THE ECOLOGY OF FIVE MAJOR SPECIES OF SMALL MAMMALS IN THE AOSERP STUDY AREA: IN REVIEW

by

JEFFREY E. GREEN

LGL LIMITED

for

ALBERTA OIL SANDS ENVIRONMENTAL RESEARCH PROGRAM

Project LS 7.1.2

August 1979

The Hon. J.W. (Jack) Cookson
Minister of the Environment
222 Legislative Building
Edmonton, Alberta

and

The Hon. John Fraser
Minister of the Environment
Environment Canada
Ottawa, Ontario

Sirs:

Enclosed is the report "The Ecology of Five Major Species of Small Mammals in the AOSERP Study Area: A Review".

This report was prepared for the Alberta Oil Sands Environmental Research Program, through its Land System, under the Canada-Alberta Agreement of February 1975 (amended September 1977).

Respectfully,

W. Solodzuk, P.Eng.
Chairman, Steering Committee, AOSERP
Deputy Minister, Alberta Environment

A.H. Macpherson, Ph.D.
Member, Steering Committee, AOSERP
Regional Director-General
Environment Canada
Western and Northern Region

DESCRIPTIVE SUMMARY

BACKGROUND AND PERSPECTIVE

Interest concerning small mammals within the oil sands area surfaced when seedlings, planted as part of the dyke reclamation project, suffered substantial mortality. The mortality originally was attributed to extensive girdling of the seedlings by small mammals.

An in-depth study of the problem was begun, including a detailed examination of the revegetation procedures currently being employed and a comprehensive examination of the small mammal population in the area.

This literature review was undertaken to provide a synopsis of species distribution, demography, food habits, and habitat utilization of northern populations of five species of small mammals and to supplement information obtained during the concurrent baseline field study Project LS 7.1.2, Part II, "Baseline States of Small Mammal Population in the AOSERP Study Area" (AOSERP Open File Report O.F. 6).

ASSESSMENT

The report "The Ecology of Five Major Species of Small Mammals in the AOSERP Study Area: A Review", which was prepared by Jeffrey E. Green of LGL Limited, has been reviewed and accepted by the Alberta Oil Sands Environmental Research Program.

The report is comprehensive and includes a discussion on the ecology of five species of small mammals common to the Alberta Oil Sands.

In view of the value of the document, AOSERP Management recommends that the report be published and made available to other AOSERP researchers and the public.

S.B. Smith, Ph.D
Program Director
Alberta Oil Sands
Environmental Research Program

B.A. Khan, Ph.D
Research Manager
Land System

TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The ecology (distribution, demography, habitat preferences and food habits) of five of the species of small mammals common to the Alberta Oil Sands are described--the species considered are *Clethrionomys gapperi*, *Microtus pennsylvanicus*, *Peromyscus maniculatus*, *Tamiasciurus hudsonicus* and *Lepus americanus*. The synthesis of available literature was restricted to these five species because these small mammals:

1. are abundant and widely distributed throughout the AOSERP study area;
2. are important prey species of many furbearers and raptors; and
3. are potential pest species of afforestation programs in the AOSERP study area.

Cyclic populations are typical for three of these species--*C. gapperi* and *M. pennsylvanicus* appear to undergo regular cycles in abundance once every three to four years whereas *L. americanus* appear to show regular 10-year cycles of abundance. *P. maniculatus* appear to undergo regular changes in density within each year but it is not clear if these species are cyclic over longer periods. *T. hudsonicus* population densities appear directly related to cone crop production.

M. pennsylvanicus is rated as a major pest species of young afforestation areas. *C. gapperi* and *L. americanus* may also become major pest species as ground, shrub and tree cover increase. *T. hudsonicus* may cause severe damage to trees, particularly coniferous species, once tree cover is abundant and trees are producing seed. *P. maniculatus* damage is restricted to the consumption of tree and shrub seed--this is not thought to be a critical problem on afforestation areas in the AOSERP study areas in light of currently used afforestation techniques.

ACKNOWLEDGEMENTS

I am especially grateful to A. Birdsall, H. Hurtak and G. Searing for their editorial comments and helpful discussions. H. Hurtak prepared the Appendix. I also thank C. Krebs and C. Findley for their reviews of the draft manuscript. K. Bruce prepared the figures. J. Bjornson, C. Furlong and D. Whitford were instrumental in the preparation of earlier and final drafts of this review. I am very grateful for all their assistance.

This research project LS 7.1.2 was funded by the Alberta Oil Sands Environmental Research Program, a joint Alberta-Canada research program established to fund, direct, and co-ordinate research in the Athabasca Oil Sands area or northeastern Alberta.

1. INTRODUCTION

A detailed study of small mammal populations in the Alberta Oil Sands Environmental Research Program (AOSERP) study area (Figure 1) was begun in the fall of 1977 to obtain long-term information on the distribution, abundance, demography and habitat utilization of these populations. Interim analyses of information obtained to date are reported in Green (1978a, 1979). An understanding of the population ecology of the major small mammal species of the oil sands area is essential because:

1. Small mammals are important herbivores in the boreal ecosystem and are one of the major preys of a number of predators. A thorough understanding of small mammal populations is therefore necessary to assess the impact of oil sands development on the ecosystems of the AOSERP study area.
2. Some species of small mammals appear capable of restricting afforestation programs on reclaimed areas--a thorough understanding of the ecology of these 'pest' species in a natural situation is essential to the formulation of an effective and ecologically acceptable program of control.

A review and synthesis of literature on northern populations of small mammals was undertaken to supplement information obtained during the baseline field study. Five major small mammal species will be considered in this review: *Clethrionomys gapperi* (Gapper's red-backed vole), *Microtus pennsylvanicus* (meadow vole), *Peromyscus maniculatus* (deer mouse), *Tamiasciurus hudsonicus* (American red squirrel) and *Lepus americanus* (snowshoe hare). The distribution, demography, habitat preferences and feeding preferences of each of these species will be discussed. I have restricted the literature synthesis to these species because:

alberta canada
ALBERTA OIL SANDS ENVIRONMENTAL RESEARCH PROGRAM

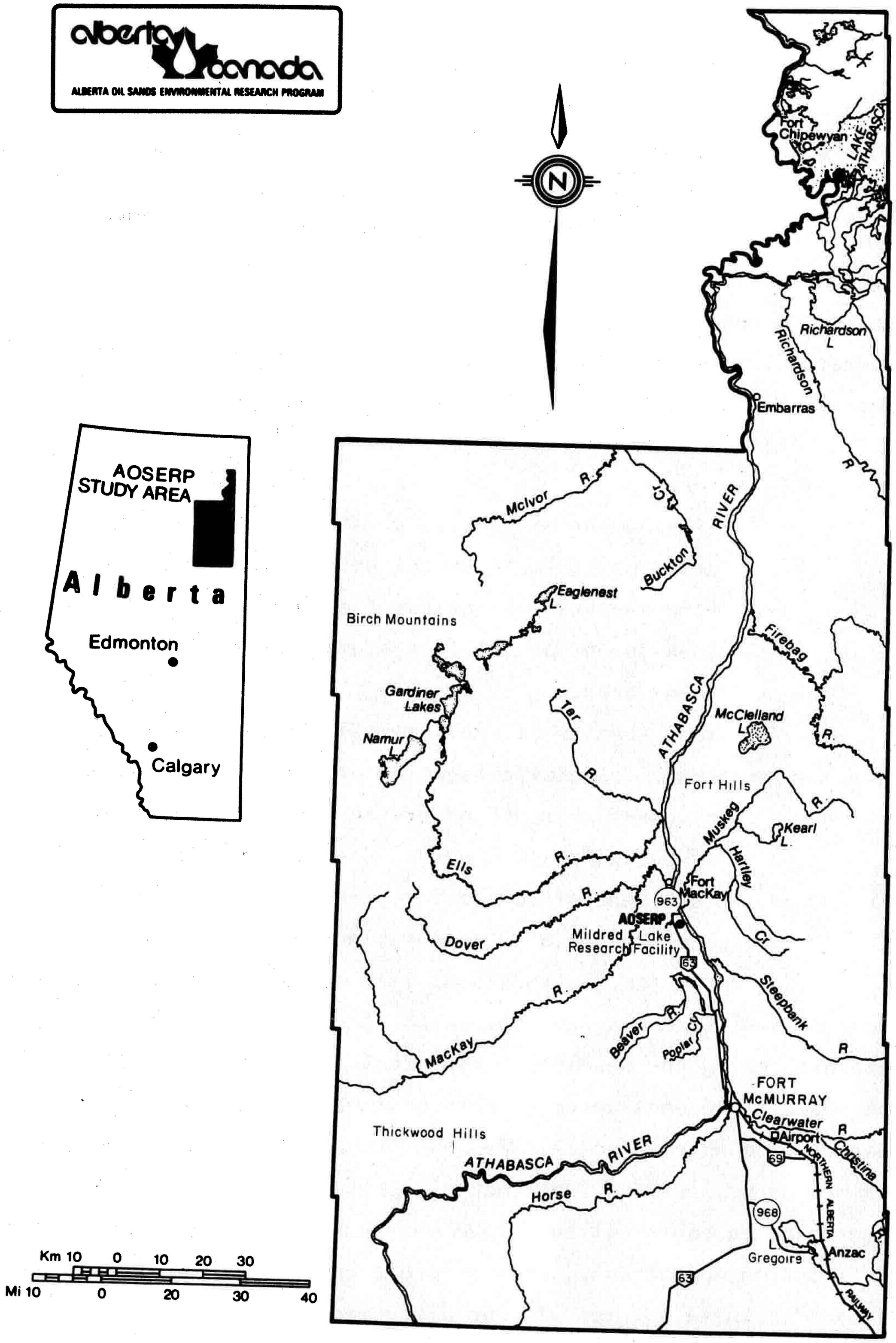

Figure 1. The Alberta Oil Sands Environmental Research Program (AOSERP) study area.

1. The three species of mice are the most abundant small mammal species in the AOSERP study area (Green 1978a, 1979; Westworth and Skinner 1978). In addition, *M. pennsylvanicus* and *C. gapperi* will consume bark (Hamilton 1941a; Thompson 1965; Zemanek 1972; Hansson 1973a, b) and are thus potential pest species on afforestation plots.
2. *T. hudsonicus* is relatively abundant in some of the mature forest vegetation types, is a moderately important furbearer of traplines in the AOSERP study area (Todd 1976; Boyd 1977) and may damage trees (Rowe 1952; Adams 1955; C. Smith 1968).
3. *L. americanus* are moderately abundant in the AOSERP study area and are presently increasing (L. Keith, Univ. of Wisconsin, pers. comm., 24 April 1978; Green 1979). Because snowshoe hares can severely damage young seedlings (Jokela and Lorenz 1959) they are also a potential pest species on afforestation plots.

Other small mammal species such as *Sorex cinereus, Sorex vagrans, Sorex arcticus, Phenacomys intermedius, Synaptomys borealis, Zapus hudsonicus, Eutamias minimus, Glaucomys sabrinus,* and *Mustela erminea* occur in the AOSERP study area (Green 1979). These species were not included in this literature synthesis because they are relatively rare or because their potential impact in terms of damage to planted seedlings in afforestation areas is small.

In this review the continental distribution, food habits, habitat utilization, demography and the potential for damage to afforestation programs are considered for each species. For most species the treatment of each of these topics is restricted to a synthesis of the available literature for northern populations of these species. In instances where information is scarce or lacking, information on closely-related North American species is also included.

It should be stressed that a discussion of the food habits, habitat preferences and demography of small mammals must include a discussion of similarities and variation between populations. Food habits and habitat utilization are obviously affected by local availability (which is often not reported) hence a wide range of responses may be observed. Similarly, estimates of demographic parameters are influenced by the method of data collection. Other factors that must be considered are interspecific competition, food supplies (particularly in the case of reproductive parameters), habitat, weather and recent population changes (i.e., the phase of the population cycle if the species is cyclic).

The term small mammals will be used to collectively describe all species of cricetids (mice and voles), sciurids (chipmunks, red squirrels and flying squirrels) and leporids (hares and rabbits) and the term small rodents to describe only mice and voles. Of the five species considered in this literature review, three are mice *(M. pennsylvanicus, C. gapperi* and *P. maniculatus*--the former two species are also voles*)*, one is a sciurid *(T. hudsonicus)* and one is a leporid *(L. americanus)*. The term microtines will be used to refer specifically to *M. pennsylvanicus* and *C. gapperi* and the term cricetine to refer specifically to *P. maniculatus*. Mammalian nomenclature otherwise follows that of Banfield (1977). Plant nomenclature follows that of Moss (1967) and Hosie (1973). Common names of most plants (when provided in the cited reference) are used throughout the text. Common names and scientific equivalents are provided in the Appendix.

2. *CLETHRIONOMYS GAPPERI*

2.1 DISTRIBUTION

Gapper's red-backed vole, *C. gapperi*, is a common vole of forest and shrub areas throughout the mainland areas of Canada as well as Prince Edward Island and Cape Breton (Banfield 1977) (Figure 2). The red-backed vole is a diurnal species and remains active throughout the year. Populations of *C. gapperi* appear to undergo wide fluctuations in densities from year to year; Fuller (1969, 1977a) suggests that regular cyclic fluctuations in population numbers occur on average once every four to five years.

2.2 FOOD HABITS

2.2.1 Fall and Winter Diets

During the winter, *C. gapperi* depend on overwintering fruits, petioles, small twigs, buds and bark as staple foods of their diet (Criddle 1932; Hamilton 1941a; Dyke 1971; Zemanek 1972). Criddle (1932) found that *C. gapperi* in Manitoba fed extensively on bark of trees and shrubs (crab apple, Manitoba maple, green ash, trembling aspen, bur oak, chokecherry, silverberry and hazel) and reported incidences where girdling by *C. gapperi* resulted in mortalities of Manitoba maple as high as 50%. Green vegetation remaining under the snow was also a staple item of the winter diet (Criddle 1932). Dyke (1971) showed that *C. gapperi* in the Northwest Territories consumed large amounts of lichens (*Parmelia* spp., *Usnea* spp. and *Alectoria jubata*) during the late fall to spring period. Overwintering fruits of bog cranberry, Canadian buffaloberry, common bearberry and common wild rose were also frequently used during the winter. Small quantities of bark and green material (leaves of trembling aspen, cranberry and feather moss) were consumed throughout the winter.

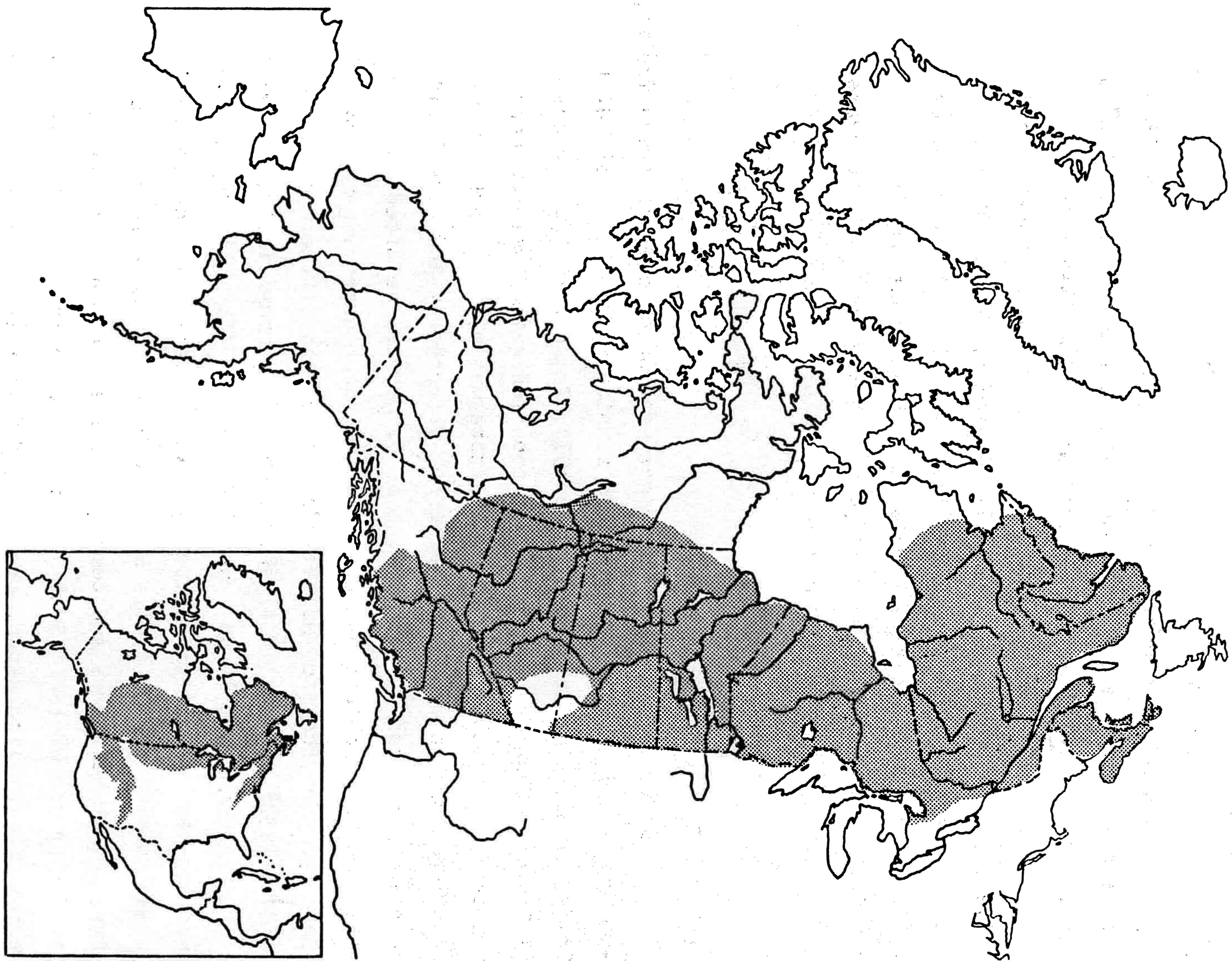

Figure 2. The distribution of *C. gapperi* (red-backed vole) in Canada and in North America (inset). (Modified from Banfield [1977], Map 75.)

