

	CLEARCUT$^{1\&2}$	FOREST$^{1\&2}$	STATISTICS
#Breed Females	13.5 (1.5)	33.5 (7.5)	T=2.22 P=0.27 df=1
#Lact/breeding F	0.95 (0.12)	0.93 (0.03)	T=0.22 P=0.86 df=1
#Juv/breeding F	0.48 (0.01)	0.33 (0.03)	T=10.3 P=0.17 df=1

Table 1-10. Reproductive output data obtained from trapping voles every two weeks in clearcut$^{3-6}$ and forest$^{3\&4}$ during summer 1995. Two sample *t* test used. (S. E.)

	CLEARCUT$^{3-6}$	FOREST$^{3\&4}$	STATISTICS
#Breed Females	17 (2.7)	23 (0)	T=1.97 P=0.12 df=3
#Lact/breeding F	0.95 (0.06)	1.02 (0.18)	T=0.60 P=0.58 df=3
#Juv/breeding F	0.39 (0.14)	0.45 (0.16)	T=0.40 P=0.71 df=3

Immigration Patterns:

In summer 1994, since I marked all deer mice born *in situ* and resident adults in clearcut^1 and forest^1 I was able to identify immigrants. Slightly more immigrants entered forest^1 than clearcut^1 (Table 1.11). The sex ratio was slightly female biased in the clearcut (29 out of 52) and slightly male biased in the forest (38 out of 69). The growth rate and recruitment of the immigrants were similar in the two habitats.

Table 1.11. Immigration data obtained from radio-collaring and trapping deer mice in clearcut^1 and forest^1 during summer 1994. (Standard Error)

	CLEARCUT^1	FOREST^1
# Immigrants	52	69
Recruitment	31%	36%
Growth of Immigrants	0.08 (0.03) g/day	0.07 (0.02) g/day

DISCUSSION

Radio telemetry and intensive trapping permitted me to compare the quality of first and second year clearcuts with the quality of original forested landscape for deer mice and red-backed voles. Similar to previous studies, in the first year of vegetative growth on clearcuts there were higher densities of deer mice in the clearcuts compared to the forests (Verme and Ozoga 1981; Monthey and Soutiere 1985; Probst and Rakstad 1987). These clearcuts, unlike those studied by Sullivan (1979), Van Horne (1982) and Martell (1983), were not acting as dispersal sinks for deer mice. The deer mice had equal summer survival rates in the clearcut and forest grids and more female deer mice were able to breed and wean young that grew and entered the breeding population in the clearcut during the first year of vegetative growth. This higher reproductive output led to an increase in deer mouse density; which translated into higher fall densities in the clearcuts than the forests. Higher immigration of deer mice into forest^1 than clearcut^1 also indicates that the clearcut does not represent a sink habitat for deer mice. However, similar to Sullivan (1979), deer mice displayed a lower over-winter survival rate in the clearcut, which indicates lower habitat quality of the clearcut compared to forests for deer mice during the winter. Even with the reduced over-winter survival the densities of deer mice in the clearcut in the spring were similar to the densities in the forest. Deer mice in the clearcuts (which were now into their second year of vegetative growth) had similar summer densities, survival rates and reproductive output compared to deer mice in the forest. These results differ from the natural sink populations studied by Krohne (1989) where although individuals demonstrated similar summer reproduction and territorial behaviour, they had lower summer densities and dramatically lower spring densities than in the high quality habitat (old-growth forest). These sink populations unlike my clearcut populations went extinct in the winter, and thus were supported by spring immigration.

There was a spring decline of deer mice in both clearcuts and forest grids in summer 1995. Low food supply (Fairbairn 1977; Hansson 1971), spacing behaviour (Fairbairn 1977; Krebs et al. 1977; Krebs and Boonstra 1978) and predation (Fitzgerald 1977) have been the suggested mechanisms behind spring declines for a variety of different small mammal species.

Many studies have tried to assess the effect of forestry on red-backed voles with the use of single-sample surveys (e.g., Clough 1987; Verme and Ozoga 1981; Kirkland 1990). When dealing with a species, such as red-backed voles, who can show dramatic changes in densities over time (Bondrup-Nielsen 1984; Gilbert and Krebs 1991; Schweiger and Boutin 1995), these single-sample surveys may not accurately represent population patterns (Wiens 1981). In particular, a single-sample survey in fall 1994 (a popular sampling period by many researchers) would have left the impression that clearcuts housed a population of red-backed voles. However, in reality it was found that red-backed voles did not live or breed in the clearcuts in summer 1994, and the vole densities in the clearcut in early October were a product of fall immigration. With trapping throughout summer 1994, I could conclude that clearcuts represent inhospitable land for red-backed voles. However, things changed dramatically during summer 1995 when red-backed voles survived, bred, weaned young that persisted and entered the breeding population in first and second year clearcuts as well as the females in the forests. The densities were generally lower in the clearcuts compared to the forests. Thus, I can conclude that habitat quality of the clearcuts was lower than that of forests for red-backed voles. The spacing behaviour and population dynamics of red-backed voles may explain the presence of voles in clearcuts in summer 1995. Spacing behaviour of small mammals has been studied extensively to understand whether this phenomenon stabilizes or destabilizes population dynamics (Bujalaska 1973; Krebs 1979; Kawata 1987; Viitala 1987; Ims 1989; Heske and Bondrup-Nielsen 1990). When a population is increasing in density spacing behaviour of territorial animals may initiate the dispersal of individuals to lower quality habitats (Wolff 1979; Gilbert 1986; Bondrup-Nielsen and Ims 1988; Stenseth and Sannes 1988). This flood of individuals into lower quality habitats may explain the appearance of red-backed voles in the clearcuts during summer 1995. The lower density of voles in the clearcut compared to the forest supports the idea that the clearcuts may be lower quality habitats. However, the high performance of voles in the clearcuts is not expected if the clearcuts are low quality habitats.

When I monitored the red-backed vole females in forest^1 with radio telemetry I found that they were not very successful. I do not know what caused the low reproductive output, however, I feel that my sampling technique was not the problem because throughout the summer I successfully trapped juveniles around some of the nests. Another trend that appeared was the higher density and reproductive output of female red-backed voles in forest^2 than in forest^1, and the higher density and reproductive output of deer mice in forest$^{1\&2}$ than forest$^{3\&4}$. At this time I am unable to determine why these similar aged forests differ greatly in vole and deer mouse productivity.

CONCLUSION

Intensive radio-telemetry and trapping around nests have provided strong evidence that first and second year clearcuts in mature mixed-wood aspen forest are not dispersal sinks for deer mice and red-backed voles. In terms of the deer mice, the clearcuts during their first year of vegetative growth seem to be higher quality habitats than the forests. However, habitat quality of the clearcut was reduced over winter, and in the second year of vegetative growth, clearcuts and forests were of similar quality for deer mice. Red-backed voles are sensitive to clearcutting and may not live in clearcuts or have smaller, equally productive populations in the clearcuts compared to the forest. Thus, I predict that deer mouse populations may increase and red-backed vole populations may decrease with increased timber harvest in the mixed-wood aspen boreal forests of northern Alberta.

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THE EFFECTS OF RESIDUAL MATERIAL ON THE NESTING AND FEEDING BEHAVIOUR OF LACTATING RED-BACKED VOLES.

CHAPTER 2

INTRODUCTION

Red-backed voles (*Clethrionomys gapperi*) live in a variety of habitat types from coniferous and deciduous forests to spruce and fir bogs (Kirkland and Griffin 1974; Bondrup-Nielsen 1987; Kirkland 1990; Zuleta and Galindo-Leal 1994). These voles are generally forest dwellers that are often sensitive to timber harvest. Many studies have found lower densities of red-backed voles in clearcuts than in forests (e.g., Gashwiler 1970; Martell and Radvanyi 1977; Provst and Rakstad 1987; Chapter 1). Martell (1983) suggested that these low densities may be due to a lack of cover or food in clearcuts. In terms of cover, the area just beneath the litter layer of the forest floor was used exclusively as the nesting site for red-backed voles in the Alberta's boreal forest (Weaver unpubl. data). Clearcuts may lack this ground cover, and thus nesting sites may not be available for red-backed voles in clearcuts. The microdistribution of red-backed voles is also strongly correlated with the presence of stumps and rotting logs (Gunderson 1959; Beare 1984; Hayes and Cross 1987; Tallmon and Mills 1994). This rotting material is a source for mycorrhiza (food source) and provides protection for small mammals against predation (Maser et al. 1978a). In many clearcuts, although slash (tree branches, etc.) may be left on the ground, snags and rotting logs are sparse.