2.2.2 Spring and Summer Diets

Dyke (1971) found *C. gapperi* near Heart Lake, Northwest Territories to be largely frugivorous during the spring and summer--overwintered common bearberry and bog cranberry were staple items in the spring diet and, as wild strawberry, wild red raspberry, bastard toad flax and Canadian buffalo-berry became available in the summer, the fruits of these species were also consumed. Leaves of Canadian buffalo-berry, trembling apsen, common bearberry and feather mosses made up a large proportion of the diets in May and June whereas mushrooms were a major component of the diet in July and August. Criddle (1932), Connor (1953) and Fisher (1968) have also reported the use of broad-leafed plants, nuts, fruits, seeds and berries by this species during the spring-summer period. Whitaker (1962), Williams and Finney (1964) and Fisher (1968) found that *C. gapperi* consumed considerable amounts of the fungi *Endogone* spp., *Hymenogaster* spp., *Melanogaster* spp., *Lactanus* spp., *Russala* spp. and *Hydriotrya cubispora* during the summer. Whitaker (1962) and Williams and Finney (1964) found fungi made up an average of 20.2% and 38.0% of the diet by volume, respectively. Insects are also consumed in small quantities throughout the summer period (Fisher 1968).

2.2.3 General Food Habits

C. gapperi is an omnivore feeding largely on petioles of broad-leafed forbs and shrubs, berries, fruits and fungi. Criddle (1932) found that there was considerable seasonal variation in the diet of *C. gapperi*. Similarly, Dyke's (1971) 4-year study of the feeding habits of *C. gapperi* showed that the food habits of this species were seasonally variable and largely reflected seasonal and annual availability--in years of poor fruit production, mushrooms and lichens became increasingly more important in the diet.

2.3 HABITAT UTILIZATION

Early studies of the distributional patterns of *C. gapperi* (Criddle 1932; Williams 1955; Gunderson 1959; Hoffman 1960) have shown that it is closely associated with the boreal montane forest biome. Within this ecotone, *C. gapperi* is limited primarily to forest situations. Connor (1953) found that *C. gapperi* were abundant in damp locations such as cedar swamps and sphagnum bogs. Gunderson (1959) reported high densities of *C. gapperi* in white cedar forests with sparse herbaceous cover. Miller and Getz (1972, 1977) showed that *C. gapperi* were abundant in most forest types, particularly those with dense tree and herb cover. Close associations of *C. gapperi* populations with moderate to dense forest cover have also been reported by Rickard (1960), Cameron (1964), Iverson *et al.* (1967), Fisher (1968), Richens (1974), Lovejoy (1975) and Kucera and Fuller (1978). Based on these and other studies, it appears the distribution of *C. gapperi* is largely affected by three factors--the amount of cover provided by vegetation, debris and litter, the amount of available water and interspecific interactions.

Local distributions of *C. gapperi* often reflect the distribution of dense vegetation cover and debris (Williams 1955; Gunderson 1959; Miller and Getz 1972, 1973, 1977; Powell 1972). Miller and Getz (1972, 1973, 1977) found that *C. gapperi* in the northeastern United States avoided fields, clearings and unforested areas. Correlation analyses of vegetation cover, debris, temperature (of air and substrate), humidity and substrate moisture with population densities of *C. gapperi* indicated a highly significant correlation between the amount of debris and abundance of *C. gapperi*. Powell (1972) compared red-backed vole population densities in a mature forest area and a recent blowdown area immediately adjacent to this forest and found that densities in the blowdown area were three times that in the forested area. Lovejoy (1975) studied a population of *C. gapperi* prior to and after logging of an area. Pre-logging populations were most dense in moist, forested areas. Following logging, *C. gapperi* were restricted to areas of heavy slash. For the first two years after logging the voles avoided partially cut and open areas--*C. gapperi* reoccupied these sites only after substantial shrub cover had begun to develop in these open areas. The association between debris and the abundance of this vole have been attributed to protection from predators (Miller and Getz 1972, 1973). West (1977), however, reported seasonal shifts in the distribution of *C. gapperi* in a black spruce forest and found that aggregations of *C. gapperi* during the winter were significantly associated with a thicker moss layer. He attributed aggregations in these areas to the superior insulating property of the ground cover (resulting from the thick moss layer).

Available moisture can also affect the distribution of *C. gapperi* (Butsch 1954; Hoffmann 1960; Miller and Getz 1972, 1973, 1977). Getz (1968) concluded from a laboratory study of water balance of *C. gapperi* that the relatively inefficient kidney of this species necessitated a relatively high daily intake of water. As a result, the species is often restricted to low, wet areas or to areas where abundant, succulent food is available (Miller and Getz 1972, 1973).

Local distributions of *C. gapperi* are significantly affected by interspecific competition, particularly with *M. pennsylvanicus* (Morris 1969; Morris and Grant 1972; Iverson and Turner 1972; Turner *et al.* 1975). Early studies of small mammals indicated that *C. gapperi* and *M. pennsylvanicus* were rarely found in similar habitats but that either species was able to exist in grassland or forest habitats in absence of the other (Cameron 1964; Grant 1972). Red-backed voles in forested areas generally prevent the occurrence of meadow voles in these areas (Cameron 1964; Morris 1969; Morris and Grant 1972) while the presence of meadow voles in grassland areas restricted red-backed voles to local forested areas (Grant 1969). Morris (1969) and Iverson and Turner (1972) showed that this habitat exclusion may break down in the fall when red-backed voles are able to coexist with meadow voles in grassland areas. Turner *et al.* (1975) showed that the reverse may occur during the fall and winter when meadow voles can coexist with red-backed voles in woodland areas. The breakdown of habitat exclusion in these two species and the re-establishment of habitat exclusion in the spring has shown to be related to changes in aggressive behavior associated with the cessation of breeding and the onset of breeding respectively (i.e., non-breeding animals in the late fall to early spring period tend to be less aggressive than breeding animals in the remainder of the year) (Turner and Iverson 1972; Turner *et al.* 1975).

2.4 DEMOGRAPHY

2.4.1 Reproduction

Female *C. gapperi* are polyoestrous and post-partum breeding appears common (Svihla 1930, cited in Banfield 1977). Fuller (1969) first captured post-partum female *C. gapperi* in the Northwest Territories in mid-June suggesting breeding first occurred in late May. The capture of visibly pregnant females before 25 May, however, suggested that first conceptions occurred in early May. Near Edmonton, Alberta, Stebbins (1976) captured female *C. gapperi* with perforate vaginas and visible ovarian follicles in early May and pregnant females were captured in early June. In New York, Fisher (1968) found the breeding season lasted from May to October. Merritt and Merritt (1978) found that *C. gapperi* in a subalpine forest in Colorado commenced breeding in late March. Males showed reproductive activity under the snow in April but most females were not reproductively active until May. Breeding intensity was high during snowmelt and throughout the summer. Elliot (1969) and Evernden and Fuller (1972) also found the onset of breeding to be related to diminishing snow cover. Evernden and

Fuller (1972) showed that sexual maturation of female *C. gapperi* was stimulated by white and blue radiation and increasing day length (penetration of white and blue radiation to the subnivean space is effectively blocked by the snow)--physiological and behavioural reactions of these voles to subnivean light conditions thus prevents subnivean winter breeding. Male *C. gapperi* in the Northwest Territories were reproductively active by early May (Fuller 1969). Fuller (1969) reported that the last pregnant females in the season were captured in late August; male with regressing testes began to appear in the population in late August. Similar dates of cessation of breeding in populations of *C. gapperi* have been reported by Merritt and Merritt (1978).

Fuller (1969) found that overwintering female *C. gapperi* usually conceived a second litter in early July and sometimes produced a third litter in late July. No females ever produced a fourth litter. Young females of the first litters in July can produce one or two litters by fall (Fuller 1969). Criddle (1932) found that *C. gapperi* in southern Manitoba produced up to four litters per year. Merritt and Merritt (1978) reported an average production of two litters per mature female each summer.

2.4.2 Litter Size

Innes (1978) found that litter size in *C. gapperi* was significantly correlated with latitude and elevation. Litter sizes of various populations of *C. gapperi* are summarized in Table 1. Patric (1962) found that mean annual litter sizes of *C. gapperi* varied significantly over the seven years of his study and that litter size was inversely related to population size--thus during periods of low population densities large litters were produced whereas during periods of high population densities small litters were produced. However, it is not clear if the correlations reported by Patric (1962) are legitimate because no corrections were made for effects of season, for effects of female condition (weight) or effects of female reproductive condition (parity) (Krebs and Myers 1974). Krebs and Myers (1974) reviewed changes

Table 1. Litter sizes of *C. gapperi* (based on Innes [1978]; Tables 1 and 2).

Species	Source	Duration of study, years	No. of months of the year sampled[1]	Latitude °	Latitude '	Elevation, m	Mean litter size	Range	n	Embryos[2] or live births[3]
C. gapperi	Barbour 1951	1	1	36	58	914	3.33	3-4	6	E
	Beer *et al.* 1957	5	-	48	04	412	6.07	3-10	107	E
	Connor 1953	1	1	39	33	15	5.30	3-7	6	E
	Connor 1960	2	5	42	30	533	4.00	3-5	9	E
	Elliot 1969	4	6	53	22	762	6.50	5-8	16	E + L
	Elliot 1969	4	6	53	22	762	7.25	4-9	12	E
	Fisher 1968	3	3	42	29	366	4.37	3-7	27	E
	Fuller 1969	3	4	60	53	229	5.70	-	84	E
	Iverson and Turner 1976	6	6	50	07	274	5.68	3-9	90	E
	Merritt and Merritt 1978	2	7	(Colorado)		3120	6.50	5-8	7	E + L
	Patric 1962	7	6	43	58	457	4.11	1-7	229	E
	Townsend 1935	2	2	43	15	152	4.50	2-6	20	E
	Vaughan 1969	3	7	40	21	3018	6.10	4-8	10	E
	Wrigley 1969	-	5	(Quebec)		-	4.60	3-7	20	E

---

[1] The number of months of the year in which pregnant females were sampled.

[2] E = litter size estimate based on counts of embryos.

[3] L = litter size estimated based on counts of live young.

in litter size with changes in population density in a number of microtine species and found no significant association with changes in litter size and population fluctuations.

2.4.3 Sex Ratios

Fuller (1969) found that males consistently formed a major portion of *C. gapperi* populations in the Northwest Territories but only one of the observed ratios was significantly different from 1:1. The significantly higher proportion of males than females in the overwintered population in 1967 suggested that females suffered heavier mortality over winter than males. Elliot (1969) reported a sex ratio of 1.04:1 for all samples combined but generally males were slightly more abundant throughout the year. Fisher (1968) also reported a trend towards a predominance of males--males made up 58.0% of the voles captured. Elliot (1969) suggested that the predominance of males in his population reflected a wider range of movements by males and a higher turnover rate of males in the population.

2.4.4 Densities and Population Fluctuations

Population densities of *C. gapperi* do not appear to fluctuate widely and do not appear to reach periodic high densities typical of some small mammal populations (i.e., *M. pennsylvanicus*) (Elliot 1969; Fuller 1969, 1977a; Dyke 1971; Kucera and Fuller 1978). Findley and Negus (1953) reported a high density of 74.1 animals/ha for a population of *C. gapperi* in a spruce forest in Colorado. Quick (1964; cited in Merritt and Merritt 1978) reported densities of *C. gapperi* in spruce-fir habitats of 5.4/ha in the spring, increasing to 8.2/ha in summer and reaching a high of 38/ha in autumn. Fuller (1977a) corrected density estimates for 'edge effect' by dividing crude density esimates by 2.5 (the size of the effective trapping area/size of the trapping grid). Density estimates obtained by this method ranged from 12 animals/ha during the peak year (1974) to 6 animals/ha during other years. Density estimates for a population of *C. gapperi* in Colorado ranged from a high of 48.3 animals/ha (in December 1974) to a low of 10 animals/ha (in March 1974) (Merritt and Merritt 1978).

Two periods of the year, the autumn and spring thermal overturns (associated with first snow fall and spring melt, respectively), appear to critically affect the survival of *C. gapperi* (Johnson 1951; Pruitt 1957; Fuller 1969; Fuller *et al.* 1969). Prior to snowfall in the late autumn, ambient temperatures fall below ground temperature and, until the accumulation of snow is sufficient for development of a subnivean layer and to insulate the substrate, small rodents are exposed to wide daily extremes in ambient temperature. During the spring thaw, snow rapidly loses its insulating capacity and meltwater may flood subnivean runways. Hence small rodents are again exposed to wide daily fluctuations in temperature. Small rodent populations have been shown to suffer high mortality during these two periods (Johnson 1951; Fuller 1969; Fuller *et al.* 1969; Vaughan 1969; Merritt and Merritt 1978).

Few population studies of *C. gapperi* have been of a sufficient duration to determine if this species undergoes cyclic fluctuations in population density. A detailed study of *C. gapperi* populations in the Northwest Territories by W.A. Fuller and associates from 1964 to 1975 (Elliot 1969; Fuller 1969, 1977a; Dyke 1971) indicated that *C. gapperi* populations underwent regular increases and decreases in numbers and suggested that peak populations occurred every four to five years.

2.5 DAMAGE POTENTIAL

Reports of damage to young trees and shrubs in reforestation areas by *Clethrionomys* spp. are limited (Gessell and Orians 1967; Black *et al.* 1969; Banfield 1977; Hornfeldt 1978). All these reports are based on circumstantial evidence but the occurrence of buds, twigs, petioles and bark of coniferous and deciduous tree species and shrubs in the winter diet of *C. gapperi* (Criddle 1932; Hamilton 1941a; Dyke 1971; Zemanek 1972) substantiates these claims.

3. *MICROTUS PENNSYLVANICUS*

3.1 DISTRIBUTION

The meadow vole *Microtus pennsylvanicus* is found throughout Canada from Newfoundland to British Columbia and as far north as the Mackenzie delta (Banfield 1977) (Figure 3). Meadow voles exhibit a diurnal activity pattern and remain active beneath the snow (in the subnivean layer) throughout the winter. Populations of *M. pennsylvanicus* exhibit marked population fluctuations that occur at three to four year intervals (Krebs and Myers 1974). Banfield (1977) rated *M. pennsylvanicus* as one of the most important small mammals within the boreal forest ecotone and the central plains region because of its role as a major prey species of furbearers and as a serious pest species in agricultural and forest areas.

3.2 FOOD HABITS

M. pennsylvanicus is largely herbivorous, feeding predominantly on grasses, sedges and to a lesser extent on forbs throughout the year (Bailey 1924; Hamilton 1940; Jameson 1955; Thompson 1965; Zimmerman 1965). Seasonal differences in diet appear to be small. Bailey (1924) found that meadow voles commonly consumed the new shoots of graminoids in the spring, the inner hearts of grass bases in early summer, seeds of various graminoids in the fall, and the bases, sprouts, roots and bulbs in the winter. The summer diet may also be augmented by flowers, leaves, and fruits of forbs and low shrubs. Thompson (1965) and Zimmerman (1965) have both conducted more detailed studies of the feeding habits and preferences of this vole.

Based on feeding trails, Thompson (1965) found that white clover was the most preferred food of *M. pennsylvanicus* in Minnesota. Alfalfa and red clover were next in rank followed by dandelion,

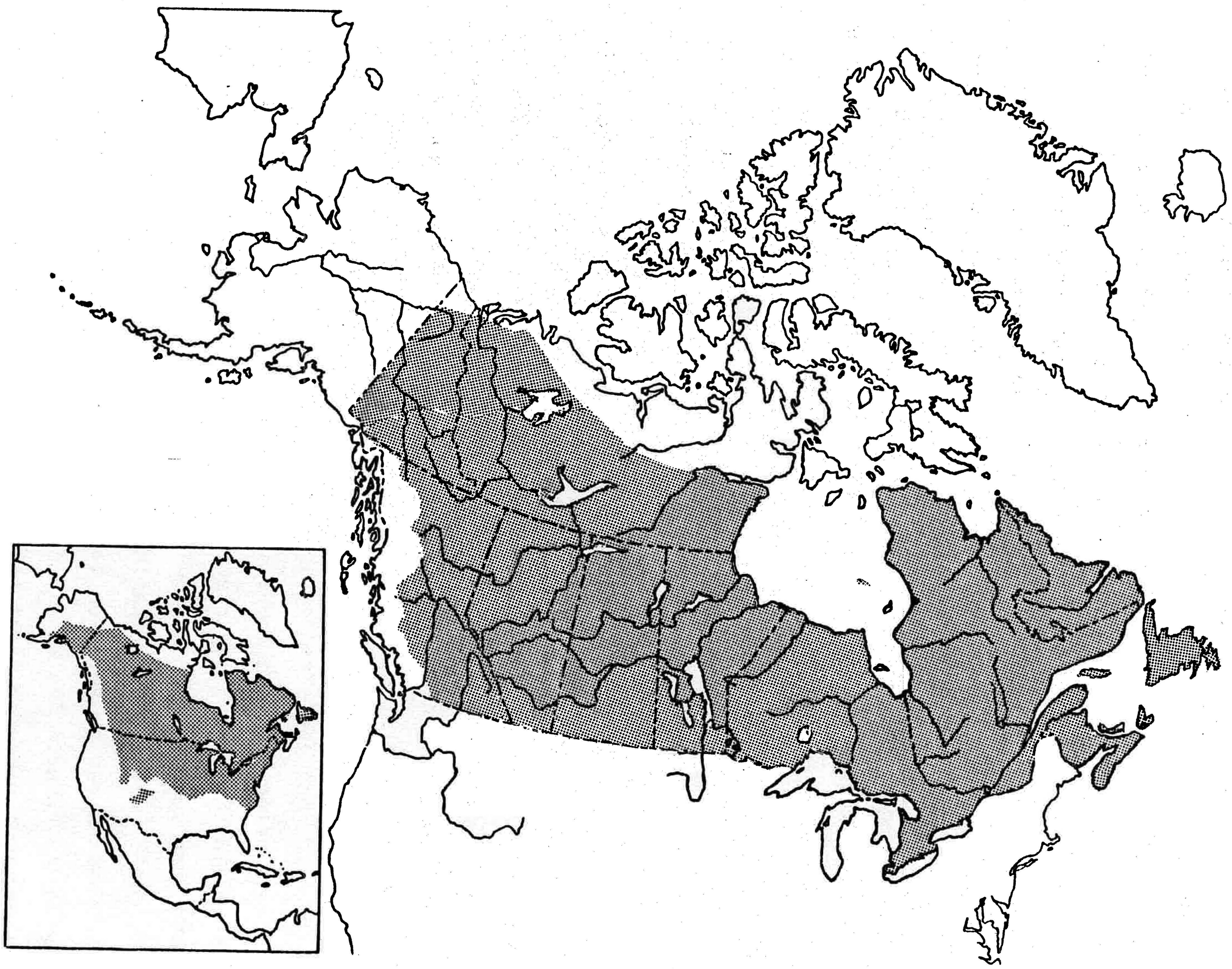

Figure 3. The distribution of *M. pennsylvanicus* (meadow vole) in Canada and in North America (inset). (Modified from Banfield [1977], Map 87.)

horsetails and a number of adventive grasses (in order of decreasing preference, Kentucky bluegrass, common timothy, smooth brome grass, short-awn fox tail, quack grass and reed canary grass). Native monocots and native boreal and bog plants were the least preferred foods of the 30 species offered during the preference trials.