Food supply can also limit the density of small mammals in an area (Smith 1971; Gilbert and Krebs 1981; Taitt and Krebs 1981; Young and Stout 1986; Schweiger and Boutin 1995). Even though northern and southern red-backed voles are thought to have a more flexible diet than other vole species (Maser et al. 1978a) fungi and lichens can constitute 80-89% of their gut contents (Martell 1981). Thus, the lack of fungi and lichens in clearcuts has been suggested as the primary reason for the decline or absence of red-backed voles in clearcuts (Maser et al. 1978a and 1978b; Martell 1981). In accordance, Mills (1995) found a decline in truffles towards the forest edge, and an absence of truffles in the clearcuts. A lack of moisture may also prevent red-backed voles from living in clearcuts. Although some controversy exists (Getz 1962) there are suggestions that red-backed voles need to consume up to 6 times more water than other small mammals of similar size (Odum 1944).

Availability of cover and food (water) in clearcuts for red-backed voles may be influenced by the amount of residual material left after timber harvest. The clearcuts studied in Alberta, which lacked red-backed voles in summer 1994, had 98% of the trees removed, but slash was left on the ground (Chapter 1). In the first year of this study, red-backed voles were only present in cutblocks that had slash retention and 40m diameter patches of undisturbed trees and associated ground cover (**residual leave**; Moses Pers. Comm.). There was about 12% residual leave in these areas, and red-backed voles had comparable densities, survival rate, and reproductive output in these cutblocks and the forested areas (Moses Pers. Comm.).

Two possible mechanisms that could have allowed the 12% residual leave to transform an inhospitable clearcut into an area that housed a red-backed vole population are: (1) the leafy layer in the patches provided nesting sites for red-backed vole females, and (2) the presence of living trees in patches ensured the survival of mycorrhizal fungi; thus, providing a food source for the red-backed voles in the clearcut (Maser et al. 1978b). To determine if either of these mechanisms enabled red-backed voles to inhabit these cutblocks I radio-collared lactating red-backed voles to find their nesting sites and determine their foraging locations.

METHODS

Study Location and Trapping Protocol

This study took place during summers 1994 and 1995 in two cutblocks in the mixed-wood aspen forest located about 50 km north of Lac La Biche, Alberta (Township 69 in Range 13, ≈ 55° N, 111° 54' W). Cutting occurred during winter 1993, and in summer 1994 the two cutblocks were overlaid with 6 ha. trapping grids (Grid^1 and Grid^2). The residual material in the grids included the slash on the ground plus several 40m diameter patches of untouched vegetation. These residual patches covered 9.3% and 14.0% of Grid^1 and Grid^2 respectively (Fig. 2-1 and 2-2). To maintain a 50m buffer between the girds and the forest edge Grid^1 and Grid^2 differed in shape.

During summers 1994 and 1995, red-backed voles were trapped from early May to the beginning of October. Trap lines on the grids were separated by 25m and Longworth live traps were placed at 25m intervals along the trap lines. Traps were pre-baited with oats and sunflower seeds for five days before the first trapping session. Cotton bedding was provided for insulation. Traps were set for three consecutive nights every two weeks. The traps were also set for one night between the trapping sessions in summer 1995. The

Fig. 2-1. The distribution of residual patches on Grid1. Scale: 0.5 cm = 25 m

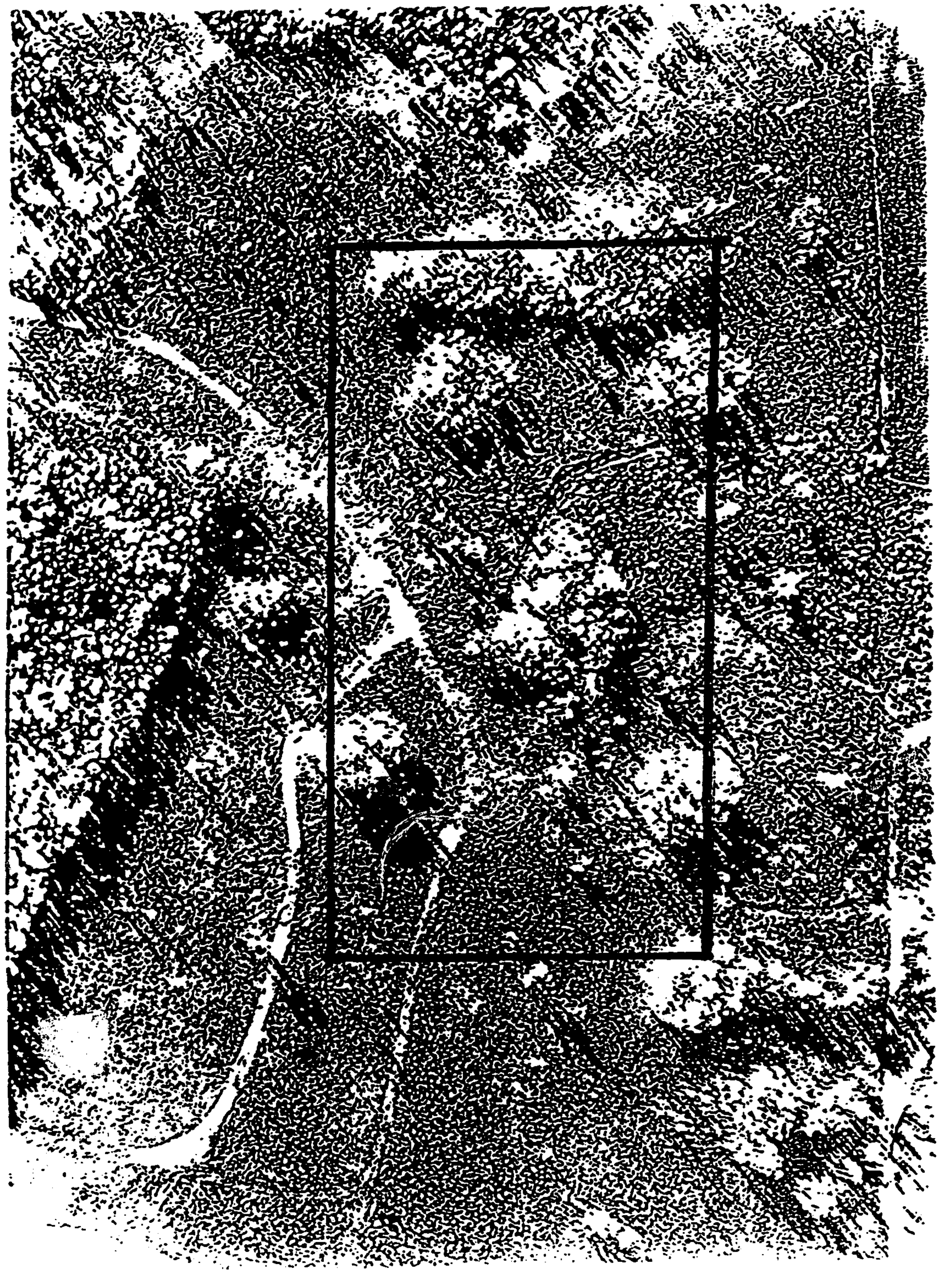

Fig. 2-2. The distribution of residual patches on Grid2. Scale: 0.5 cm = 25 m

location where red-backed voles were caught was recorded, and they were tagged with a numbered eartag at initial capture, sexed, and weighed. Reproductive status was also recorded and included the following categories: Breeding males - distended testes, Non-breeding males - abdominal testes, Breeding females - pregnant or lactating, Non-breeding females - not pregnant or lactating.