Zimmerman (1965) examined the stomach contents of *M. pennsylvanicus* collected in Indiana and, on the basis of percent volume, rated *Poa compressa* as the most common food species (a mean of 32.1%). Other important food species included *Panicum capillare, Muhlenbergia sobolifera, Plantago lanceolata* and *Achillea millefolium.* Comparing the frequency of occurrence of each plant species in the collection area to the volume consumed, Zimmerman (1965) concluded that meadow voles most often consume those plants which are most abundant, particularly if they are green and succulent.

Insects and fungi are also consumed in small amounts (Bailey 1924; Zimmerman 1965) and the cambium of woody plants is included in the diet during some winters (Bailey 1924; Jameson 1955; Zimmerman 1965). The consumption of bark by meadow voles is supposedly highest during periods of food scarcity (Bailey 1924). *Microtus agrestis,* the European ecological equivalent of the meadow vole in North America, commonly consumed bark only when food supplies were limited (Hansson 1971; Larrson and Hansson 1977). Hansson (1971) showed in a laboratory experiment that no girdling occurred when preferred carbohydrates were available suggesting that barking of young trees is indicative of nutritional stress (i.e., a shortage of nutrients in more commonly consumed graminoid and herb species).

Grant (1978) examined dispersal tendencies of *M. pennsylvanicus* in relation to the carrying capacity of a grassland area in Quebec. The weekly energy requirements of the study population never exceeded 1% of the standing crop of grass and was usually 0.1%. However, sodium and phosphorous were limited in the food supply. By feeding selectively and/or copiously (on foods rich in sodium and phosphorous), voles could compensate for these nutrient deficiencies (Grant 1978). In doing so, Grant (1978) estimated that voles consumed only 10% of the standing crop during the summer. During the winter, however, consumption of grasses sufficient to fulfill both the energy and nutrient requirements of the vole population approached 100% of the standing stock of grass. Thus, meadow vole populations in grassland situations may regularly undergo periods of nutrient stress during the mid- to late winter. Grant (1978) suggested that dispersal from *M. pennsylvanicus* populations increases as the 'nutrient' carrying capacity of an area is approached.

3.3 HABITAT UTILIZATION

The distribution of *M. pennsylvanicus* has been shown to be closely related to the type and amount of vegetative cover. *M. pennsylvanicus* most commonly occurs in moist habitats with dense grass-dominated or sedge-dominated ground cover (Findley 1951, 1954; Connor 1953; Eadie 1953; Mossman 1955; Getz 1960; Hoffman 1960; Zimmerman 1965; Iverson *et al.* 1967; Wrigley 1969; Grant 1971a; Hodgson 1972). Hodgson (1972) examined the local distribution of *M. pennsylvanicus* in nine different habitat types in Montana. Densities were highest in grass-sedge meadows (6.78 voles/100 trap-nights [TN]), followed by mesic grasslands (5.25 voles/100 TN), forb-dominated areas (2.00 voles/100 TN), grass-forb dominated areas (1.84 voles/100 TN), aspen groves (0.67 voles/100 TN) and dry grasslands (0.27 voles/100 TN). No meadow voles were captured in sagebrush areas, coniferous forest or mountain parkland. However, *M. pennsylvanicus* is able to and does occupy woodland areas, particularly areas comprised of open woods and grassy vegetation (Buckner 1957; Smith and Foster 1957; Clough 1964; Connor 1960; Morris 1969; Grant 1971a; Krebs and Wingate 1976).

Some plant species appear to affect the local distribution of the meadow vole. Hodgson (1972) reported that *M. pennsylvanicus* favoured habitats dominated by *Bromus marginatus, Dactylis glomerata* and *Poa pratensis*. Areas of abundant *Medicago sativa* also supported high densities of this vole. Hoffman (1960) found densities of *M. pennsylvanicus* to be highest in habitats dominated by *Carex* spp. Zimmerman (1965) found a positive association between the density of *Poa compressa* and *Muhlenbergia sobolifera* and densities of *M. pennsylvanicus*. M'Closkey (1975) found that the habitat favoured by meadow voles was composed primarily of *Agropyron trachycaulum*.

The density of ground cover and structure of the canopy also influences *M. pennsylvanicus* populations. Eadie (1953) showed that areas of a grassland in New York with high indices of mouse density had almost double the amount of ground cover (by weight) of areas with low indices of mouse density. Birney *et al.* (1976) found that densities of *Microtus* sp. were directly related to the amounts of vegetation cover and suggested that a threshold level of vegetation cover was necessary before cyclic fluctuations in population densities could occur. Wirtz and Pearson (1960) offered meadow voles a choice of a simulated grassland habitat or a simulated *Solidago*-dominated habitat and found that most animals chose the grassland habitat. Hodgson (1972) found that distribution of *M. pennsylvanicus* was significantly correlated with the amount of plant biomass and the total coverage of the herbaceous and shrub canopy--areas with plant biomass greater than 700 g/m^2 or with herb-shrub cover greater than 85% appeared to be the most favourable habitats. Zimmerman (1965) concluded that the optimum habitat of *M. pennsylvanicus* was those areas where grasses formed 50% or more of the vegetation and cover was fair to good.

LoBue and Darnell (1959) showed that abrupt changes in amounts of cover led to rapid changes in the local distribution of meadow voles. In an area consisting of a plowed field and edge areas, *M. pennsylvanicus* was restricted to areas of dense cover during the spring but, as the crops developed in the field, they gradually utilized larger portions of this area. However, following the cutting of the field crop in the fall, *M. pennsylvanicus* showed a negative response to reduced cover and restricted their movements to the edge areas.

Soil moisture and composition can, of course, affect small mammal distribution indirectly through influences on vegetation. Several studies have also indicated that local distributions of small mammals can be directly affected by soil properties. Miller (1969) showed that the distribution of *M. pennsylvanicus* in Indiana was associated with areas of greater amounts of soil moisture. Aumann and Emlen (1965) suggested that peak densities of microtine rodents were correlated with the relative abundance of sodium in the soil--as sodium levels increased, higher peak densities were attained. Krebs *et al.* (1971), however, found no significant relationships between percent organic matter, calcium, magnesium, phosphorous or sodium levels of soils and peak densities or mean densities of *M. pennsylvanicus.* However, 38% of the variation in peak densities of *M. pennsylvanicus* could be explained by differences in soil pH and potassium levels. Krebs *et al.* (1971) suggested that soil nutrients per se were not significant to voles but that nutritional differences in plants, resulting from differences in the soil, could influence population densities.

Interspecific competition with other small rodent species may affect local distributions of *M. pennsylvanicus.* In Quebec, Grant (1970, 1971a) showed that isolated groups of *M. pennsylvanicus* in enclosures preferred grassland habitat to woodland areas--movement into woodland areas occurred only when densities of meadow voles in the grassland exceeded densities of 168-198 voles/ha. Morris and Grant (1972), however, showed that *C. gapperi* in aspen groves in Saskatchewan excluded *M. pennsylvanicus* from woodland areas. It would appear that *M. pennsylvanicus* normally occupies grassland areas (by choice) but density-dependent dispersal may occur into woodland habitats. Occupation of woodland areas would then be possible only when *C. gapperi* are absent or in low numbers. In southern areas of its range, Findley (1954) and Miller (1969) suggested that competition with *Microtus ochrogaster* and *Microtus montanus* restricted *M. pennsylvanicus* to the hydrosere community. A more recent study by Krebs (1977), however, suggested that *M. pennsylvanicus* and *M. ochrogaster* coexist in Indiana grassland with little interspecific competition.

3.4 DEMOGRAPHY

3.4.1 Reproduction

The breeding season normally commences in late March to early April and terminates in September or October (Coventry 1937; Gunderson 1950; Getz 1960; Beer and MacLeod 1961; Krebs *et al.* 1969; Wrigley 1969; Iverson and Turner 1976). Getz (1960) suggested that the onset of breeding in spring was related to the appearance of new green food. The length of the breeding may vary depending on the weather conditions, availability of food and phase of the population cycle. For example, Cole and Batzli (1978) provided high quality food to a population of *M. ochrogaster* and found that breeding intensity (e.g., length of breeding season, percentage of males and females in breeding condition, pregnancy rates) increased. Winter breeding by this species has been reported in Indiana (Corthum 1967; Krebs *et al.* 1969; Tamarin 1977), in Manitoba (Iverson and Turner 1976) and in Minnesota (Beer and MacLeod 1961). Banfield (1977) suggested that winter breeding may occur if good quality food was abundant and if snow conditions were good (i.e., a well-developed subnivean layer). Krebs *et al.* (1969) and Tamarin (1977) reported winter breeding (or an extended summer breeding period) only during the population increase--reproductive effort decreased just prior to the population peak and continued to decrease during the peak period and the population decline. Tamarin (1977) found that only older animals tended to breed when winter breeding occurred.

Females are polyestrous and post-partum mating is common (Hoffman 1958; Hasler 1975). Gestation is 21 days with embryos becoming visible by the sixth day after conception (Hamilton 1941b; Hoffman 1958). Young born in the first or second litter of each year are capable of reproducing--females may breed for the first time at an age of 25 days, males may breed at an age of 35-45 days (Hamilton 1941b). Young females may produce two litters in their first summer (Iverson and Turner 1976).

3.4.2 Litter Size

Unlike *C. gapperi*, *M. pennsylvanicus* does not show a significant relationship between litter size and latitude (Innes 1978). Litter sizes of various populations of *M. pennsylvanicus* are summarized in Table 2. Litter size in microtines, however, does appear to be related to body weight, age of females, season and food supplies. Larger females (hence older females) have been shown to produce large litters (Beer *et al.* 1957; Keller and Krebs 1970; Iverson and Turner 1976; Anderson and Boonstra 1979 [for *Microtus townsendi*]). Litter sizes also tend to be larger in the spring and decrease in size throughout the summer, with winter litters (if they occur) being the smallest (Kott and Robinson 1963; Keller and Krebs 1970; Iverson and Turner 1976; Anderson and Boonstra 1979). This may be a real seasonal effect or may simply reflect the recruitment of young females into the breeding population as the summer progresses. (Because young females produce smaller litters, their inclusion in mean litter sizes for late summer would tend to lower the mean for that period.) Cole and Batzli (1978) found that the litter sizes of a *M. ochrogaster* population provided with supplemental food tended to be larger than litter sizes in

Table 2. Litter sizes of *M. pennsylvanicus* (based on Innes [1978]; Tables 1 and 2).

Species	Source	Duration of study in years	No. of months of the year sampled[1]	Latitude °	Latitude '	Elevation, m	Mean Litter size	Range	n	Embryos[2] or live births[3]
M. pennsylvanicus	Beer and MacLeod 1961	3	12	45	40	290	5.70	1-11	>100	E
	Christian and Davis 1966	4	7	40	01	213	4.25	-	51	E
	Connor 1960	2	6	42	30	168	5.31	2-10	13	E
	Corthum 1967	1	11	39	28	183	4.46	1-9	153	E
	Corthum 1967	1	-	39	28	183	4.18	-	51	L
	Coventry 1937	1	-	47	02	305	4.35	3-7	23	E
	Coventry 1937	1	7	43	45	152	5.83	3-9	18	E
	Criddle 1956	23	10	49	43	351	5.03	1-9	246	E
	Goin 1943	2	2	41	34	373	5.73	1-8	19	E
	Hamilton 1937a	1?	-	42	29	229	6.30	-	24	L
	Hamilton 1937b	4	12	42	29	229	5.07	1-11	>100	E
	Harris 1953	3	4	38	23	15	3.65	-	19	E
	Iverson and Turner 1976	6	10	50	07	274	3.82	1-11	312	E
	Keller and Krebs 1970	3	12	39	10	265	4.54	-	152	E
	Kott and Robinson 1963	5	5	43	45	152	4.90	1-8	124	L
	Kott and Robinson 1963	5	4	43	45	152	5.60	1-8	37	E
	Smith and Foster 1957	5	4	58	45	15	6.90	4-12	17	E
	Townsend 1935 (cited in Innes [1978])	3	3	43	15	168	5.07	2-9	41	E
	Wrigley 1969	-	5	(Quebec)		-	5.80	4-9	11	E

[1] The number of months of the year in which pregnant females were sampled.

[2] E = litter size estimate based on counts of embryos.

[3] L = litter size estimate based on counts of live young.

the control population. Hoffman (1958) reported that litter sizes of *Microtus californicus* and *M. montanus* were inversely related to population density and suggested this was a means of damping population fluctuations. Krebs and Myers (1974), however, reviewed a number of studies of litter size in microtine rodents and found no conclusive evidence to substantiate Hoffman's (1958) claim.

3.4.3 Sex Ratio

Males are typically more abundant than females in populations of *M. pennsylvanicus* (Blair 1940; Beer *et al.* 1958; Getz 1960; Myers and Krebs 1971a, b; Krebs and Myers 1974) but in almost all cases differences from equality are not significant. Some studies have found seasonal trends in changes of sex ratios. Getz (1960) found that sex ratios were usually near 1:1 but the proportion of males (in marsh habitat) increased in March of each year. Iverson and Turner (1976) reported a predominance of females from July to September (0.40-0.49 males) whereas males predominated from October to June (0.51-0.59 males). Tendencies for sex ratios to favour males are usually attributed to higher ranges of movement of males (Blair 1940; Beer *et al.* 1958; Getz 1960; Myers and Krebs 1971b). Myers and Krebs (1971b) also showed that over a long period of time resident populations tended to show a slight but not significant deficiency of males whereas dispersing populations showed a slight but not significant excess of males. They also considered the effects of secondary sex ratio, differential survival, differential trappability and differential growth on sex ratios of *M. pennsylvanicus* populations in Indiana. Male voles survived less well than females but because of higher growth rates and greater ranges of movement were more likely to be captured as adults (Myers and Krebs 1971b).

3.4.4 Densities and Population Fluctuations

Populations of *M. pennsylvanicus* undergo wide fluctuations in number and periodic outbreaks or plagues of this and related species have been known for thousands of years (Elton 1942; Krebs and Myers 1974). Based on a review of long-term population studies of microtine rodents, Krebs and Myers (1974) concluded that most microtines undergo cyclic fluctuations in population size and that these cycles occur regularly over a period of three to four years. Population cycles occurred once every three years in a meadow vole population studied by Bole (1939, cited in Tamarin 1977). Krebs *et al.* (1969) found that *M. pennsylvanicus* populations in Indiana underwent two-year population cycles but attributed this short cyclic behaviour to influences of nearby agricultural areas. Tamarin (1977) reported three to four year density cycles in *M. pennsylvanicus* populations in Massachusetts.

Densities of meadow vole populations during population lows and highs show considerable variability. Bole (1939, cited in Tamarin 1977) reported peak densities of 583 voles/ha. Maximum densities of 26-74 voles/ha were reported by Blair (1948). Getz (1960) reported densities of 6-18 voles/ha in old field habitat and 18-63 voles/ha in marsh habitat in Michigan during a 2-year study. Another study of meadow vole populations in Michigan reported an increase from a low of 6 voles/ha to a high of 140 voles/ha (Golley 1961). Over a three year period in Indiana, populations of *M. pennsylvanicus* on three control areas showed peak population densities varying from 53-163 voles/ha and declined to lows of 3-19 voles/ha (Krebs *et al.* 1969; Myers and Krebs 1971a). Notably, meadow vole populations in 0.8 ha fenced grids (Krebs *et al.* 1969) where dispersal was prevented reached densities of 388 voles/ha. Tamarin (1977) reported peak densities of 160-181 voles/ha and low densities of 2-23 voles/ha in two *M. pennsylvanicus* populations in Massachusetts.

Detailed studies of cyclic fluctuations of *M. pennsylvanicus* populations have indicated that a characteristic set of changes in reproduction and mortality are associated with the cycle (Krebs 1970; Schaffer and Tamarin 1973; Krebs and Myers 1974; Tamarin 1977). Krebs and Myers (1974) summarized these changes as follows:

1. Reproductive rates are highest in the increase phase resulting from a longer breeding season including winter breeding and a lower age at sexual maturity. In the peak and decline phases, reproductive rates are reduced. Litter size, pregnancy rates and sex ratios do not appear to change systematically with the cycle.
2. Mortality rates in all sexes and age groups are lowest in the increase phase, remain low during the peak but sharply increase in the decline phase. Juvenile mortality is very high during the decline.
3. Prenatal mortality varies over the cycle but is not a major causative factor of the decline.
4. Dispersal is most frequent from increasing populations but is uncommon from declining populations.
5. Adult animals in peak populations are typically larger.
6. Changes in allelic frequency at marker loci occur in association with density fluctuations.
7. Aggressive behaviour of males and females increases with increased density.

Krebs (1970) proposed that population changes in control populations were influenced primarily by four variables--reproductive rates, juvenile survival (number of young recruiting to the trappable population per lactating female), male survival, and female survival

(survival included both mortality and emigration). Using multiple regression analyses, Krebs (1970) found that reproductive rates, early juvenile survival and female survival were significantly correlated with population growth. Voles in increasing populations tended to survive well and reproduce rapidly whereas those in peak populations tended to show poor reproductive success and low juvenile survival (Keller and Krebs 1970). During the decline, female survival, reproductive rates and juvenile survival continued to decrease. Population cycles of *M. pennsylvanicus* thus appear to involve complex interactions between several factors and affect all age groups.

3.5 DAMAGE POTENTIAL

Voles of the genus *Microtus* are considered to be one of the major small rodent pest species in North America and Europe. Bailey (1924) reported severe damage by *M. pennsylvanicus* to agricultural crops and to young trees in years of peak population densities. Banfield (1977) cites an example of a moderate population of meadow voles consuming as much as one ton of hay per year from one hundred acres of alfalfa. Hansson (1971, 1975) and Larsson (1975) reported extensive damage by voles to young trees in afforestation areas in Sweden. Similar types of damage have been noted in tree farms in the eastern United States (Littlefield *et al.* 1946; Jokela and Lorenz 1959; Sartz 1970), in Oregon (Black *et al.* 1969), in Manitoba (Cayford and Haig 1961; Buckner 1970), and in Ontario (Von Althen 1971; Radvanyi 1974, 1976).

The consumption of the cambium layer of the bark and the resulting girdling or barking of trees by *M. pennsylvanicus* have been shown to or are believed to have limited afforestation programs in North America (Jokela and Lorenz 1952; Cayford and Haig 1961; Buckner 1970; Radvanyi 1976, 1978). As discussed earlier, bark consumption by microtines is believed to be indicative of nutritional stress--when food of adequate nutritional and energy content is available, bark consumption is greatly reduced (Hansson 1971).

4. *PEROMYSCUS MANICULATUS*

4.1 DISTRIBUTION

Peromyscus maniculatus, the deer mouse, is one of the most widely distributed small rodent species in North America (Figure 4)--it ranges from the Atlantic to Pacific coasts and from the Mexican plateau north to the vicinity of the treeline of Canada. Notably, *P. maniculatus* is absent in Newfoundland. *P. maniculatus* is a highly plastic species (Baker 1968; Blair 1968) and occupies many ecological niches throughout its range. Banfield (1977) describes 32 subspecies in Canada, many of which differ in size, length of appendages and colour. Baker (1968) classified the North American species according to two morphological types: short eared, short-tailed and short-footed groups common to open habitats; and long-eared, long-tailed and long-footed groups occupying woodlands and brushlands. Deer mice are nocturnal and, like most North American cricetid species, remain active all winter. Unlike voles, however, they are often active above the snow and do not build extensive systems of subnivean tunnels. Banfield (1977) considered the deer mouse to be an important prey species of owls, weasels and foxes as well as an important predator of insect species deterimental to regenerating and mature forests.

4.2 FOOD HABITS

4.2.1 Fall and Winter Diets

During the fall and winter, seeds and fruit of trees and shrubs are the most important food items of populations in forested areas (Jameson 1952; Williams 1959; Baker 1968; Gashwiler 1969; Drickhamer 1970; Dyke 1971; Everett *et al.* 1978) while seeds of grasses, herbs and in some cases commercial grain species are the most important food items of populations in more open, unforested areas (Hamilton 1941a; Brown 1964; Frischknecht 1965; Whitaker 1966).

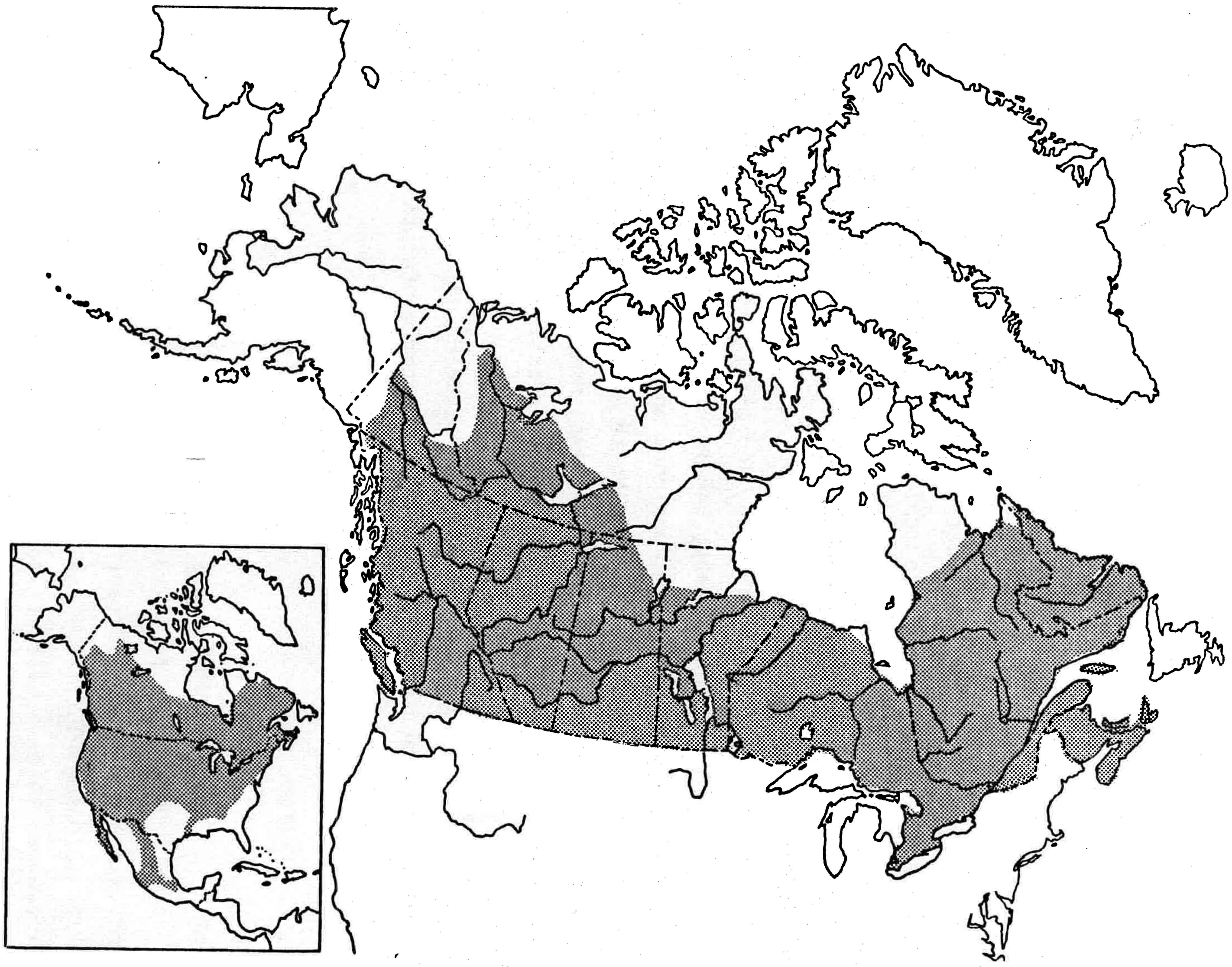

Figure 4. The distribution of *P. maniculatus* (deer mouse) in Canada and in North America (inset). (Modified from Banfield [1977], Map 70.)

In forested areas, seed of coniferous species such as white spruce (Radvanyi 1970a) and Douglas Fir (Gashwiler 1969; Sullivan 1978a, b) have been found to be common foods in the late fall to early spring period--Williams (1959) reported that 38%-79% of the diet of deer mice in Wyoming and Colorado consisted of the integument of coniferous seed. In the Northwest Territories, Dyke (1971) found that fruits of Canadian buffalo-berry, wild strawberry, wild red raspberry and bastard toad flax comprised most of the late fall diet. Arthropods and overwintering fruits of bog cranberry, common bearberry and wild rose were also eaten to a lesser degree. Jameson (1952) found that deer mice would also browse on needles of various conifers during periods of deep snow (which results in poor food availability).

4.2.2 Spring and Summer Diets

In spring, newly sprouting seeds, leaves and overwintered fruits became more common in the diet. By late spring, however, insects became increasingly more important in the diet (Jameson 1952; Williams 1959; Brown 1964; Gashwiler 1969; Dyke 1971). In the four years of his study, Dyke (1971) found that arthropods made up at least 90% of the diet in late May to July of each year. Williams (1959) and Brown (1964) found insects composed 8-28% and 34% of the summer diet by volume, respectively. Whitaker (1966) reported that 15.4% of the diet of *P. maniculatus* in New York was composed of lepidopterous larvae. Berries, fruits and seeds of grasses, shrubs and trees are used as they become available and gradually comprise more of the diet in the late summer and early fall (Hamilton 1941a; Jameson 1952; Brown 1964; Frischknecht 1964; Whitaker 1966; Gashwiler 1969; Dyke 1971). Leaves may also be consumed in the fall (Jameson 1952). Fungi when abundant may form a large part of the diet--Williams and Finney (1964) found that 8-92% of the diet of *P. maniculatus* in Wyoming and Colorado was made up of the fungi *Endogone*. Limited use of fungi by *P. maniculatus* has been reported by Jameson (1952), Dowding (1955), Bakerspigel (1958), Whitaker (1962) and Dyke (1971).

4.2.3 General Food Habits

The food habits of *P. maniculatus* can best be described as opportunistic and omnivorous (Jameson 1952, 1955). Generally seeds and arthropods are the most important items in the diet. Long-term studies of the feeding habits of this species by Jameson (1952), Williams (1959) and Dyke (1971) have clearly indicated that there are regular seasonal shifts in the types of foods eaten and that variations in the quality and quantity of food in different habitats greatly affect the composition of the diet. For example, Dyke (1971) found that *P. maniculatus* populations depended on over-wintering fruits during the winter but, in years of fruit crop failures, readily utilized insects. Local food shortages were overcome by more extensive foraging excursions.

4.3 HABITAT UTILIZATION

P. maniculatus is a widely distributed species and shows few restrictions in habitat use (Williams 1955; Rickard 1960; Baker 1968). Based on an extensive survey of small mammals in 18 habitat types in the southwestern Yukon, Krebs and Wingate (1976) calculated standardized niche breadth estimates for eight species of cricetid rodents and found that *P. maniculatus* had the largest niche breadth. The species is chiefly an inhabitant of woodlands and brushlands but it does occur in open areas such as grasslands or early successional areas. In the latter habitats it is usually second in abundance to *Microtus* sp. (Baker 1968).

Relatively high densities of *P. maniculatus* in forested areas have been reported by Hoffman (1960), Iverson *et al.* (1967), Sheppe (1967), Baker (1968), Wrigley (1969), Dyke (1971), Grant (1971b), Richens (1974), Lovejoy (1975), and Krebs and Wingate (1976). In Washington State and Idaho, Hoffman (1960) reported the highest densities of *P. maniculatus* in cedar-dominated stands with various understories and in Ponderosa pine forests with *Agropyron*-dominated ground cover. In Quebec, Wrigley (1969) captured most deer mice in mature, damp, mixed deciduous-coniferous forests although moderate densities were noted in second growth hardwoods and coniferous forests. Richens (1974) similarly noted a preference for mixed-woods by deer mice in Maine. Hardwoods were also preferred whereas softwood forests and open areas were not. Krebs and Wingate (1976) found that *P. maniculatus* was most common in closed spruce forests with buffalo-berry understory followed by beach ridge areas, closed spruce forests, aspen woods, closed spruce-aspen forests and balsam poplar forests with buffalo-berry understory. Moderate to low numbers of *P. maniculatus* were also captured in grass-fireweed meadows, spruce-birch forests, *Dryas drummondi* flats, closed spruce forests with moss or willow understory, and willow scrub.

In much of the north-central United States, *P. maniculatus* is also a common resident of prairie habitats (Hays 1958; LoBue and Darnell 1959; Wecker 1963; Brown 1964; Iverson *et al.* 1967; Beck and Vogl 1972). Wecker (1963) studied the habitat preferences of this ecotype by introducing animals into field exclosures that contained approximately equal proportions of grassland and forest habitat. Animals that had been raised in a laboratory colony for several generations and animals from natural field situations both showed a preference for grassland habitat. Early experience thus did not appear to affect habitat preferences. Wecker (1963) suggested that habitat preferences of some *P. maniculatus* ecotypes are hereditary--early experience can reinforce these preferences but is not a necessary prerequisite.

A number of studies have suggested that disturbed areas such as post-burn or post-logging successional areas are more readily utilized by *P. maniculatus* than forest sites (Williams 1955; Tevis 1956a, b; Gashwiler 1959, 1970; Ahlgren 1966; Lawrence 1966; Hooven 1969, 1973; Sims and Buckner 1973; Krefting and Ahlgren 1974; Hooven and Black 1976; Martell and Radvanyi 1976). Recently, however, several detailed studies of small mammal populations in disturbed sites and natural forest habitats have indicated there are very few differences in the numbers of mice in these areas (Petticrew and Sadlier 1974; Lovejoy 1975; Sullivan 1978a). Sullivan (1978a) points out that most of the authors that indicated that densities of deer mouse populations on disturbed sites are higher than in adjacent forested areas have based their conclusions on relatively short trapping programs in the fall. Because recruitment to disturbed areas has been found to be highest in the fall (Petticrew and Sadlier 1974; Sullivan 1978a), short fall trapping programs provide biased estimates of population densities in these areas. Petticrew and Sadlier (1974) and Sullivan (1978a) studied several populations of *P. maniculatus* in disturbed and forested sites for 3-4 year periods and showed that, although recruitment to disturbed areas is high, overwinter mortality and rates of emigration from these disturbed areas are also much higher than forested areas. Thus by spring, population densities on forested and disturbed areas are actually quite similar--however, the turnover of animals on disturbed areas is more rapid. On the basis of this rapid turnover of animals, Sullivan (1978a) suggests that disturbed sites are actually less preferable to forested areas--food supplies and cover would be limited and animals would be more vulnerable to predation.

It has been suggested that food availability influences habitat preferences and use of *P. maniculatus*. Fairbairn (1978) suggested that seasonal changes in habitat suitability may be associated with a changing pattern of food availability. She found that major seed and fruit producing plants tended to be concentrated in low, moist areas during the summer in coastal forests of southwestern British Columbia. Thus preferred foods and cover were localized in distinct areas. However, these areas became saturated with water and flooded quickly during the winter rainy season. Thus the best food supplies and nest sites would be in better drained areas of the forest during the late fall and winter. Dyke (1971) similarly found that food availability and cover were important factors in the local distribution of *P. maniculatus* in the Northwest Territories.

Interspecific competition (as previously discussed for *C. gapperi* and *M. pennsylvanicus)* has also been shown to be an important determinant of habitat use by *P. maniculatus*. Grant (1971b) introduced *P. maniculatus* and *M. pennsylvanicus* to exclosures containing grassland and woodland habitat. By itself, *P. maniculatus* was initially trapped only in the woodland area but, as recruitment occurred, animals began to inhabit the grassland areas. However, in the presence of *M. pennsylvanicus*, *P. maniculatus* rarely entered the grassland area. Based on these and several successive introductions, Grant (1971b) concluded that *P. maniculatus* normally chose woodland habitats but, when deer mouse densities reached 'saturation' levels, intraspecific competition forced animals out into the grassland. However, in the presence of high density populations of *M. pennsylvanicus*, *P. maniculatus* were totally excluded from grassland habitats. Thus the presence of *P. maniculatus* populations in grassland areas reflect density-dependent effects of intraspecific and interspecific interactions. Studies of sympatric *P. maniculatus* and *Microtus oregoni* populations in British Columbia also suggested that interspecific interactions affect the local abundance of *P. maniculatus* (Petticrew and Sadlier 1974; Taitt 1978).

4.4 DEMOGRAPHY

4.4.1 Reproduction

Female *P. maniculatus* are seasonally polyestrous. The vulva is normally sealed during the winter anestrous period but becomes perforate with the onset of breeding in spring (Banfield 1977). Like many small rodent species, *P. maniculatus* shows highly variable breeding seasons. Male and female *P. maniculatus* typically become reproductively active in March to

April of each year (Jameson 1953; Beer *et al.* 1957; Dunmire 1960; Sheppe 1963; Vaughan 1969; Wrigley 1969; Sadlier *et al.* 1973; Sadlier 1974; Fairbairn 1977a, b; Sullivan 1977). Jameson (1953) reported slightly earlier onsets of breeding in some years in California whereas Fuller (1969) first reported breeding activity in *P. maniculatus* in the Northwest Territories in early May. Vaughan (1969) found that *P. maniculatus* in alpine areas of Colorado did not become reproductively active until just after snowmelt. Sullivan (1977) noted large differences in the onset of breeding in populations of *P. maniculatus* on two islands and the mainland in British Columbia and attributed these to differences in food availability and aggressive (territorial) behaviour in each population.