Radio-telemetry

In summer 1995, lactating red-backed voles caught on the one additional trap night between the trapping sessions were radio-collared. To radio-collar these females, they were first placed in a 250 ml beaker with a plastic bag used as a lid. Inside the 250 ml beaker was a 50 ml beaker with cotton containing 1 ml of Metofine. Gauze padding separated the animal from the 50 ml beaker. After the female became unconscious (about 4-5 minutes) she was removed and a radio-collar was placed around her neck. The antenna of the radio-collar was used as the collar. When the female regained consciousness she was released (about 20 minutes).

To find the female's nest she was located during the day for three consecutive days. Nest characteristics were recorded, as well as nest location (clearcut or residual patch). To determine where the females foraged I used radio-telemetry and plotted territories of lactating red-backed voles on aerial photographs. In terms of radio-telemetry, the females were located every 20 to 30 minutes from dusk (approximately 10:00 P.M.) to midnight for at least two nights. The female was approached until her activity (active or not active) and her location (clearcut or residual) were determined. Activity was based on the consistency of signal strength when the researcher and antenna were stationary. To determine her location I first tested the accuracy of the signal direction by locating the female nest during the day. Once a signal was heard I was able to walk directly to the nest. Thus, the direction and strength of the signal in the evening allowed me to determine the position of female (clearcut or residual). If the female was close to a residual patch and it was difficult to determine her position I approached the female from several different directions until I could determine if she was in the patch or the clearcut. A female had to be located at least 10 times while she was active to be included in the foraging analysis. When the female was caught in the following trapping session her radio-collar was removed without the use of Metofine.

I identified the traps that were frequented by lactating red-backed voles and plotted their location on aerial photographs. Radio-telemetry in the evening indicated that lactating females were never further than 25m away from the trap she frequented. Thus, a 50 m diameter circle (an indication of the maximum territory size) was placed on the aerial photograph around the trap site most frequented by each lactating red-backed vole. It was then noted whether the territory was located in the clearcut or overlapped with a residual patch. Since these circles represented the maximum territory size, these data were used to determine if there were females that foraged exclusively in the clearcut portion of the grids.

Red-backed vole mothers may suppress maturation of juvenile females (Gilbert et al. 1986). Thus, to breed, juvenile females may need to leave the natal area and set up territories in less suitable habitats - perhaps the clearcut portion of grid (Bondrup-Nielsen and Ims 1988; Stenseth and Sannes 1988). Thus, the presence of territories in the clearcut may be a function of juvenile dispersal. To determine if this trend occurred, I compared the placement of territories at the beginning of the summer (May and June - before juveniles breed) with the placement of territories after juveniles were breeding (July and August).

RESULTS

Nest Location

Twenty-one nests were located in the two cutblocks (12 in grid1 and 9 in grid2). Seventy-six percent of nests were located in the clearcut portion of the grids, and thus red-backed voles were not restricted to nesting in the residual patches. Using chi-square analysis, and expected values based on the coverage of residual patches on the grids (average 12% of grid covered by patches), the pattern of nest location does not deviate significantly from expected ($X^2=0.35$, $P>0.05$, df=1). Nests in the residual patches were located as expected under the leafy layer of the residual floor, whereas nests in the clearcuts were located in various places from under rotting logs and slash piles to the base of old or new stumps. At the beginning of the breeding season (late May) 7 of the 9 females already had their nest in the clearcut portion of the grids.

Foraging Location

The foraging behaviours of 20 females were included in the chi-square analysis. Using expected values based on coverage of residual patches on the grids (average 12% of grid covered), there were almost significantly more of these females than expected foraging in the residual patches ($X^2 = 3.51$, $0.1<P>0.05$, df=1). However, 12 of the 20 female red-backed voles foraged exclusively in the clearcut. Only 1 female foraged exclusively in the residual patches, and the other 7 females spent 50-90% of their time foraging in both the clearcut and the residual patches. Six of the 9 breeding females in late May foraged exclusively in the clearcut portion of the grids.

Fig. 3-6 illustrates that 44% - 50% of the 74 lactating red-backed vole territories were completely in the clearcut portion of the grids. There was no seasonal effect on territory placement with generally half of the territories being in the clearcut and half overlapping the residual patches in May and June 1994 and 1995 and a similar pattern was observed in July and August 1994 and 1995.

DISCUSSION

In contrast to summer 1994, when red-backed voles only lived in cutblocks with about 12% residual leave, in summer 1995, red-backed voles began to live in all clearcuts in the study area, including those with <2% residual leave (Chapter 1). Thus, in summer 1995, it is not surprising that radio-collared red-backed voles used a variety of nesting materials, and were not restricted to having their nests beneath the leafy layer in residual patches. Since voles could use these other materials for nesting sites, I concluded that the availability of leafy layer in the residual patches was not the mechanism that allowed red-backed voles to live in cutblocks in summer 1994.

Although lactating voles foraged almost more than expected in the residual patches in the cutblocks in summer 1995, 12 of the 21 radio-collared females in the cutblocks were not associated with any residual patches.

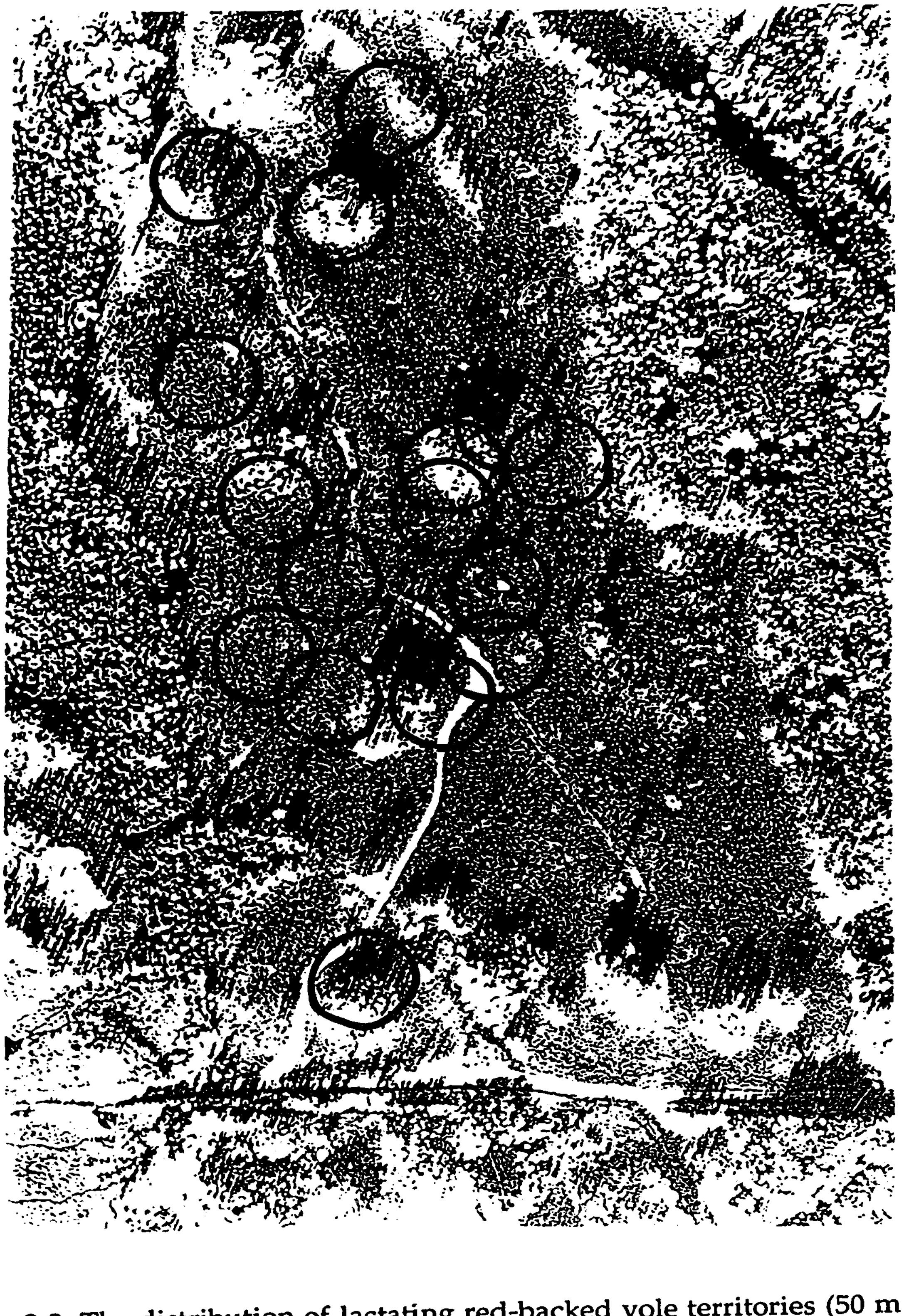

Fig. 2-3. The distribution of lactating red-backed vole territories (50 m diameter - maximum size) in relation to residual patches on Grid^1, during summe. 1994. Scale: 0.5 cm = 25 m