Males generally cease breeding in late July to August and females cease breeding in mid-August to September (Jameson 1953; Beer *et al.* 1957; Dunmire 1960; Sheppe 1963; Vaughan 1969; Wrigley 1969; Sadlier *et al.* 1973; Sadlier 1974; Fairbairn 1977a, b; Sullivan 1977). Again some variation was noted within localities and between widely separated geographic locations (Jameson 1953; Sheppe 1963; Sadlier 1965, 1974; Canham 1969; Fairbairn 1977a). Limited winter breeding in deer mice has been reported by Brown (1945), Jameson (1953) and Dunmire (1960).

Dunmire (1960) examined altitudinal effects on the reproductive activity of *P. maniculatus* in California. Populations at lower altitudes were characterized by two main breeding seasons in the spring and fall; mice at mid-altitudes bred throughout the spring and summer, and mice in the highest study area bred only in the late summer and early fall.

Gestation in *P. maniculatus* is approximately 23 days (Svihla 1932, cited in Beer *et al.* 1957; Layne 1968). Post-partum mating is common although implantation may be delayed during lactation (Jameson 1953). Promiscuity is common in wild *P. maniculatus*--Birdsall and Nash (1973) found conclusive evidence that 11 of 107 litters tested had more than one male parent. Young females of the first litter of the season may breed and produce one and possibly two litters in their first summer (Jameson 1953; Fuller 1969; Vaughan 1969; Wrigley 1969; Iverson and Turner 1976).

Annual variations in the length of the breeding period appear to be associated with food availability and weather. Sadlier *et al.* (1973) suggested that female *P. maniculatus* were unable to obtain sufficient food during the winter to maintain themselves and breed as well and as a result remained reproductively inactive during times of energy stress. The onset of breeding in spring was found to be related to environmental cues--both day length and increasing temperatures were important (Sadlier *et al.* 1973). Food abundance, however, strongly affected the influence of temperature and day length on the onset of breeding. Thus if temperatures were above normal but food was still limited, reproduction was delayed. Experimental increases in food supplies of *Peromyscus* spp. have clearly shown that reproductive activity is related to food supplies. Provision of supplementary food supplies in the winter or early spring resulted in sharp increases in reproductive activity and early maturation of young animals (Fordham 1971; Hansen and Batzli 1978; Taitt 1978). Taitt (1978) found that the addition of supplemental food enabled mice to breed earlier and for longer periods despite poor weather. This suggests that energy limitation is a major influence in reproductive activity and that female *P. maniculatus* restrict reproduction to the most favourable seasons when food is more abundant.

Fairbairn (1977a) found that some female *P. maniculatus* consistently attempted to breed before conditions were suitable. Over the two and half years of her study, some females always attempted to breed in late winter to early spring. Of these early breeding females, only 25% survived to the first six weeks of the breeding period whereas 69% of the non-breeding females survived this period. The strategic disadvantage of poor survival (from an evolutionary point of view) was thought to be offset by the occasional high productivity (number of offspring produced per breeding season) of early breeders when their early breeding efforts were successful (Fairbairn 1977b).

4.4.2 Litter Size

Litter sizes of *P. maniculatus* are variable but are usually within the range of four to six young per litter (Table 3). Litter sizes in *P. maniculatus* have been shown to vary with the age of the female, with the season of the year, length of growing season and altitude. Jameson (1953) found that younger female *P. maniculatus* shed fewer ova than overwintered females (a mean of 3.8 vs 5.4, respectively). Rolan and Gier (1967) found that litter size increased from an average of 3.0 in young females to 5.3 in older females. However, litter sizes of very old females were smaller than females in the previous age class. Beer *et al.* (1957) and Iverson and Turner (1976) have noted similar trends. The latter study also reported higher fetal mortality rates in young mothers than in overwintered females.

Jameson (1953) noted that litters at the height of the breeding period (May) tended to be larger than litters born early in the season. Fuller (1969), however, found that in years with late springs and delayed breeding litters tended to be smaller.

Spencer and Steinhoff (1968) reviewed geographic variations in litter sizes of small rodents and found that *P. maniculatus* populations with shorter growing seasons (i.e., high latitudes or altitudes) tended to have large litter sizes. Dunmire (1960) similarly found a positive correlation between altitude and litter size in *P. maniculatus* in eastern California.

Table 3. Litter sizes of *P. maniculatus*.

Species	Source	Location of Study Area	Mean Litter Size	Range	N	Method[1]
P. maniculatus	Beer *et al.* 1957	Minn.[2]	5.86	3-12	251	C
			5.45	3- 8	251	PS
			5.32	2- 9	251	E
	Beer *et al.* 1957	Minn.[3]	5.77	1-10	217	C
			5.25	2- 9	217	PS
			5.08	2- 9	217	E
	Birdsall and Nash 1973	Alberta	4.99	3- 7	100	L
	Brown 1945	Nebraska	3.64	2- 5	17	E
	Coventry 1937	Ontario	5.38	-	-	E
	Dunmire 1960	California[4]	4.63	-	8	E
			4.01	-	19	E
			3.64	-	11	E
			4.00	-	2	E
	Fuller 1969	Northwest Territories[5]	5.57-5.58	-	233	PS
			5.33-6.10	-	109	E
	Howard 1949	Michigan	4.28	-	25	L
	Iverson and Turner 1976	Manitoba[6]	5.8	3- 9	22	PS
			5.8	1-10	26	E
		Manitoba[7]	6.6	1-10	33	PS
			4.8	1- 7	7	E
	Jameson 1953	California	4.6	-	96	E
	Price 1967	Michigan	3.8	2- 6	26	L
	Rolan and Gier 1967	Kansas	4.38	-	405	PS
			4.29	1- 7	405	E
	Sadlier 1974	British Columbia	4.52	-	57	PS
			4.52	-	57	E
	Scheffer 1924	Washington	5.10	-	48	E
	Sheppe 1963	British Columbia	5.50	2- 9	53	L
	Vaughan 1969	Colorado	5.9	2-10	34	PS
			5.6	2- 9	111	E
	Wrigley 1969	Quebec	5.3	4- 7	18	PS
			5.6	3- 7	17	E

---

[1] C=counts of corpora lutea; PS=counts of placental scars; E=counts of embryos; L=counts of young at birth.

[2] means for *P. m. gracilis*.

[3] means for *P. m. bairdii*.

[4] means for animals from study areas at 3780 m, 2990 m, 2165 m and 1370 m, respectively.

[5] range of mean values for the three years of study shown.

[6] means for adult animals only.

[7] means for young-of-the-year females only.

4.4.3 Sex Ratio

Males tend to be slightly more abundant than females in most populations of *P. maniculatus* (Terman and Sassaman 1967; Terman 1968). Verts (1957) found that sex ratios of both juvenile and adult age classes favoured males. Sheppe (1963) noted a tendency for young males to outnumber young females but in adult age classes the ratio was close to equality. In older age classes females predominated, suggesting adult females live longer than males. Terman and Sassaman (1967) reviewed sex ratios of *P. maniculatus* populations obtained in the North American Census of Small Mammals (NACSM)--a mean sex ratio of 55.8% males was obtained which was significantly different from equality ($P<0.001$). Fuller (1969) found sex ratios of *P. maniculatus* favoured males but at no time in the 4-year study did ratios vary significantly from equality. Redfield (1976) and Sullivan (1977) found that sex ratios of *P. maniculatus* on the Gulf Islands of British Columbia usually favoured males, but differences were not significant. Although few populations of *P. maniculatus* show sex ratios significantly different from 1:1, Terman and Sassaman (1967) found that the proportion of males (0.54) in litters born in the laboratory significantly exceeded the number of females. Terman (1968) suggested that small differences in secondary sex ratios accentuated by the increased trappability of males (resulting from increased movements and larger home ranges) result in the observed slight predominance of males in the field situations.

It is not clear if changes in sex ratios and population trends are related. Based on an analysis of NACSM data for 130 trapping periods, over a two year period, Terman and Sassaman (1967) found that the proportion of males in a population and population density were negatively correlated. Fuller (1969), however, found the opposite trend in his study populations--as the population density increased so did the proportion of males.

4.4.4 Densities and Population Fluctuations

Although populations of *P. maniculatus* exhibit some features of cyclic fluctuations in density, they do not appear to undergo the regular changes in population density common to microtine rodents (Fuller 1969) but instead undergo an annual cycle in numbers. Typically, the number of mice reach a peak at the end of the breeding season followed by a slow decline throughout the non-breeding period (Petticrew and Sadlier 1974; Fairbairn 1977a). In more temperate areas, stress associated with cold fall periods with little snow cover, long, cold winters, and spring meltoff appears to increase winter mortality (Fuller 1969). With the onset of breeding in spring, the population may decline further depending on the density of the overwintered-breeding population (Sadlier 1965; Fairbairn 1977a). Densities of the spring breeding population are typically very low. The density of mice then increases gradually until the cessation of breeding when recruitment of juveniles to the population increased rapidly (Verts 1957; Petticrew and Sadlier 1974; Fairbairn 1977a, 1978; Sullivan 1978a). Spring breeding densities and fall (non-breeding) densities are thus important in the yearly fluctuations of population density.

Fuller (1969) found that, while late spring densities (3-9 mice/ha) were similar in the four years of his study, fall densities varied from 4 mice/ha in 1964 to 42 mice/ha in 1966. Petticrew and Sadlier (1974) reported mean densities for breeding and non-breeding seasons of between 15.7-34.9 mice/ha and 7.8-33.8 mice/ha, respectively for *P. manciulatus* populations on their three control grids over the three years of their study. Sullivan (1977) reported mean annual densities of 18.7 mice/ha on the mainland, 22.0 mice/ha on Samuel Island and 43.5 mice/ha on Saturna Island in British Columbia. Spring densities of two study populations of *P. maniculatus* near Vancouver, British Columbia varied between 7-24 mice/ha; summer densities varied between 12-24 mice/ha and fall densities varied between 18-41 mice/ha (Fairbairn 1978).

Most long-term population studies of *P. maniculatus* have been conducted in the coastal forests of southwestern British Columbia. Low density breeding populations in the early spring and higher density non-breeding populations appear to be typical of these populations. Sadlier (1965) suggested and Healey (1967) later confirmed that juveniles survive poorly and do not recruit to the population because they are competing with aggressive breeding adults (particularly adult males). Increased recruitment and improved juvenile survival in the fall was directly correlated with a decline in the aggressiveness of adult males (associated with the cessation of breeding activity) and resulted in a rapid increase in the population size. These results have been supported by more recent studies of population regulation in this species (Fairbairn 1978; Taitt 1978).

Fuller (1969) conducted a study of *P. maniculatus* populations in the Northwest Territories from 1964 to 1966. Similar to coastal populations of *P. maniculatus*, spring densities were quite low. Rapid increases in population size occurred in August of each year except 1964 (the population density was consistently low in 1964). This generally coincided with cessation of breeding in males supporting Sadlier's (1965) and Healey's (1967) hypothesis that male aggression (during the breeding period) limited juvenile recruitment. However, most adult (overwintering) animals survived only to late July or August. Thus, if adult aggression does prevent juvenile recruitment, the death of adult animals would also allow increased juvenile recruitment. Fall densities were high in all years, but declined to low numbers by the next spring.

Factors related to the spring decline or reorganization (Fairbairn 1977a) are not as well defined as those related to the fall increase. Low breeding densities in the spring appear to be the result of overwinter mortality and a density-dependent decline in the early spring--large declines are associated with high overwintering densities whereas little or no decline in spring numbers is associated with low overwintering densities (Petticrew and Sadlier 1974).

Fordham (1971) provided supplemental food to a population of deer mice in the early spring and found that the number of females almost doubled while the number of males remained the same. This suggested that the numbers of males and females in the spring breeding population were determined differently. Petticrew and Sadlier (1974) suggested that the number of breeding adult males was determined by agonisitic interactions. Aggressive interactions between adult males were common during this period and likely accounted for the reduced adult male survival. However, females that survived or immigrated were tolerated and the number of breeding females slowly increased. Recently Fairbairn (1977a) showed that males disappearing from the spring breeding populations were most often light-weight, subordinate animals suggesting that socially-motivated (i.e., aggressive behaviour) dispersal was the cause of the spring decline of adult males. The disappearance of females, however, appeared to be due to mortality of early-breeding females rather than to socially-motivated dispersal.

Fairbairn (1978) suggested that resource availability may affect social pressure (i.e., spacing behaviour) and that this in turn would determine spring breeding densities of adult males. Based on a series of experiments in which supplemental food supplies were made available or withdrawn at various seasons of the years, Taitt (1978) suggested that adult males defend a territory in the spring which will provide sufficient food for them to gain weight and reproduce. She found that the size of male home ranges during the spring reorganization decreased when abundant supplemental food was provided.

Food supplies during the spring reorganization thus appear to play a critical role in determining the density of breeding adult males. As discussed earlier with respect to reproduction, food supplies also partly determine the onset of breeding in a population (in association with day length and temperature). Survival of females also appears to be affected by food supplies--female survival of early breeding females was better in years with early springs (Fairbairn 1977b) and supposedly better food resources.

4.5 DAMAGE POTENTIAL

P. maniculatus is an important small rodent species because of its importance as a major prey of some furbearers and raptors and its value as a predator on some species of forest-damaging insects. It is also important as a potential pest species because it is one of the major consumers of coniferous seed. *P. maniculatus* is considered to be one of the major causes of failures to re-establish forest cover by artifical seeding (Howard 1950; Jameson 1952; Nord 1965; Black 1969; Gashwiler 1969; Radwan 1970; Radvanyi 1973; Everett *et al.* 1978; Sullivan 1978a, b, c). *P. maniculatus* is not known to destroy or damage trees or shrubs by consumption of bark (i.e., girdling) or by browsing.

Because reforestation of cleared areas by direct seeding techniques offers an economical alternative to more costly, seedling planting programs, numerous methods have been tried to protect seed from birds and rodents. To date, mechanical devices, chemical repellent seed coatings and poison baits have been most commonly used. Mechanical devices such as screens or fencing are obviously not suitable for large-scale reforestation programs. Various repellents have been shown to be of limited value in reducing seed consumption and have often had the additional disadvantage of lowering the viability of the seed (Casebeer 1954; Kverno 1954; Spencer 1954; Radwan 1969, 1970; Radvanyi 1970b; Lindsey *et al.* 1974; Passof *et al.* 1974). Broadcast spraying of some poisons or the use of poisoned baits has proved effective in eliminating resident animals, but long-term control of rodent populations was not possible because of the rapid reinvasion of these areas by new animals (Gashwiler 1969; Radwan 1969; Morris 1970, 1972; Radvanyi 1974). Poisons also are hazardous to non-target species and their eventual fate in the environment is as yet unknown--thus care must be taken in their application. Evans (1974) and Sullivan (1978b) have discussed recent trends away from chemical control towards non-chemical methods of control. Methods of biological control appear to offer some means of long-term control of small mammal pest problems in reforestation programs (Green 1978b; Sullivan 1978b).

Evans (1974) suggested that the use of 'sacrifice' foods (the broadcasting of preferred seeds or food in conjunction with broadcasting of tree seed) may provide a means of lessening small rodent predation on tree seed. Everett *et al.* (1978) conducted a series of seed preference tests to determine which seeds might be best used as sacrifice foods. Sullivan (1978a, b) tested the use of sacrifice foods under field conditions as a means of controlling small rodent seed predation. He used a mixture of conifer seed (Douglas fir seed) and alternative foods (sunflower seed and oat groats) which was evenly broadcast over the treatment area. Survival of Douglas fir seeds in the presence of these alternative foods was much greater than when Douglas fir was applied without sacrifice foods. Sullivan (1978a, b) suggested that seeding with mixes of conifer seed and alternative food should be carried out in early spring because (a) other seed predators such as birds or chipmunks are absent or inactive in clearcut areas from late October to early April, and (b) *P. maniculatus* populations are also at their lowest densities in the early spring. Initial results suggest that the use of this technique should greatly increase the success of seeding as an afforestation technique (Sullivan 1978a).

5. *TAMIASCIURUS HUDSONICUS*

5.1 DISTRIBUTION

T. hudsonicus is a common inhabitant of the entire coniferous forest region and much of the deciduous forest region of Canada (Figure 5). The species has been the focus of detailed population studies in Alaska (Brink 1964; M. Smith 1968; Krasnowski 1969; Streubel 1968; Modafferi 1972; Nodler 1973; Searing 1975), in Alberta (Wood 1967; Kemp and Keith 1970; Zirul 1970; Rusch and Reeder 1978), in British Columbia (C. Smith 1968, 1970; Millar 1970a, b) and in the eastern United States (Layne 1954; Reige 1976).

5.2 FOOD HABITS

A wide range of food types are used by red squirrels throughout their range but the diet of northern populations is apparently more limited than that of populations at lower latitudes (M. Smith 1968). However, the importance of conifer seed to northern and southern populations of the red squirrel has been documented by intensive studies of their feeding ecology (C. Smith 1968; M. Smith 1968; Nodler 1973; Rusch and Reeder 1978).

The more diverse diet of southern populations probably reflects a more diverse availability of food. A study of *T. hudsonicus* in New Brunswick and Ontario (Klugh 1927) showed that the major food was coniferous seed with white spruce and red spruce being the more preferred species. Buds of various deciduous tree species (sugar maple, soft maple, elm, beech, ironwood, yellow birch, hybrid willow and trembling aspen) and spruces were also commonly consumed in the spring. Bark, primarily of deciduous species, was eaten in small amounts at all times of the year, even when green food was abundant. Fruits and berries made up a small proportion of the summer diet. Mushrooms were often eaten

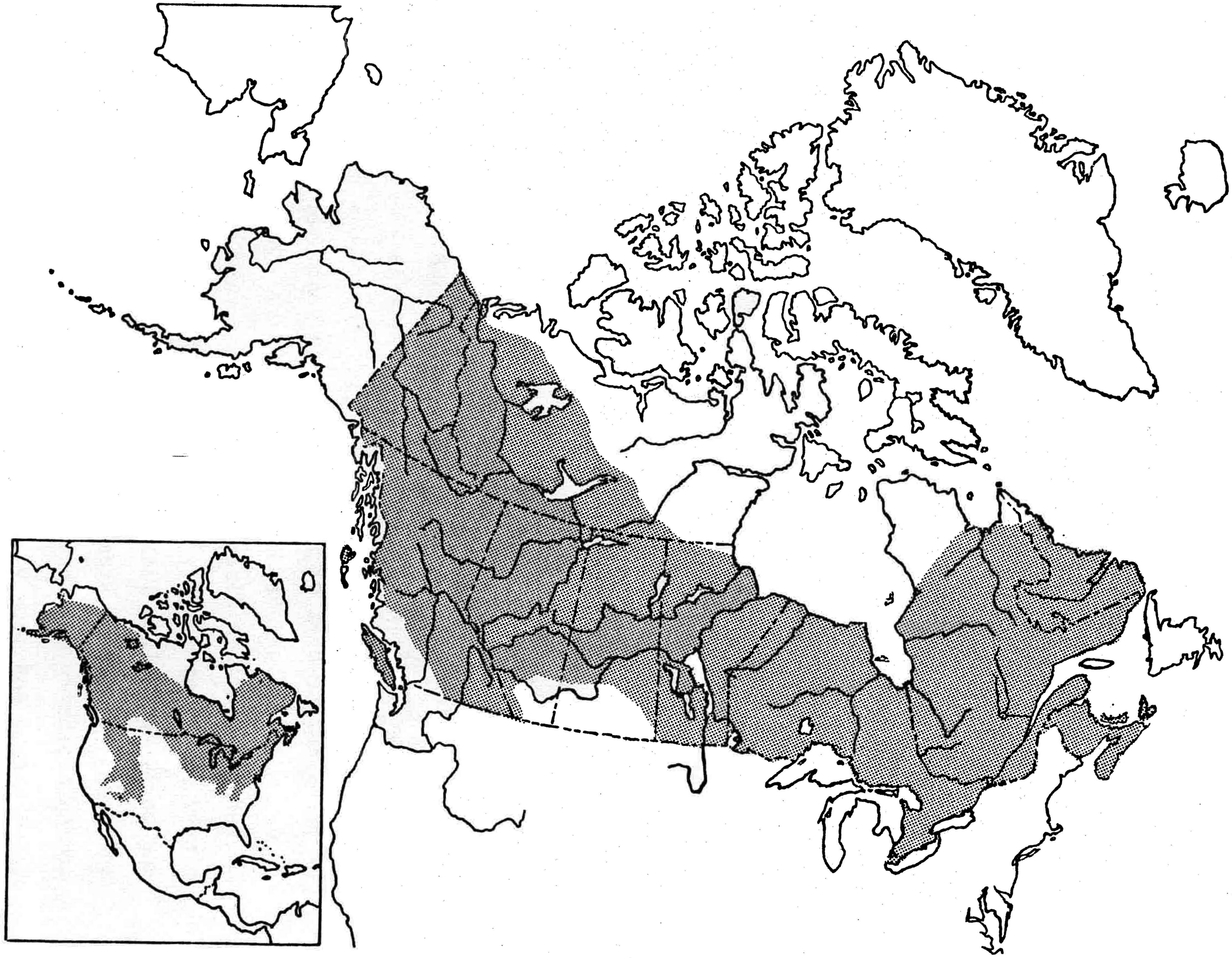

Figure 5. The distribution of *T. hudsonicus* (American red squirrel) in Canada and in North America (inset). (Modified from Banfield [1977], Map 60.)

in the late summer and early fall and were often stored for winter consumption. More recent studies of the diet of eastern North American populations of *T. hudsonicus* (Layne 1954; Reige 1976) have described similar seasonal trends although the plant species consumed may differ slightly depending on the habitat and availability. Conifer seed and tree buds were again heavily utilized at all times of the year and the bark of some deciduous species was consumed in small amounts throughout the year.

Red squirrels in Colorado (Hatt 1943) consumed a variety of foods but seeds of lodgepole and limber pine, Engelmann and blue spruce, Douglas and alpine fir and staminate flowers of the lodgepole pine comprised virtually the entire food supply during the early summer. Consumption of the bark of lodgepole pines was also noted.

C. Smith (1968, 1970) studied the energy budgets of red squirrels in southern British Columbia. These *T. hudsonicus* commonly consumed seeds of conifers (seeds of Pacific silver fir, Douglas fir, Engelmann spruce and hemlock were preferred in that order), seeds of some deciduous trees and shrubs (vine and dwarf maples, cottonwood, wild rose, bearberry), pollen of some conifer species, various fruits and berries (western red raspberry, blueberry), some herbs, mushrooms (*Chroogmphus rutilus, Suillus* spp.), false truffles (*Rhizopogon* spp.), rusts (*Peridermium harknessi*) and some animal matter. Millar (1970a) reported a similar variety of items in the diet of *T. hudsonicus* on Vancouver Island.

Rusch and Reeder (1978) considered the dietary composition of red squirrels in Alberta during a long-term population study. Continuous daily observations of single squirrels in March and early April in a jack pine study area indicated that pine buds and cones were their staple foods while fungi, rosehips and common bearberry were only of minor importance. White spruce, black spruce and jack pine seed were heavily utilized by squirrels in coniferous stands while hazelnuts were a major food of squirrels in deciduous stands with dense hazelnut undergrowth. Preference studies suggested that black spruce seeds were more frequently consumed than white spruce seeds.

M. Smith (1968) suggested that the variety in the diet of the red squirrel in interior Alaska was limited largely by the homogeneous character of the white and black spruce forests it inhabits. Spruce seed constitutes the major portion of the diet throughout most of the year (Dice 1921; Murie 1927; Brink 1964; M. Smith 1968; Streubel 1968; Nodler 1973) but other items become more important in years of poor cone production (M. Smith 1968). For example, M. Smith (1968) found that when the availability of spruce seed decreased, fungi and spruce buds made up larger portions (by volume) of the diet. Green plant material, insects and fleshy fruits also became important (when available). Studies of the spruce seed preferences of Alaskan squirrels (Brink and Dean 1966; M. Smith 1968) have shown that white spruce seed is highly preferred over black spruce seed. Although white spruce seed contains 9% more calories per gram than black spruce seed, Brink (1964) felt this difference was too small to account for this preference and instead attributed it to a comparative lack of essential nutrients in black spruce seed. Brink and Dean (1966) suggested that competition for territories within white spruce habitat was intense with less successful squirrels being forced into marginal black spruce habitat. Nodler (1973) found that black spruce seed was most heavily utilized in years when white spruce cone production failed.

Food storing by red squirrels is more common in the northern portion of its range than in the southern latitudes (Dice 1921; Murie 1927; Layne 1954; C. Smith 1968; M. Smith 1968). In northern populations, cones and buds are cut and stored in caches for use during the winter. Because cones are utilized on or near the cache, the result is an accumulation of bracts and stalks of shredded cones known as middens. Middens are the center of most squirrel activity (M. Smith 1968; Streubel 1968; Searing 1975) and may be used continuously for long periods of time by a series of different squirrels, providing both an area for shelter and cone storage during the winter (Clarke 1939; Soper 1942; Pruitt and Lucier 1958; Wagg 1963). Middens are defended by the occupant and no more than one squirrel will occupy a midden at a time (Gordon 1936; C. Smith 1968). Fleshy foods such as mushrooms are often stored in the branches of trees surrounding the midden (C. Smith 1968; M. Smith 1968; Streubel 1968).

Food has been cited as one of the ultimate regulating factors of red squirrel populations both through its effects on reproduction (Wood 1967; Millar 1970a, b; Searing 1975) and on population densities through changes in the size of territories (Brink and Dean 1966; C. Smith 1968; M. Smith 1968; Rusch and Reeder 1978). Fecundity may fluctuate with the type and amount of food available. Both C. Smith (1968) and Millar (1970a) showed that, when larger amounts of high quality food were available (i.e., lodgepole pine), high reproductive rates resulted but, when preferred foods were scarce and poor quality foods (i.e., Douglas fir) were consumed, reproduction rates decreased. C. Smith (1968) found that territory size was adjusted to the food supply and suggested that territorial behaviour allowed each individual to optimize conditions for harvesting, storing and defending a seasonal food supply so that it was available throughout the year. More recent studies by Streubel (1968), Nodler (1973), Searing (1975) and Rusch and Reeder (1978) have supported these conclusions.

5.3 HABITAT UTILIZATION

The distribution of red squirrels often appears to be closely related to that of coniferous forests and hence the availability of cones (Hatt 1929; Layne 1954; Reige 1976)--this has been related to the role of conifer seed as a staple food item, important to overwinter survival.

In Alaska, squirrels are predominantly found in white and black spruce forests. White spruce forests are the preferred habitat and animals failing to obtain territories in areas of white spruce forest are probably forced to establish themselves in less preferred black spruce habitat (Brink and Dean 1966).

In northern Alberta, red squirrels again prefer white spruce habitat. Wood (1967) found that densities of red squirrels in white spruce habitat were always high whereas populations in jack pine forests only increased in years in which large cone crops developed. Based on food habits, Kemp and Keith (1970) ranked white spruce as prime habitat, followed by black spruce and aspen-dominated deciduous stands. A recent study of squirrel populations near Rochester, Alberta (Rusch and Reeder 1978) showed that squirrels were most abundant in spruce *(Picea mariana* and *P. alba)* stands, less abundant in jack pine forests and least abundant in aspen woods.

Eastern populations of red squirrel appear to heavily utilize a number of habitat types. Hatt (1929) found that the red squirrel was most often associated with white pine in New York while Layne (1954) rated beech-maple-hemlock and mixed hardwoods-scattered conifer forests as good squirrel habitat in this area. Reige (1976) found squirrel densities in Wisconsin were highest in balsam fir-white cedar forests or white spruce-black spruce forests followed by white pine-red pine forests and maple-oak woods.

Despite wide variation in habitat use by red squirrels, white spruce or mixed white spruce-black spruce forests appear to consistently support the highest squirrel densities (Table 4). Because white spruce and black spruce forests are common throughout the southern and northwestern portions of the AOSERP study (based on a systematic survey of furbearer habitat, Searing [1979]

Table 4. Spring densities of adult red squirrels in various habitats and areas[1]. (Adult squirrels were considered as animals greater than 4 months of age.)

Habitat	Province/State	Reference	ha/adult squirrel
Spruce (*Picea* sp.)	New Brunswick	Klugh (1927)	0.4
	New York	Hatt (1929)	0.4
	Massachusetts	Hatt (1929)	0.4
	Alaska	Brink (1964)	0.5
	Alaska	M. Smith (1968)	2.1 - 5.3[2]
	Alaska	Streubel (1968)	0.9[2]
	Saskatchewan	Davis (1969, cited *in* Rusch and Reeder 1978)	0.4
	Alberta	Rusch and Reeder (1978)	0.4
Mixed conifers	Massachusetts	Hatt (1929)	0.6
	Montana	Halvorson (1965, cited *in* Rusch and Reeder 1978)	0.5 - 1.2
	British Columbia	C. Smith (1968)	0.4
	Wisconsin	Reige (1976)	1.1 - 1.5[2]
Hardwoods and conifers	Ontario	Klugh (1927)	0.04[2]
	Massachusetts	Hatt (1929)	0.8
	Ohio	Baumgartner (1938)	1.2
	New York	Fitzwater (1941, cited *in* Rusch and Reeder 1978)	0.7
	New York	Layne (1954)	0.2, 0.4, 0.6
	Alberta	Wood (1967)	1.0
Pine (*Pinus* sp.)	Manitoba	Seton (1909, cited *in* Rusch and Reeder 1978)	1.2
	Ontario	Klugh (1927)	8.1
	Massachusetts	Hatt (1929)	1.2 - 1.8
	British Columbia	C. Smith (1968)	0.9
	Wisconsin	Reige (1976)	2.1 - 2.5[2]
	Alberta	Rusch and Reeder (1978)	1.0
Hardwoods	Ontario	Klugh (1927)	8.1
	New York	Williams (1936)	0.8 - 1.6[2]
	Michigan	Linduska (1950, cited *in* Rusch and Reeder 1978)	0.6 - 1.3
	New York	Layne (1954)	1.5
	Alberta	Rusch and Reeder (1978)	4.0 - 8.1

[1] Modified from Rusch and Reeder (1978: Table 13).

[2] Squirrels censused in the fall; probably providing overestimates of adult densities and underestimates of hectares per adult squirrel.

reported that 8.5% and 57.2% of the AOSERP study area were composed of white spruce forests and black spruce-tamarack associations) it would appear that the study area would have a moderate carrying capacity for red squirrels.

5.4 DEMOGRAPHY

5.4.1 Reproduction

Periods of reproductive activity, the onset of breeding and the number of breeding periods each year vary between populations--geographic location, weather and food resources appear responsible for some variation in reproduction.

The breeding season (as defined by the presence of males with scrotal testes and females in estrous) varied from February to March in Alaska (Krasnowski 1969; Modafferi 1972), from January to early May in Alberta (Wood 1967; Zirul 1970) and January to May in southern British Columbia (C. Smith 1968; Millar 1970b). In more southerly populations two breeding peaks may occur, one in the early spring (February-March) and one in the summer (June-July) (Layne 1954; Reige 1976). In most reproductively active populations, almost all adults are capable of breeding but the proportion of the sub-adult age class that breeds varies considerably between years (within a population) and between populations (Wood 1967; C. Smith 1968; Krasnowski 1969; Millar 1970b; Modafferi 1972; Dolbeer 1973).

The onset of the breeding period has been shown to be affected by the abundance of food resources (Brink and Dean 1966; C. Smith 1968; Krasnowski 1969; Millar 1970b) and environmental factors (i.e., a late spring) (Hatt 1929; Zirul 1970; Modafferi 1972; Dolbeer 1973). Shortages of food and high densities can severely curtail breeding activity (Searing 1975). Searing (1975) observed only two attempted copulations and no young were produced during a year of extreme food shortages.

The gestation period of *T. hudsonicus* is approximately 40 days (Hamilton 1939). Dates of first parturition in a population vary considerably (in response to varying dates for onset of breeding activity). In all northern populations, females produce only one litter per year (Soper 1972; Wood 1967; Krasnowski 1969; Modafferi 1972; Rusch and Reeder 1978) whereas populations in more southerly latitudes often produce two litters per year (Layne 1954; Reige 1976). In British Columbia, Millar (1970b) found females produced two litters a year if the onset of breeding was early enough. In 1966, females first bred in February and some females produced two litters that year. In 1967, however, females did not breed until May and breeding females produced only one litter.

5.4.2 Litter Size

Litter sizes have been estimated for *T. hudsonicus* based on counts of corpora lutea, placental scar counts, embryos and number of young. Hatt (1929) reported that a litter size of six was common in New York. Layne (1954) reported mean litter sizes (based on placental scar counts, embryos and number of young) in the spring of 4.0 and in the summer of 5.3 for *T. hudsonicus* in New York. Two subspecies of red squirrel in southern British Columbia had litter sizes (based on counts of corpora lutea) of 3.6 *(T. hudsonicus streatori)* and 4.1-5.1 *(T. hudsonicus lanuginosus)* (Millar 1970a). Litter sizes of red squirrels in Alberta ranged from 3.1-4.3 young/litter (Kemp and Keith 1970; based on placental scar counts) and from 3.1-4.6 young/litter (Rusch and Reeder 1978; based on embryo and placental scar counts). In Alaska, Krasnowski (1969) found that the mean litter size of *T. hudsonicus* based on counts of corpora lutea, placental scars and embryos were 5.6, 3.9, and 4.2, respectively. Modafferi (1972) reported mean litter sizes of 4.4 and 3.4 for *T. hudsonicus* in the same area of Alaska, based on corpora lutea and combined placental scar-embryo counts, respectively.

The observed variance in litter size may reflect the abundance and quality of food supplies. Following a winter of good lodgepole pine seed availability (the preferred food for red squirrels in that particular area of British Columbia), Millar (1970a) found that females produced large litters (a mean of 5.1 young/litter). The following winter, squirrels depended more on Douglas fir seed and litter sizes were smaller (a mean of 4.1 young/litter) (Millar 1970a)。 Data collected by C. Smith (1968) support this hypothesis although the inter-year differences were small. Millar (1970a) pointed out that a correlation between large litter sizes and late breeding (Layne 1954; C. Smith 1968; Millar 1970a) also supports this hypothesis.

5.4.3 Sex Ratio

Juvenile sex ratios usually approximated a 1:1 ratio (Zirul 1970; Rusch and Reeder) but Krasnowski (1969) reported an immature sex ratio of 0.64 (proportion of males) which was significantly different from 0.50. However, it appears common for adult age classes to significantly favour males (Krasnowski 1969; Searing 1975; Rusch and Reeder 1978). Exceptions include a study by Kemp and Keith (1970) which reported sex ratios closely approximating a ratio of 1 male:1 female and a study by Zirul (1970) which reported an increasing predominance of females in one year and older age classes (the oldest age class was 100% females). Although males were more common in red squirrel populations in the early fall (as a result of high female mortality), Rusch and Reeder (1978) found that equality of sex ratios was restored during the breeding season when males experienced high mortality.

5.4.4 Densities and Population Fluctuations

Variation in the densities of red squirrel populations in northern and southern areas has already been indirectly discussed in relation to habitat utilization (Table 4). The highest densities of *T. hudsonicus* in both northern and southern areas are in most cases in spruce forests. Densities of 0.4 ha/adult squirrel appear to represent high population densities.

Territorial behaviour appears to be the mechanism by which densities are regulated. Studies by C. Smith (1968), Kemp and Keith (1970) and Rusch and Reeder (1978) have shown that territorial behaviour can regulate densities at levels determined by food abundance. In years of poor mast crops, production of young decreases (Kemp and Keith 1970; Rusch and Reeder 1978) and loss of non-territorial or young animals increased because of the enlarged territory size of resident animals resulting in a decrease in population density (Kemp and Keith 1970).