Fig. 2-4. The distribution of lactating red-backed vole territories (50 m diameter - maximum size) in relation to residual patches on Grid1, during summer 1995. Scale: 0.5 cm = 25 m

Fig. 2-5. The distribution of lactating red-backed vole territories (50 m diameter - maximum size) in relation to residual patches on Grid2, during summer 1994. Scale: 0.5 cm = 25 m

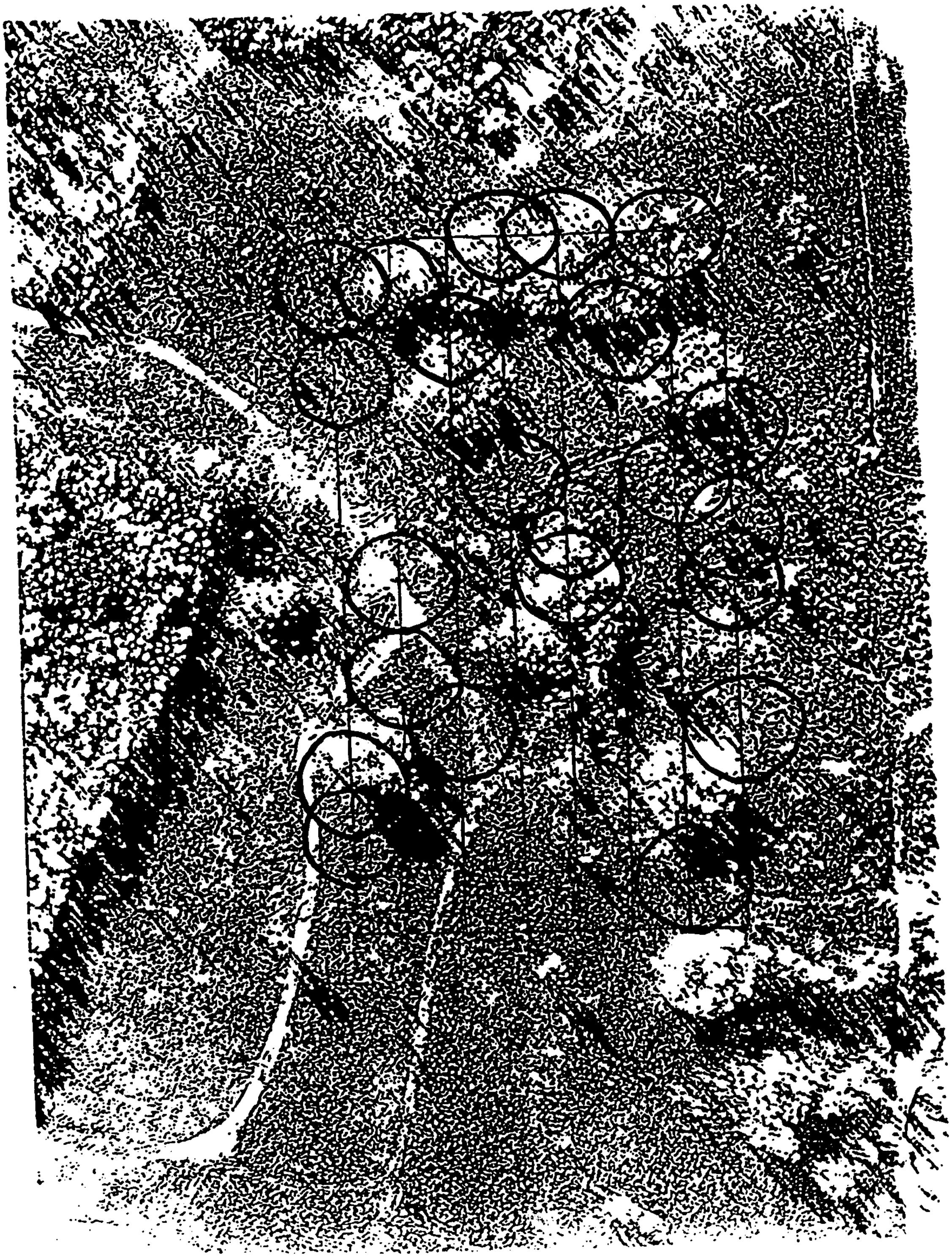

Fig. 2-6. The distribution of lactating red-backed vole territories (50 m diameter - maximum size) in relation to residual patches on Grid2, during summer 1995. Scale: 0.5 cm = 25 m

Likewise, almost half of the female territories were exclusively in the clearcut portion of the cutblocks in summers 1994 and 1995. The high number of females in the clearcut portion was not a function of the young of the year leaving their natal place in the residual patches and setting up territories in the surrounding, potentially lower quality, clearcut (Wolff 1979; Gilbert 1986; Bondrup-Nielsen and Ims 1988; Stenseth and Sannes 1988). Instead, many over-wintered adult red-backed vole females placed their nests in the clearcut portion early in the breeding season (late May) and most of these females foraged exclusively in the clearcut portion of the cutblocks. This pattern may indicate that fungus may be present in the clearcut, or these red-backed voles were surviving on another food source - berries or green vegetation - that was present in the clearcuts.

The most interesting trend in this study is appearance of vole territories in the clearcut portion of cutblocks in summer 1994. Red-backed voles lived did not live in any other clearcuts in the study area, and thus there was something unique that made clearcut portion of the cutblocks hospitable or higher quality than these other clearcuts. There may be several explanations for this trend. For example, a dry summer 1994 may have restricted red-backed voles to clearcut portion close to residual patches where moisture may have been greater (less wind), whereas a wet summer 1995 allowed red-backed voles to exploit all clearcuts. On the other hand, only two cutblocks with residual leave were studied, and the presence of red-backed voles in these areas may be independent of residual leave. For example, meadow voles (*Microtus pennsylvanicus*) may exclude red-backed voles from an area; thus densities of meadow voles may determine the presence or absence of red-backed voles irrespective of residual leave (Iverson and Turner 1972).

Future studies should be directed towards including more cutblocks with 12% residual leave to ensure that the trends observed are caused by the manipulation of residual leave and not some other variable. Continued monitoring of red-backed voles in cutblocks with 12% residual leave and clearcuts with <2% residual leave is also necessary to determine if these populations remain viable. It would also be interesting to determine mycorrhizal abundance and the diet of red-backed voles in the cutblocks and clearcuts, for red-backed voles may be able to alter their diet to match food availability allowing them to exploit a variety of areas (Martell 1981).

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"PACKING" AND EDGE EFFECTS: THE INFLUENCE OF TIMBER HARVEST ON DEER MICE AND RED-BACKED VOLES

CHAPTER 3

INTRODUCTION

Disturbances such as forestry produce vegetation types (clearcuts) which differ in abiotic and biotic features from adjacent vegetation type (forests). Depending on time elapsed since disturbance a distinct edge can be formed between the two vegetation types (Sekqororoane and Dilworth 1995). There are flows of energy, nutrients and species between the vegetation types, and the penetration of these flows into adjacent vegetation is known as edge effects (Murcia 1995). Negative edge effects can reduce the quality of the remnant forest. Thus, the distance penetrated by edge effects is directly related to the functional size of remnant forests (Mills 1995).

The functional size of remnant forests is critical to the persistence of forest dwelling species (Yahner 1988; Matlack 1993). Thus, many conservation biologists have directed their attention toward measuring edge effects on abiotic and biotic features in the forest (Laurance and Yensen 1991). In terms of abiotic features, researchers have studied the edge effect on light, temperature, litter moisture, vapor pressure deficit, humidity, and chemical substances (i.e., Lovejoy et al. 1986; Kapos 1989; Saunders et al. 1991; Hester and Hobbs 1992; Matlack 1993). Murcia (1995), in a review of this literature, suggested that edge effects on these abiotic features disappear within the first 50 m into the forest. Similarly, edge effects on biotic features such as shrub cover and mycorrhizal fungi density did not penetrate further than 40 m into the forest (Saunders 1991; Matlack 1993; Mills 1995). There is also a rapidly growing literature concerning edge effects on animal species. However, due to recent declines in neotropical migrant populations (Diamond 1993) this literature is dominated by the effect of edge on brood parasitism or egg predation (Paton 1994; Murcia 1995). In contrast, although small mammals such as deer mice and red-backed voles are known as important predators on eggs (Maxson and Oring 1978; Cotterill 1996), dispersers of seeds and mycorrhizal fungi (Sullivan 1979; Martell 1981), and an important prey base for many mammalian and avian predators (Thompson and Colgan 1987; Boutin 1995; Jedrzejewski 1995) few studies have addressed the effect of edge on small mammal populations (Mills 1995).

The importance of such studies has been addressed by Nour et al. (1993) who believes that to understand the effect of edge on egg predation one must study the effect of edge on the predator population. Santos and Telleria (1992) theorized that high levels of egg predation in the edge may be due to "packing" of small mammals into forest remnants after surrounding habitats were changed into inhospitable land. In particular, red-backed voles are known to be forest dwellers who typically have low densities in clearcuts (Martell 1983). If the adjacent clearcut is inhospitable one may also see the pooling of frustrated dispersers at the forest edge, because the edge is not permeable to these species (Wiens 1985; Yahner 1988). In contrast, high densities of small mammals may occur in the edge if numbers in the clearcut increases dramatically and there is overflow of individuals from the clearcut into the edge; or, as with bird species (Gates and Gysel 1978; Lovejoy et al. 1986; Ratti and Reese 1988; Noss 1991; Cieslak 1992), higher abundance of food may draw small mammals towards the edge (edge effect). Determining which of these factors causes an increase in predation rates on eggs in the edge may dictate the management strategy used. For example if the first theory is supported then managers may consider improving the quality of the surrounding habitat for small mammals to reduce "packing" in remnant forests.

In this study, intensive trapping of small mammals (deer mice and red-backed voles) in clearcuts, through the edge and into the forest allowed me to first use density estimates to determine whether clearcuts are inhospitable for small mammals thus leading to "packing" of small mammals into the forest, and second to determine whether there is a relationship between distance from edge and numbers of individuals, numbers of breeders and survival rates of small mammals. The predictions of this study are that (1) the clearcuts would be inhospitable to red-backed voles, and thus voles would "pack" into the forest causing high densities in the edge. And (2) Deer mice will also have higher densities in the edge due to an attracted to the edge - increased vegetative complexity (Van Horne 1981) - or an "overflow" from the higher density clearcuts.

METHODS

Study Location and Trapping Protocol

This study took place during summers 1994 and 1995, in the mixed-wood aspen forest about 50 km north of Lac La Biche, Alberta (Township 69 in Range 13, ≈ 55° N, 111° 54' W). Three study sites were overlaid with trapping grids. One of these sites (grid^{1}) was trapped during summer 1994. The trapping grid was 10 ha. in size and extended from 75m into the clearcut through the forest edge to 125m into the forest interior. In summer 1995, the other two sites (grid^{2} and grid^{3}; 6.5 ha. each) were trapped. Grid^{2} and grid^{3} extend further into the clearcut (125m) than grid^{1}, but penetrated an equal distance into the forest (125m). Sherman live traps were used in summer 1994 while Longworth live traps were used in summer 1995. In summer 1994, Longworth live traps were used, less than 1km away, and similar species of small mammals were trapped with Longworth and Sherman live traps. Trap lines, on all three grids, were separated by 25m and traps were placed at 25m intervals along a trap line. All three clearcuts were trapped in their first year of vegetative growth after timber harvest. Timber harvest included the removal of most trees (>98%) and retention of slash (tree branches, etc.) on the ground.

Traps were pre-baited with oats and sunflower seeds for five days before the first trapping season. Cotton bedding was provided for insulation. Traps were set for three consecutive nights every two weeks from the beginning of May to the end of August 1994 and 1995. When small mammals were caught trap location was noted and the animals were identified (deer mice or red-backed voles), tagged with a numbered eartag at initial capture, sexed, and weighed. Reproductive status was also recorded and includes the following categories: Breeding males - distended testes, Non-breeding males - abdominal testes, Breeding females - pregnant or lactating, Non-breeding females - not pregnant or lactating.

Density Estimates in Clearcuts and Forests

Closed population models used by CAPTURE (Otis et al. 1978) provided a density estimate for each species, for each trapping session, in the clearcut and the forest portion of grid^{2} and grid^{3}. The best fit model was always chosen for the density estimate. The number of trapping occasions (3 nights), the number of individuals captured, and the total number of captures over the three nights are used by the CAPTURE to generate these density estimates. Grid^{1} was not included because the clearcut portion was smaller than the forest portion.

Relationship of Animal Numbers and Survival with Distance from Edge

To determine the average distance that individual animals and breeders lived in the forest away from the edge I recorded which traps were frequented over the summer by each individual animal. The distance of these traps into the forest away from the edge were added together and divided by the total number of times the individual was captured. To determine if there was a relationship between the numbers of animals and average distance lived in the forest away from the edge I used a linear regression. In this analysis, the three grids were considered separately for the individuals and the grids were considered together for breeders; due to their low numbers.

I also compared the survival rates of small mammals living at different average distances into the forest away from the edge. Survival rates of deer mice and red-backed voles could not be directly measured. Instead program POLLOCK (Pollock et al. 1989) was used to calculate persistence of individuals on a grid, and this persistence was used as an indication of survival. Individuals were grouped into several categories based on average distance they were living in the forest (less than or greater than 75m away from edge into the forest), and species (deer mice or red-backed vole). Individuals had to be captured for more than one session to be included in the model. The fate of each individual was determined by trapping. For each individual there was an initial capture date, subsequent captures (every two weeks) which were used as an indication of survival, and the final date that the animal was trapped was used as an indication of disappearance. The three grids were considered separately in the analysis.

RESULTS

Density Estimates in Clearcuts and Forests

Densities of deer mice in summer 1995 were typically two times higher in the clearcuts than the forests (Fig. 3-1). In contrast, in May 1995, red-backed vole densities were two times higher in the forests than the clearcuts (Fig. 3-2). However, by late June densities of voles in the clearcut and the forest were very similar, and by late August densities were slightly higher in the clearcut than the forest.

Fig. 3-1. Densities of deer mice from early May 1995 to late August 1995 on Grid2 and Grid3. Bars represent 1 S.E.