Cyclic population fluctuations similar to those observed in microtine rodents do not appear to occur in *T. hudsonicus* populations. Kemp and Keith (1970) suggested that cycles did occur and analysed fur returns for Alberta, Saskatchewan and Manitoba for the period 1946-62 to determine the synchrony and periodicity of red squirrel fluctuations. Peak populations were defined as any year in which fur returns were higher than in the years immediately preceding and following. Using this definition, the mean interval between population peaks was 2.6, 2.8 and 2.9 years, respectively, in Alberta, Saskatchewan and Manitoba. This cyclic behaviour was related to regular fluctuations in mast crops which in turn were suspected to be related to weather conditions. However, long-term population studies of red squirrel populations in Alaska (Smith 1968; Streubel 1968; Krasnowski 1969; Nodler 1973; Searing 1975) and in Alberta (Rusch and Reeder 1978) suggest no cyclic changes in population densities. Large changes in population density do appear to be partly related to changes in food supply and, should cone failure failurs occur at regular intervals, a cyclic-like behaviour may occur.

5.5 DAMAGE

Red squirrels have been reported to damage mature trees and in some cases young seedlings by clipping of terminal and lateral buds, by removal of cones and by barking. Hosley (1928) found that Scotch pine, Norway spruce and European larch in older plantations were all severely damaged by red squirrels and that levels of damage tended to be higher during winters of heavy snow cover. An average of 93.2% of Scotch pines and 68.0% of Norway spruce suffered damage in a winter with heavy snow cover whereas 55.6% and 23.0%, respectively, were damaged during a winter with light snow cover. Hosley (1928) reported that damage usually involved extensive clipping of the terminal and lateral buds of Scotch pines, the terminal buds of Norway spruce, the lateral branches of European larch and the terminal buds of white spruce. All species, except Scotch pine, were able to recover from these levels of damage. Hosley (1928) attributed high damage years primarily to failure of natural cone crops and poor availability of food as a result of heavy snow cover. Hart (1936) also reported high levels of damage by red squirrels during winters of heavy snow--77.2% of Norway spruce, 53.5% of white spruce and 29.0% of red spruce were damaged by clipping of terminal buds. Adams (1955) found that clipping of cones of Ponderosa pines often resulted in the removal of small portions of the lateral branches containing immature cones and terminal buds. Balch (1942) noted that red squirrels most often clipped conifers in late winter and spring and suggested that buds served as a supplement to the diet.

Barking of trees by red squirrels has been reported by Hatt (1929), Moore (1940), Rowe (1952), Adams (1955) and Lutz (1956). Barking most commonly involved girdling of young trees 6-7 cm in diameter or girdling of the tops of mature trees. In the former case, most young trees that were girdled survived poorly (Lutz 1956) while, in the latter case, the upper portions of the mature trees were killed. Lutz (1956) concluded that damage by red squirrels was highest following peak years when food supplies may be limited and, as a result, foods of lower nutritional value are consumed.

No information on methods of controlling red squirrel damage was available. It appears red squirrel damage is most often confined to mature trees hence the likelihood of severely deforming young trees or stunting tree growth is small. Fisch and Dimock (1978) found that clipping of plantation stock, particularly in younger stands, was usually confined to areas closely adjacent to older stands. Use of cleared buffer strips between plantation areas and undisturbed mature forests may thus be one method of controlling squirrel damage.

6. *LEPUS AMERICANUS*

6.1 DISTRIBUTION

The snowshoe hare, *L. americanus*, is a common inhabitant of the forested regions of Canada from the Atlantic to Pacific coast (Banfield 1977) (Figure 6). Agricultural development along the southern fringe of the boreal forest has eliminated some snowshoe hare habitat but small populations still occur in woodland pockets in these areas (Windberg and Keith 1978). Snowshoe hares exhibit cyclic fluctuations in abundance becoming very numerous about every ten years (Keith 1963). Howell (1923) suggested that leporids in northern areas undergo large population fluctuations while those of the western United States maintain more stable population densities. More recent studies of snowshoe hare populations in Alaska (Trapp 1962; Wolff 1978), in Alberta (see Keith and Windberg 1978 for a review), in British Columbia (Chitty and Elton 1937; Chitty 1950) and in Colorado (Dolbeer and Clark 1975) have supported this concept.

6.2 FOOD HABITS

6.2.1 Fall and Winter Diets

In late fall and winter, the diet is composed almost entirely of hardwood browse and the bark and needles of coniferous trees. The winter diet of hares in central Alaska consists largely of small twigs and buds of white and black spruce, willow, birch, alders, Labrador tea, blueberries, raspberry and rose (Trapp 1962; O'Farrell 1965; Wolff 1978). Wolff (1978) found that woody browse made up 82% of the diet in mid-winter and 56% of the diet in April. The winter diet of *L. americanus* in Newfoundland (Dodds 1960) was quite similar to this, but high-bush cranberry was reported as a more highly preferred food. In eastern Canada (MacLulich 1937; Bider 1961; de Vos 1964), snowshoe hares appear to prefer pines, trembling aspen, alder, hazel, willows and balsam poplars as winter foods. Telfer (1972) also reported preferences for beech, white and black spruce, hobblebush, hazel, mountain maple and alder in New Brunswick.

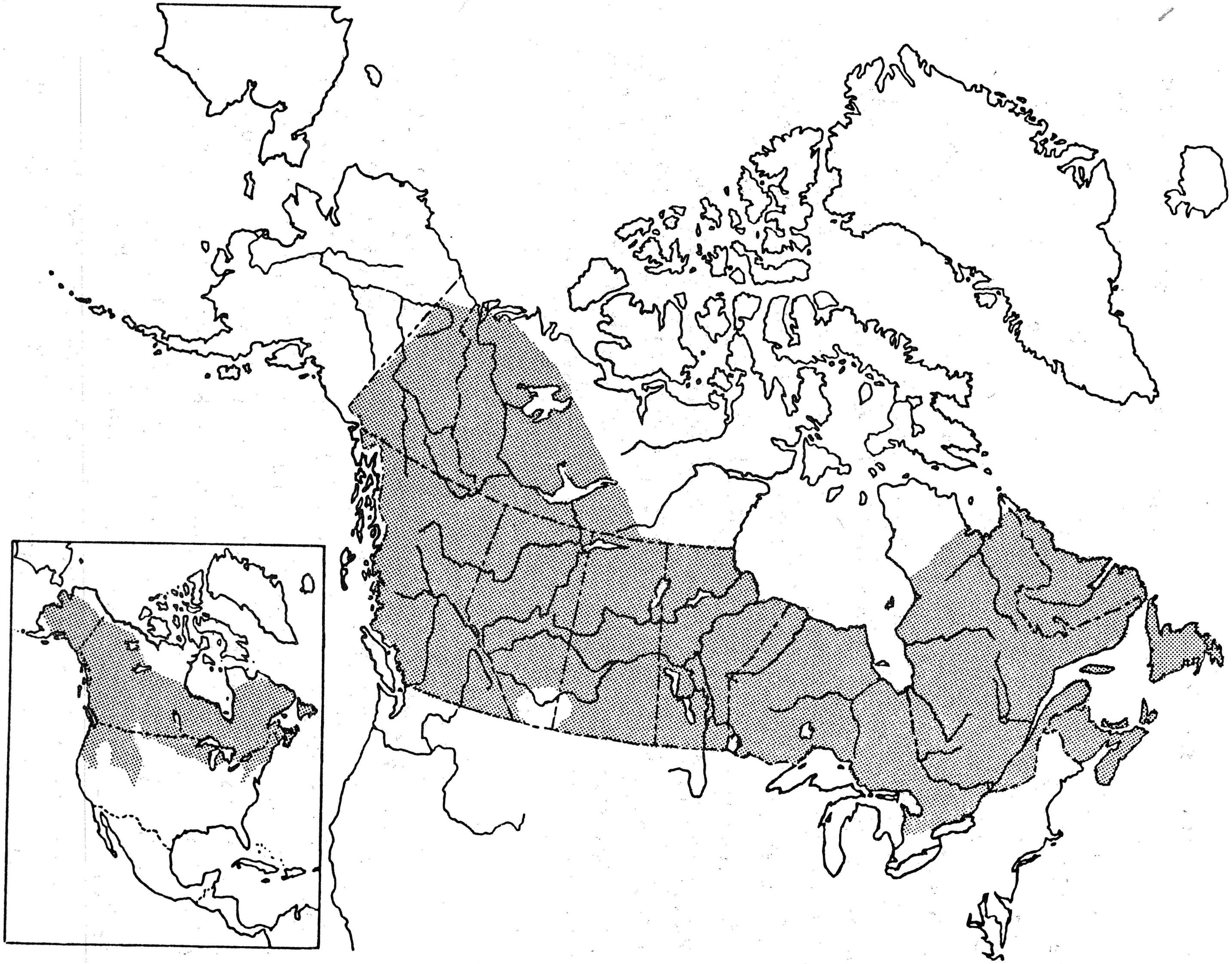

Figure 6. The distribution of *L. americanus* (snowshoe hare) in Canada and in North America (inset). (Modified from Banfield [1977], Map 38.)

6.2.2 Spring and Summer Diets

In general, the diversity of the summer diet appears to be greater than that of the winter diet (Wolff 1978). In late spring, summer, and early fall, snowshoe hares feed on a variety of leaves, herbs, and green plant material (Bider 1961; Trapp 1962; Wolff 1978). Wolff (1978) found that blueberry, low-bush cranberry, fireweed, and horsetails made up 47% of the spring diet of hares in Alaska, while leaves of birch, willow, rose and other deciduous shrubs made up 76% of the summer diet. Adams (1959) provided no quantitative estimates for food consumption but listed Douglas fir, hollygrape, balsam-root, arnica, junegrass and white spirea as major summer foods of snowshoe hares in Montana.

6.2.3 General Food Habits

The food habits of *L. americanus* are largely herbivorous (Adams 1959; Trapp 1962; Dodds 1960; de Vos 1964; Hansen and Flinders 1969, cited in Wolff 1978; Telfer 1972; Wolff 1978). Hardwood browse, conifer needles and bark are staple winter foods--leaves green plant material, herbs and some hardwood browse are staple summer foods.

Telfer (1972) and Wolff (1978) suggested that the density and frequency of occurrence of a plant species in a given habitat are important in the determination of the composition of a hare's diet. Nutritive value and palatibility may also be important factors. Holter *et al.* (1974) and Lindlof *et al.* (1974) have shown that several species of plants may be required in the daily diet of leporids to provide minimum energy, protein and nutrient requirements. Hares may thus change food preferences within a season to correct for nutrient deficiencies. Population densities may also affect food habits. Windberg and Keith (1976) established high density experimental populations by transplanting hares onto two islands during the summer and found that woody browse as well as all available herbaceous growth was heavily utilized by late June. Keith (1974) and Windberg and Keith (1978) have suggested that the decline in the availability of woody browse associated with increasing densities of snowshoe hares initiates the decline of snowshoe hare populations and is partly responsible for the cyclic fluctuations in populations of snowshoe hares.

6.3 HABITAT UTILIZATION

Snowshoe hares appear to prefer black spruce forest, spruce-fir forests, mixed spruce-fir-lodgepole forests and post-fire successional areas dominated by aspen regrowth (Bider 1961; Keith 1972; Dolbeer and Clark 1975). Keith (1963) considered changes in overall habitat use throughout a cycle and concluded that snowshoe hares are largely restricted to islands or foci of favourable habitat during low years but disperse into less favourable habitat as densities increase. Keith and Windberg (1978) showed that, during a population low (1966-67), snowshoe hares near Rochester, Alberta used areas of aspen upland with well-developed understory. However, by the population peak (1970-71), hares were found in all habitats except those in which cover was very sparse. During the population decline, hares disappeared from the more open habitat types as well as from many of the areas with good cover. Destruction of forest cover by fire can also restrict local distribution although hares will reoccupy badly burned areas once revegetation has begun (Keith and Surrendi 1971).

Keith (1972) concluded that optimal cover for snowshoe hares in northern Alberta was in areas of aspen regrowth following fires. The hazel, willow, and alder understory that is common in these areas offered both good cover and good winter food supplies. Mature conifer forests or mixed wood areas generally had low densities of snowshoe hares. Resident populations in these areas occurred chiefly in shrub-dominated areas or young coniferous cover along bog edges, water courses or natural openings. In eastern Canada, snowshoe hares utilized subclimax bog habitat, mesophytic coniferous forest and hygrophytic mature conifer-alder stands (MacLulich 1937; Wood and Munroe 1977). Areas of mixed northern hardwood regeneration were used as browsing areas while the mixed coniferous and hardwood association was used as both food and cover. Snowshoe hares in Colorado used spruce-fir or mixed spruce-fir-lodgepole pine forests much more extensively than aspen woods (Dolbeer and Clark 1975). This was attributed to a preference for the dense understory of the coniferous forests. However, juvenile snowshoe hares appeared to use open habitat areas shortly after weaning (July and August). Dolbeer and Clark (1975) attributed this to the exclusion of juvenile hares from areas of good habitat by resident adults during the breeding period when adults are more territorial than in the fall and winter.

6.4 DEMOGRAPHY

6.4.1 Reproduction

L. americanus is a seasonal breeder producing from 3-4 litters each year. Males show a distinct annual cycle of reproductive activity. From late winter (February) to late summer (August), most adult males are reproductively active but from early fall to late winter no males are in breeding condition (Rowan and Keith 1956; Bookhout 1965; Keith 1972). Females also show an annual cycle of reproductive activity but the onset of breeding is about 6 weeks later than in males (Bookhout 1965). First litters are usually conceived in late March to early April (Adams 1959; Newson 1964; Bookhout 1965; Dodds 1965; Keith *et al.* 1966; Dolbeer and Clark 1975; Wood and Munroe 1977) although, in Alaska, first conceptions may not occur until mid-April (Trapp 1962). The gestation period in snowshoe hares is 35-37 days (Sevaraid 1945; Keith *et al.* 1966). Immediate post-partum mating results in well-defined litter groups with a mean interval between groups of approximately 35 days (Keith *et al.* 1966; Wood and Munroe 1977; Keith and Windberg 1978).

The annual number of litters per year per adult female is generally highest in central areas of the range and lower in the northern and southern extremes of the range (Keith *et al.* 1966) (Table 5). Within an area, spring weather conditions (through effects on the onset of breeding and date of first conception) appear important in determining the number of litters each year (Dolbeer and Clark 1975). Populations in Alberta commonly have 3-4 litters per year per female (Keith *et al.* 1966; Keith 1972). Populations in Utah and Colorado commonly produce 2 litters per year and, in Utha, some females produced three litters per year (Dolbeer and Clark 1975). In Minnesota (Green and Evans 1940c), Maine (Severaid 1945) and Montana (Adams 1959), the average number of litters produced per female per year was 2.33, 2.89 and 2.90, respectively. The last litter is usually conceived by early August (Keith *et al.* 1966).

6.4.2 Litter Size

Within populations, the size of first litters (per breeding female) tend to be significantly smaller than the sizes of subsequent litters (Table 5). Litter size may also vary between years in a population suggesting changes over a population cycle. Keith (1963), however, found no significant correlations between year to year variations in litter size and cyclic population trends. Meslow and Keith (1971) found annual changes in litter size to be correlated with temperature and snow depth. Litter sizes were larger following winters with cold temperatures and deep snow.

Rowan and Keith (1956) and Keith (1963) suggested that snowshoe hare litter sizes increase from the south to north of their range. Keith *et al.* (1966) found a highly significant correlation ($r=0.80$; $p<0.01$) between litter size and latitude (when an aberrant value from Manitoba was ignored). The results of population studies by Trapp (1962) and Wood and Munroe (1977) appear to agree with this finding but values reported by Dolbeer and Clark (1975) for populations in Colorado and Utah are high. Dolbeer and Clark (1975) discussed this inconsistency and attributed the high mean litter sizes of their study populations to altitudinal effects (their study areas were at altitudes of 3100-3145 m in Colorado and 2230-2490 m in Utah), hence their study population is probably equivalent to populations in more northerly areas.

6.4.3 Sex Ratio

Sex ratios of both juvenile and adult snowshoe hares generally approximate a ratio of 1 male:1 female. *In utero* sex ratios and ratios at birth indicate that the proportions of males and females produced each year are similar (Dodds 1965; Meslow and Keith 1968; Wood and Monroe 1977). Juvenile sex ratios (at 2-4 months of age) approximate a ratio of 1 male:1 female (Trapp 1962; Newson and de Vos 1964; Dodds 1965; Meslow and Keith 1968; Wood and Monroe 1977). However, Rowan and Keith (1956) reported significant deficiencies of juvenile males in snowshoe hare populations near Anzac, Alberta in the early 1950's during a population high. Adult sex ratios do not generally differ significantly from equality (Aldous 1937; Webb 1937; Adams 1959; Dodds 1960; Trapp 1962; Newson and de Vos 1964; Meslow and Keith 1968; Wood and Munroe 1977). The one exception was again in the snowshoe hare populations near Anzac, Alberta where only 30.3% of a peak population were male (Rowan and Keith 1956). The preponderance of females in the population gradually diminished during the decline.

6.4.4 Densities and Population Fluctuations

Densities of snowshoe hare populations show considerable variation between the number of hares/ha during population lows and population highs. In eastern Canada, MacLulich (1937) reported densities of 0.004 hares/ha (1/sq. mi) during a population low and densities as high as 13.13 hare/ha during a population high. From 1932-39 in the northeastern United States, Green and Evans (1940a) reported lows of 0.04 snowshoe hares/ha and highs of 1.93 hares/ha. The minimum densities of snowshoe hare populations during short term studies in Colorado and Utah were 0.73 hares/ha and 0.46 hares/ha, respectively (Dolbeer and Clark 1975). A population study of snowshoe hares conducted by L.B. Keith and associates in the vicinity of Rochester, Alberta from 1961 to 1976 is the most detailed study of long-term population changes of snowshoe hares. Within the main study area, comprised largely of post-fire successional aspen woods

Table 5. Average litter size, number of litters per adult female per year and average number of young produced per adult female per year for *L. americanus*. (Modified from Keith *et al.* [1966], Table 1.)