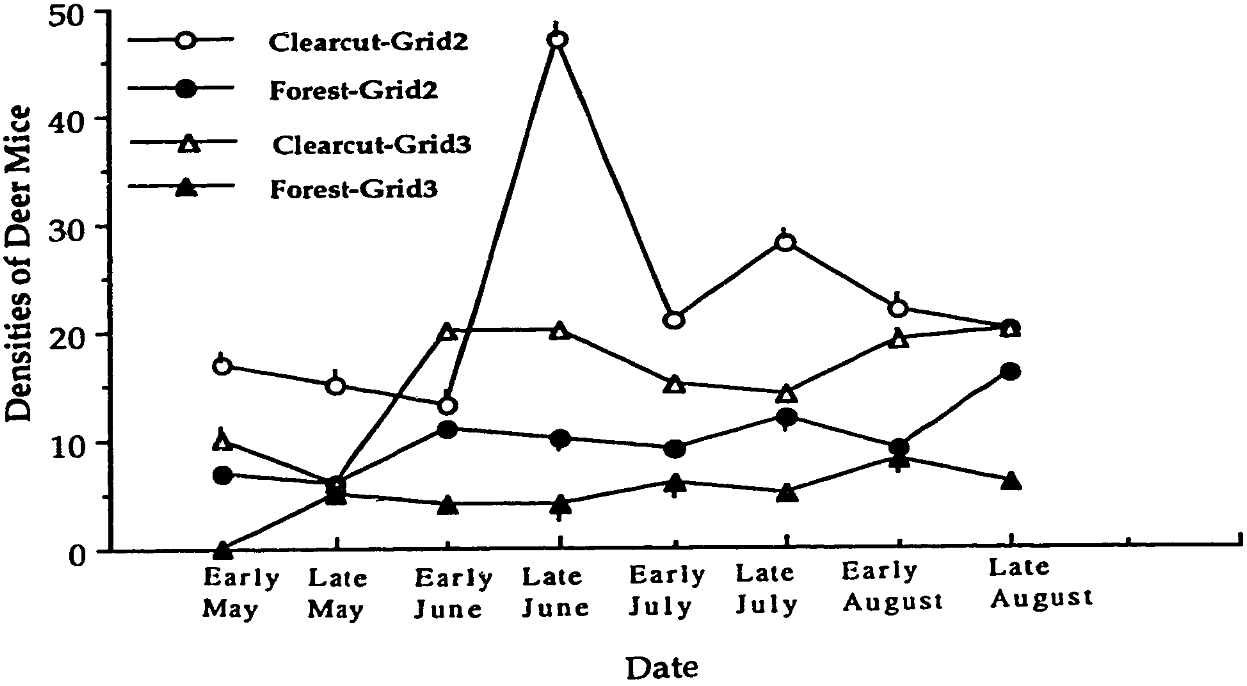
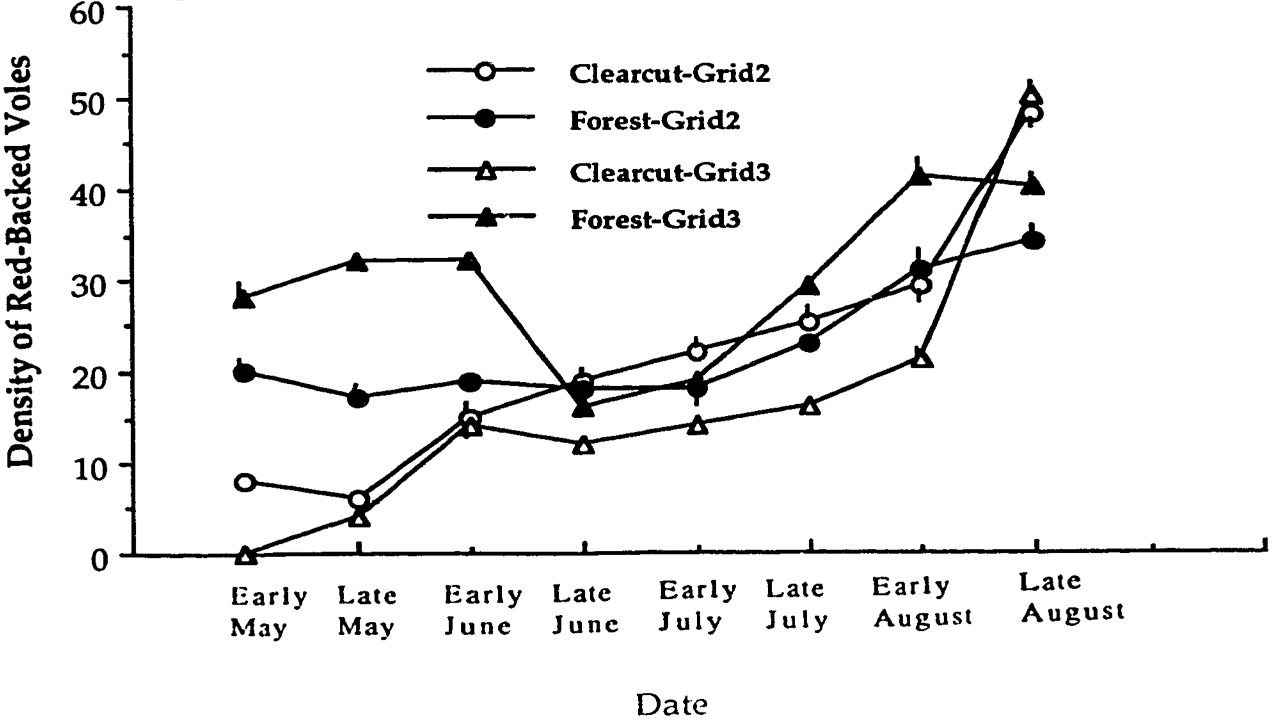


Fig. 3-2. Densities of red-backed voles from early May 1995 to late August 1995 on Grid2 and Grid3. Bars represent 1 S.E.



Relationship of Animal Numbers and Survival with Distance from Edge

Numbers of female deer mice increased significantly from 0 individuals in the forest interior to 6 individuals in the forest edge on Grid^2 (F=16.12, P=0.001, R^2=0.59, df=1; Fig. 3-3). However, there were no significant relationships between numbers and distance in the forest away from edge on Grid^1 and Grid^3 or with breeding females on all three grids. In contrast, individual male deer mice increased significantly in numbers towards the edge in Grid^1 (F=6.05, P=0.03, R^2=0.35, df=1) and grid^2 (F=7.88, P=0.02, R^2=0.41, df=1; Fig. 3-4). Male breeders also increased significantly from 2 breeders in the forest interior to 12 breeders in the forest edge (F=4.78, P=0.05, R^2=0.3, df=1). There was no significant relationship between numbers of male deer mice and distance from edge for Grid^3.

Fig. 3-3. The numbers of individual female deer mice and female breeders caught at different distances in the forest away from the edge.

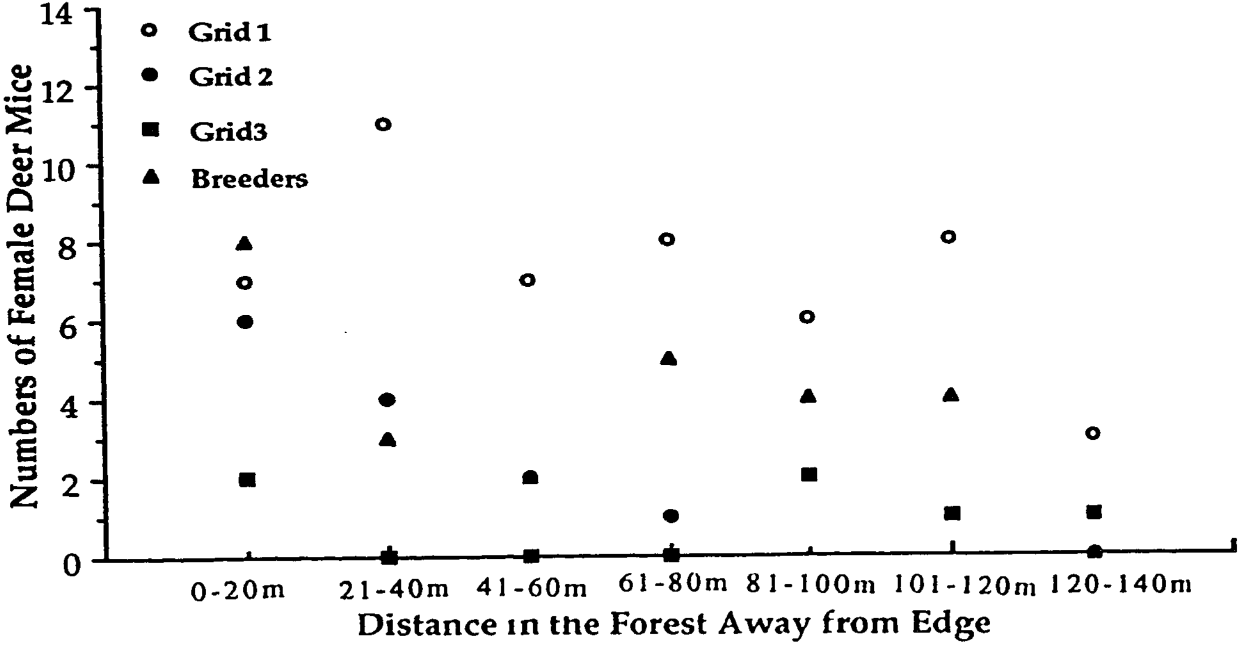
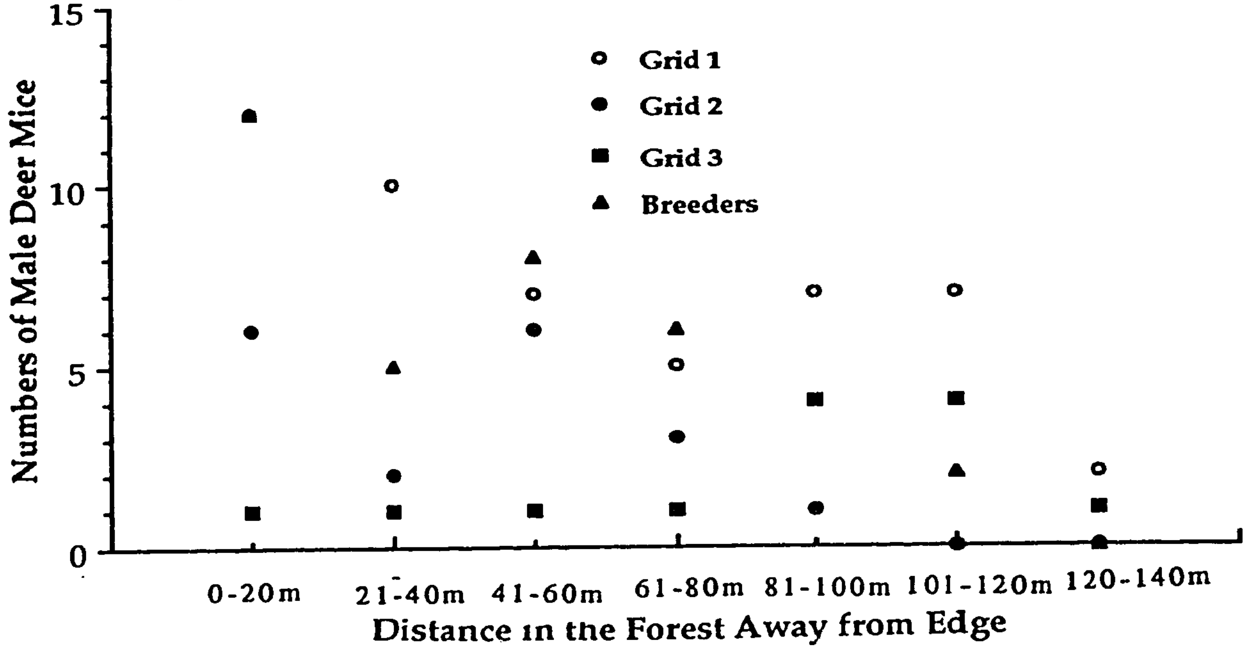


Fig. 3-4. The numbers of individual male deer mice and male breeders caught at different distances in the forest away from the edge.



There were no significant relationships between numbers of individual female red-backed voles and female breeders and distance in forest away from edge on any of the three grids (Fig. 3-5). Male red-backed voles had varied trends with significantly higher numbers towards the forest edge in Grid^1 (F=9.15, P=0.01, R^2=0.45, df=1; Fig. 3-6) and almost significantly higher numbers towards the forest interior in grid^2 (F=4.1, P=0.07, R^2=0.3, df=1). There was no significant relationship between numbers of male voles and distance to edge on Grid^3 or for the male breeders.

Fig. 3-5. The numbers of female red-backed voles and female breeders caught at different distances in the forest away from the edge.

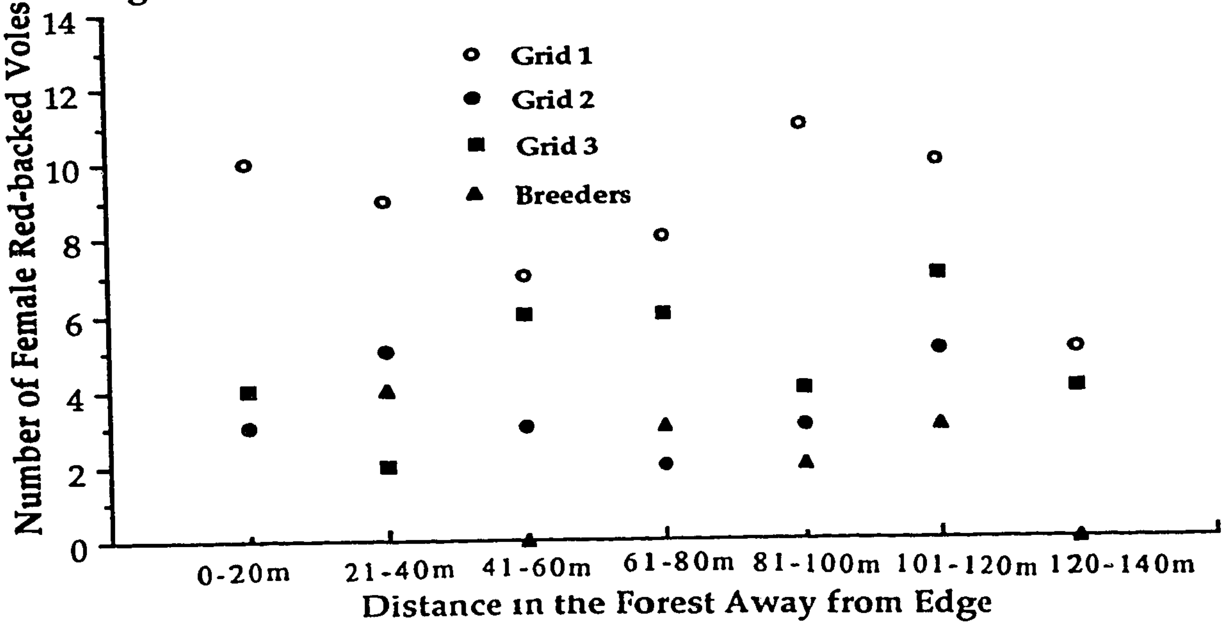
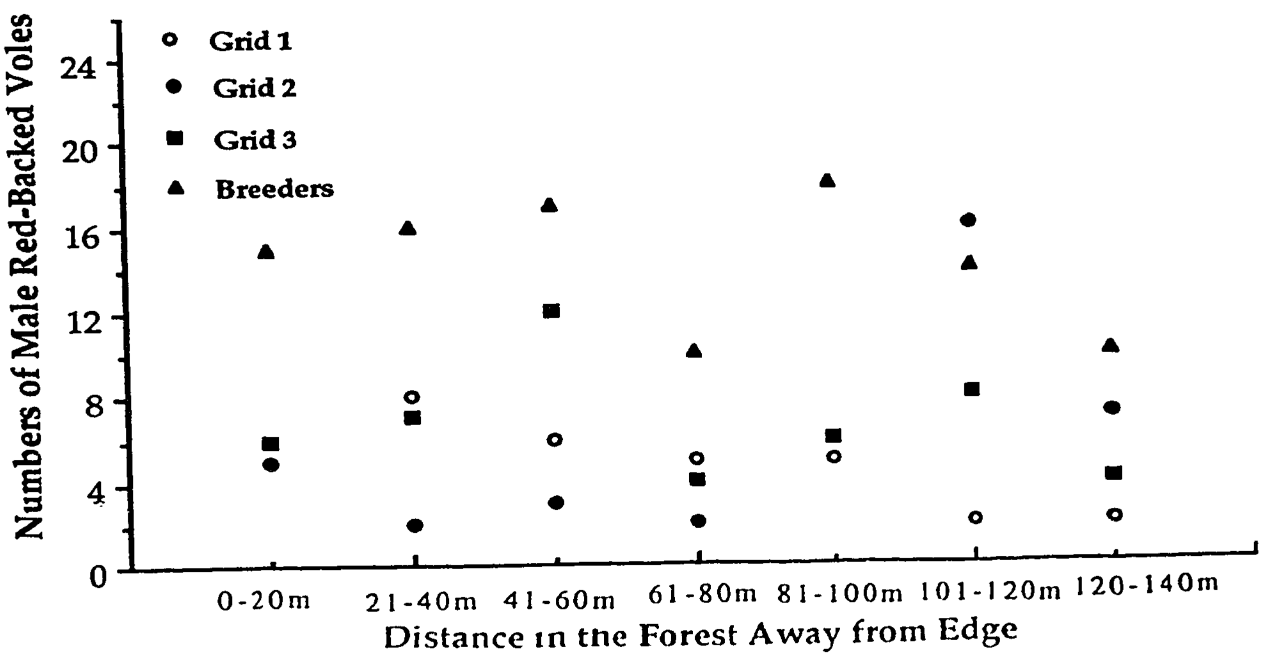


Fig. 3-6. The numbers of male red-backed voles and male breeders caught at different distances in the forest away from the edge.



Survival rates were high for deer mice and red-backed voles, and due to the overlapping confidence limits there were no significant differences between sexes or between individuals living from the 0m (right at the forest edge) to 75m into the forest and from 76m to 125m into the forests (Tables 3-01, 3-02).

Table 3-01. Two week survival rates calculated by program POLLOCK for female and male deer mice living from 0-75m and 76-125m into the forest on Grids$^{1-3}$. Numbers in brackets indicate confidence limits and "n" represents number of mice included in the analysis.

	0-75m grid1	76-125m grid1	0-75m grid2	76-125m grid2	0-75m grid3	76-125m grid3
Female	0.84 (0.07) n=20	0.87 (0.05) n=10	0.90 (0.07) n=9	0.89 (0.1) n=2	0.89 (0.1) n=2	0.92 (0.04) n=3
Male	0.81 (0.06) n=22	0.90 (0.06) n=14	0.92 (0.05) n=7	0.89 (0.1) n=2	1.0 (0.0) n=2	0.96 (0.04) n=4

Table 3-02. Two week survival rates calculated by program POLLOCK for female and male red-backed voles living from 0-75m and 76-125m into the forest on Grids$^{1-3}$. Numbers in brackets indicate confidence limits and "n" represents number of mice included in the analysis.

	0-75m grid1	76-125m grid1	0-75m grid2	76-125m grid2	0-75m grid3	76-125m grid3
Female	0.83 (0.08) n=8	0.88 (0.05) n=5	0.90 (0.07) n=9	0.89 (0.09) n=12	0.84 (0.09) n=12	0.81 (0.05) n=8
Male	0.91 (0.07) n=7	0.86 (0.09) n=4	0.92 (0.07) n=7	0.90 (0.05) n=15	0.88 (0.06) n=10	0.86 (0.04) n=11

DISCUSSION

Unlike previous studies in aspen forests (i.e., Probst and Rakstad 1987; Kirkland 1990), after one year of timber harvest in the aspen mixed-wood forest in northern Alberta there were high densities of both deer mice and red-backed voles in clearcuts. These high densities indicate that clearcuts are hospitable for these small mammal populations. Thus, the first hypothesis that small mammals are "packed" into the remnant forest due to the conversion of the surrounding area into inhospitable land is not supported.

The second hypothesis, that there are relationships between numbers of individuals, breeders, and survival rates with distance from edge (i.e., edge effects), is partly supported by male deer mice who had higher numbers of individuals and breeders toward the forest edge. Individual female deer mice showed this trend only for 1 of the 3 grids. The higher numbers of male deer mice in the edge may indicate that deer mice are drawn toward the edge area. However, these higher numbers may also be caused by increased densities of deer mice in the adjacent clearcuts. Large increases in deer mouse density in clearcuts are often recorded (Verme and Ozoga 1981; Monthey and Soutiere 1985; Probst and Rakstad 1987). However, influences of these high densities on adjacent habitats have been rarely addressed (Sullivan and Krebs 1981). The influence of high densities would be dependent on the permeability of the forest edge to deer mice (Wiens et al. 1985). Since deer mice are naturally resident in the forest I believe that the edge would be very permeable to deer mice, and thus the increased deer mouse density in the edge may be due to an overflow of individuals from the higher density clearcut. Sekgororoane and Dilworth (1995) also found higher densities of deer mice right at the forest edge. However, they did not observe higher densities of deer mice in the clearcut compared to the forest, thus reducing the likelihood of the overflow hypothesis.

However, irrespective of what caused the increased density of male deer mice in the edge one may expect that egg predation rates would also increase towards the edge accordingly. However, the numbers of male deer mice at the edge (≈ 1 ha. area) only reach a maximum of 12 individuals during the summer, and thus although there is a relationship between numbers and distance from edge this trend may not translate into an edge effect on egg predation rates. Male red-backed voles also responded in an opposite manner to distance from edge on one grid (Grid2) which may also mitigate edge effects on egg predation rates. In support, Cotterill (1996), in a study located 125 km north-west of my study site, found that there was no relationship between distance from edge and egg predation rates in artificial nests. Small mammals were the major predators on eggs in this study.

The number of female red-backed voles showed no pattern with distance from edge on any grid. In contrast, lower densities of red-backed voles have been found towards the forest edge by Mills (1995) and Sekgororoane and Dilworth (1995). These reduced densities have been related to reduced densities of truffles (a main food source; Maser *et .al.* 1978a and

1978b; Martell 1981) at the edge (Mills 1995). However, red-backed voles may be able to alter diet depending on food availability. Thus, even if fungus is reduced towards the edge in my study sites; the females may compensate by increasing their consumption of green vegetation or berries (Martell 1981).

Morris (1989) found that the survival of juvenile white footed mice was lower in the edge than the forest interior. In this study, however, survival rates were generally high for both deer mice and red-backed voles and showed no relationship with distance from edge.

In summary, deer mice and red-backed voles were able to live in the clearcuts and thus were not forced to "pack" into the surrounding forests. Although there were some edge effects on numbers of deer mice, the low numbers of deer mice in the forests and the opposite edge effects on red-backed vole males would reduce the appearance of edge effects on egg predation rates.

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CONCLUSION

This study provided information on the quality of clearcuts, the effects of residual leave, and the effects of forest edge on deer mice and red-backed voles. However, several unanswered questions have arisen in this study: (1) Deer mice in clearcuts had significantly lower over-winter survival than deer mice in forests. Is this lower survival a constant feature of clearcuts, and if so, what is the full effect on the viability of clearcut populations? (2) In the second year of the study, red-backed voles appeared in the clearcuts. What are the over-winter survival rates for these clearcut individuals compared to the forest individuals? And do these clearcut populations remain viable over time? And (3) what are the effects of continued regrowth in clearcuts, and annual changes in small mammal abundance on the patterns observed in this study? To answer these questions one needs longer-term monitoring programs in these areas.

The techniques (i.e., radio telemetry) and indexes (<12 gm = *in situ* reproduction) used in this study may enhance these monitoring programs and other small mammal studies. The data generated in this study and from future monitoring programs can be used (1) to determine the effect of harvesting mature aspen forest on density and productivity of small mammal populations in the mixed-wood aspen forests. And (2) by comparing these data to data collected from burned areas one can determine if current harvesting practices emulate natural disturbance of fire.