		Average litter size				Litters/ adult females per year		Av. young/ adult females per year
		First litters		Later litters				
	Region	Corpora lutea	Embryos	Corpora lutea	Embryos	Av.	Max.	
Dolbeer and Clark (1975)	Colorado Utah	3.43 3.47	3.00 3.56	5.03 6.49	4.75 5.91			
Bookhout (1965)	Michigan				2.83 ± ? (48)	2.42	4	6.5
Aldous (1937)	Minnesota		2.04 ± 0.15 (28)		2.79 ± 0.04 (194)		4	
Green and Evans (1940a)	Minnesota		2.40 ± 0.11 (45)		3.17 ± 0.15 (36)	2.35	3	6.8
Newson (1964)	Ontario	2.38 ± 0.05 (225)		3.48 ± 0.04 (433)			4	6.3
Adams (1959)	Montana					2.94	3	8.2
MacLulich (1937)	Ontario		2.25 ± 0.22 (12)		3.39 ± 0.24 (13)			
Dodds (1965)	Newfoundland		2.77 ± ? (15)		4.23 ± ? (164)	3.20	4	12.2
Wood and Munroe (1977)	Nova Scotia New Brunswick		2.27 2.56		2.27-3.26 3.40-4.00			
MacLulich (1937)	Manitoba		4.18 ± 0.21 (23)					
Keith *et al.* (1966)	Alberta	3.20 ± 0.15 (41)	2.71 ± 0.13 (45)	4.94 ± 0.16 (70)	4.49 ± 0.15 (87)	3.15	4	12.8
Rowan and Keith (1956)	Alberta		2.88 ± 0.26 (9)		4.06 ± 0.14 (63)	2.75	5?	10.5
Philip (1939)	Alaska		3.72 ± 0.23 (29)		4.33 ± 0.13 (88)	1.79	3	7.2
Trapp (1962)	Alaska				4.6			

and black spruce forests, snowshoe hare populations fluctuated between lows of 1.3-2.6 hares/ha (April 1966) to highs of 5.88-11.77 hares/ha (Windberg and Keith 1978). One study area with a history of recurrent fires of varying intensity (and hence a wide variation in habitat types) increased from a low of 0.17-0.33 hares/ha to a high of 11.45-22.91 hares/ha. Keith (1963) analyzed indices of population change from six provinces and the Northwest Territories and found that major peaks occurred on average once every 8.9 years (range of 8-11 years). Amplitudes of these population cycles involved 15- to 100- fold changes in density (Keith 1963). The long-term periodicity of these cycles has discouraged detailed demographic studies--exceptions to this include the seven-year study by Green and Evans (1940a, b, c) in Minnesota and the 15-year study by L.B. Keith and associates (see Keith and Windberg [1978] for a summary analysis of the studies comprising the 15-year study of these populations).

Green and Evans (1940a, b, c) were the first to obtain long-term quantitative information on snowshoe hare demography. They concluded that, although reproductive rates remained similar throughout the period from a population high to a population low, a sharp reduction in juvenile survival was associated with a decline in the population. Adult survival showed little change during the initial decline. However, during the fifth to sixth year after the decline, both adult and juvenile survival rose.

On the basis of a 15-year study which spanned two periods of decline and a single period of increase, Keith and Windberg (1978) found a number of conditions to be predictably associated with the hare cycle in northern Alberta:

1. Overwinter survival of juveniles declined rapidly in the peak year and continued to decline for four to five years. Although variable, the overwinter survival rate of juveniles during the period of population increase was three to four times higher than during years of decline.

2. Adult survival in late winter, one year after the population peak, declined and continued to decline throughout the population low.
3. Average overwinter weight loss increased immediately before the peak summer and fall; overwinter weight losses gradually declined prior to the cyclic low.
4. Mean growth rates of young hares in summer were inversely correlated with mean adult weight losses during the previous winter to spring.
5. The number of young born per adult female declined in the peak summer, and throughout the first 2-3 years of the decline but recovered just prior to the cyclic low. Changes in natality resulted from changes in ovulation rates, third and fourth litter pregnancy rates and length of breeding season which in turn were inversely correlated with mean weight losses during previous winters.

Keith and Windberg (1978) concluded that two distinct sequences of events (involving the above conditions) significantly affected the cyclic behavior of the population. The first began about three years after the peak winter resulting in a lower rate of decline. This sequence included lower winter-spring weight loss, increased reproduction, increased juvenile growth rates and increased overwinter survival of juveniles. The second sequence included high winter-spring weight loss, decreased reproduction, decreased juvenile growth rates and decreased juvenile survival over winter. This sequence of events preceded the peak winter and tended to slow the rate of increase. These two sequences are consistent with predictions from a conceptual model of cyclic fluctuations in snowshoe hare populations presented by Keith (1974).

Keith (1974) suggested that interactions between hares and their winter food supply and between hares and predators were involved in the cyclic fluctuations. Increased numbers of snowshoe hare gradually over-utilize the winter food supply (woody browse) resulting in quantitative and qualitative declines in browse. Keith (1974) suggests that these changes initiate the decline. Delayed increases in the population size of predators (resulting from high snowshoe hare populations one to two years earlier) lead to increased predation on the snowshoe hare population and so extend the period of decline. Nutritional problems are reflected in increased overwinter weight losses, reduced reproduction and reduced juvenile growth. After the major decline, juvenile survival and later adult survival declines in response to increased predation. Improving food supplies during this period result in increased reproductive rates and growth rates and decreased overwinter weight losses. Until predator populations decline, however, the effects of high reproduction and recruitment are not apparent. Keith (1974) suggests that by this time the browse has recovered from the previous over-utilization.

6.5 DAMAGE POTENTIAL

Snowshoe hares have been known to cause severe damage to young trees in natural situations and in plantations by girdling or barking and by clipping. MacLulich (1937) reported snowshoe hare girdling of poplars up to 7 cm (2.5 in) in diameter up to an average height of 0.6 m (2 ft) above the snowline. Willows, alders, white birch, juneberry and jack pine were also girdled. Besser and Welch (1959) found that snowshoe hares caused considerable damage to Douglas fir seedlings in Colorado and Washington. Trapp (1962) reported barking of willows, alders, poplars, white spruce, and black spruce by hares in Alaska. Snowshoe hares were rated as the second most damaging pest species on plantations in Oregon and Washington (Black *et al.* 1969). Keith (1972) similarly reported clipping and girdling of plantation stock by snowshoe hares in the Peace River district of Alberta. Barking appears to most frequently occur in the late winter-early spring (Aldous and Aldous 1944; Trapp 1962). Clipping of the terminal and lateral twigs and buds is also common and can deform the plant and retard growth

(Aldous and Aldous 1944; Black *et al.* 1969). Black *et al.* (1969), for example, found that young trees damaged by snowshow hares obtained an average height of only 59.4 cm (23.4 in) by three years of age whereas undamaged seedlings (caged) obtained an average height of 84.1 cm (33.1 in). It would appear that snowshoe hare populations, particularly peak populations, are capable of causing sufficient damage so as to be an important limiting factor in afforestation programs (Trapp 1962; Keith 1972).

Aldous and Aldous (1944) recommended that impacts of snowshoe hare damage could be limited by planting less preferred but fast growing species (based on levels of damage, snowshoe hares appeared to prefer [in order of decreasing preferences] jack pine, red pine, white pine, and white spruce), by planting during population lows, by planting in open areas and maintaining these areas free of cover and by the use of repellents. Supplemental food supplies (i.e., aspen cuttings) did not appear to be effective. Keith (1972) recommended the use of older stock (3 years or older) as well as the use of less palatable species and planting during lows. Besser and Welch (1959) found the three repellents they tested (ZAC, TMTD, and TNB-A) to be effective in controlling hare damage to Douglas firs in Colorado and Washington State.

7. CONCLUSIONS

Cyclic population fluctuations are exhibited by three of the five species considered--*M. pennsylvanicus* and *C. gapperi* populations exhibit regular population fluctuations every 3-4 years whereas *L. americanus* populations undergo regular 8-11 year cycles of abundance. *P. maniculatus* exhibit regular annual changes in abundance but it is not clear if this species exhibits cyclic population fluctuations over longer periods. *T. hudsonicus* population densities appear to be directly influenced by the quality and quantity of mast produced by preferred coniferous tree species. Changes in cone crop production thus influence long-term density changes in this species.

At present, the population dynamics of small mammal species in the AOSERP study areas are only partly understood. Most species of small mammals can undergo very large changes in population densities (between populations lows and peak population periods) in relatively short periods. Because of their importance as herbivores and as prey of various raptors and furbearers, it is important that we at least determine cyclic trends in these populations if we are to make meaningful predictions on the environmental impact of oil sands development in the AOSERP study area. An understanding of the population ecology of small mammals in natural areas will also provide information important to the eventual formulation of effective reforestation programs in reclamation areas.

M. pennsylvanicus is potentially one of the most serious small rodent pest species of recent afforestation areas. Severe barking (consumption of the cambium layer of the bark) of young trees by this species has been reported in many reforestation programs in North America. *C. gapperi* also has a high damage potential but because this species prefers mature forest or thick shrub habitats, its distribution in newly reclaimed areas will be limited--however, as grass, herb and shrub cover increase in afforestation areas, the species could become a serious pest species. *L. americanus* is also known to severely browse and bark trees, particularly during periods of high population density. Like *C. gapperi*, *L. americanus* prefer areas of dense cover. As a result, the damage potential for this species will be limited in younger afforestation areas but, as tree and shrub cover increase, damage by *L. americanus* may increase. The damage potential of this species, however, could increase sharply during years of peak population densities. *P. maniculatus* is known to be a major pest species (seed predator) only in areas reforested by direct seeding techniques--the damage potential for *P. maniculatus* is thus extremely low on afforestation areas in the AOSERP study area in light of the currently used afforestation techniques (seedling planting program).

8. LITERATURE CITED

Adams, L. 1955. Pine squirrels reduce future crops of ponderosa pine cones. J. Forest. 53:35.

Adams, L. 1959. An analysis of a population of snowshoe hares in northwestern Montana. Ecol. Monogr. 29:141-170.

Ahlgren, C.E. 1966. Small mammals and reforestation following prescribed burning. J. Forest. 64:614-618.

Aldous, C.M. 1937. Notes on the life history of the snowshoe hare. J. Mammal. 18:46-57.

Aldous, C.M. and S.E. Aldous. 1944. The snowshoe hare: a serious enemy of forest plantations. J. Forest. 42:88-94.

Anderson, J.L. and R. Boonstra. 1979. Some aspects of reproduction in the vole *Microtus townsendii*. Can. J. Zool. 57:18-24.

Aumann, G.D. and J.T. Emlen. 1965. Relation of population density to sodium availability and sodium selection by microtine rodents. Nature. 208:198-199.

Bailey, V. 1924. Breeding, feeding and other life habits of meadow mouse *(Microtus)*. J. Agric. Res. 8:523-535.

Baker, R.H. 1968. Habitats and Distribution. Pages 98-126 *in* J.A. King ed., Biology of *Peromyscus* (Rodentia). Am. Soc. Mammal., Spec. Publ. No. 2.

Bakerspigel, A. 1958. The spores of *Endogone* and *Melanogaster* in the digestive tracts of rodents. Mycologia. 50:440-442.

Balch, R.E. 1942. A note on squirrel damage to conifers. Forest. Chron. 18:42.

Banfield, A.W.F. 1977. The mammals of Canada. National Museum of Canada. Univ. of Toronto Press, Toronto. 438 p.

Barbour, R.W. 1951. The mammals of Big Black Mountain, Harlan County, Kentucky. J. Mammal. 32:100-110.

Baumgartner, L.L. 1938. Population studies of the fox squirrel in Ohio. Trans. N. Amer. Wildl. Nat. Res. Conf. 3:685-689.

Beck, A.M. and R.J. Vogl. 1972. The effects of spring burning on rodent populations in a brush prairie savanna. J. Mammal. 53:336-346.

Beer, J.R., L.D. Frenzel and C.F. MacLeod. 1958. Sex ratios of some Minnesota rodents. Am. Midl. Nat. 59:518-524.

Beer, J.R. and C.F. MacLeod. 1961. Seasonal reproduction in the meadow vole. J. Mammal. 42:483-489.

Beer, J.R., C.F. MacLeod and L.D. Frenzel. 1957. Prenatal survival and loss in some cricetid rodents. J. Mammal. 38:392-402.

Besser, J.F. and J.F. Welch. 1959. Chemical repellents for the control of mammal damage to plants. Trans. N. Amer. Wildl. Conf. 24:166-173.

Bider, J.R. 1961. An ecological study of the hare *Lepus americanus*. Can. J. Zool. 39:81-103.

Birdsall, D.A. and D. Nash. 1973. Occurrence of successful multiple insemination of females in natural populations of deer mice. Evolution. 27:106-110.

Birney, E.C., W.E. Grant and D.D. Baird. 1976. Importance of vegetative cover to cycles of *Microtus* populations. Ecology. 57:1043-1051.

Black, H.C. 1969. Fate of sown coniferous seeds. Pages 42-51 *in* H.C. Black, ed. Wildlife and reforestation in the Pacific northwest. School of Forestry, Oreg. State Univ., Corvallis.

Black, H.C., E.J. Dimock II, W.E. Dodge and W.H. Lawrence. 1969. Survey of animal damage on forest plantations in Oregon and Washington. Trans. N. Amer. Wildl. Conf. 34:388-407.

Blair, W.F. 1940. Home ranges and populations of the meadow vole in southern Michigan. J. Wildl. Manage. 4:149-161.

Blair, W.F. 1948. Population density, life span and mortality rates of small mammals in the blue-grass meadow and blue-grass field associations of southern Michigan. Am. Midl. Nat. 40:395-419.

Blair, W.F. 1968. Introduction. Pages 1-5 *in* J.A. King, ed. The biology of *Peromyscus* (Rodentia). Am. Soc. Mammal., Spec. Publ. No. 2.

Bole, B.P. Jr. 1939. The quadrat method of studying small mammal populations. Sci. Publ. Cleveland Mus. Nat. Hist. 5:15-77. Cited *in* Tamarin (1977).

Bookhout, T.A. 1965. Breeding biology of snowshoe hares in Michigan's upper peninsula. J. Wildl. Manage. 29:296-303.

Boyd, M. 1977. Analysis of fur production records by individual furbearing species for registered trapping areas in Alberta, 1970-75. Unpubl. Rep., Alberta Recreation, Parks and Wildl., Fish and Wildl. Div., Edmonton. 72 p.

Brink, C.H. 1964. Spruce seed as a food of the squirrels *Tamiasciurus hudsonicus* and *Glaucomys sabrinus* in interior Alaska. M.Sc. Thesis. Univ. of Alaska, College. 73 p.

Brink, C.H. and F.C. Dean. 1966. Spruce seed as a food of red squirrels and flying squirrels in interior Alaska. J. Wildl. Manage. 30:503-512.

Brown, H.L. 1945. Evidence of winter breeding of *Peromyscus*. Ecology. 26:308-309.

Brown, L.N. 1964. Ecology of three species of *Peromyscus* from southern Missouri. J. Mammal. 45:189-202.

Buckner, C.H. 1957. Population studies on small mammals of southeastern Manitoba. J. Mammal. 38:87-97.

Buckner, C.H. 1970. The strategy for controlling rodent damage to pines in the Canadian mid-west. Proc. Vert. Pest Conf. 4:43-48.

Butsch, R.S. 1954. Life history and ecology of the red backed vole, *Clethrionomys gapperi*. Diss. Abstr. 14:1115.

Cameron, A.W. 1964. Competitive exclusion between the rodent genera *Microtus* and *Clethrionomys*. Evolution. 18:630-634.

Canham, R.P. 1969. Early cessation of breeding in an unusually abundant population of *Peromysous maniculatus borealis*. Can. Field-Nat. 83:279.

Cary, J.R. and L.B. Keith. 1979. Reproductive change in a 10-year cycle of snowshoe hares. Can. J. Zool. 57:375-390.

Casebeer, R.L. 1954. The use of tetramine in bitterbrush revegetation. J. Forest. 152:829-830.

Cayford, J.H. and R.A. Haig. 1961. Mouse damage to forest plantations in southeastern Manitoba. J. Forest. 59:124-125.

Chitty, H. 1950. The snowshoe rabbit enquiry, 1946-48. J. Anim. Ecol. 19:15-20.

Chitty, D.H. and C. Elton. 1937. The snowshoe rabbit enquiry, 1935-1936. Can. Field-Nat. 51:63-73.

Christian, J.J. and D.E. Davis. 1966. Adrenal glands in female voles *(Microtus pennsylvanicus)* as related to reproduction and population size. J. Mammal. 47:1-18.

Clarke, C.H.D. 1939. Some notes on hoarding and territorial behaviour of the red squirrel *Sciurus hudsonicus* (Erxleben). Can. Field-Nat. 53:42-43.

Clough, G.C. 1964. Local distribution of two voles: evidence for interspecific interaction. Can. Field-Nat. 78:188-197.

Cole, F.R. and G.O. Batzli. 1978. Influence of supplemental food on a vole population. J. Mammal. 59:809-819.

Connor, P.F. 1953. Notes on the mammals of a New Jersey pine barrens area. J. Mammal. 34:227-235.

Connor, P.F. 1960. The small mammals of Otsego and Schoharie counties. N.Y. State Museum Sci. Serv. Bull. No. 382. Cited *in* Innes (1978).

Corthum, K.W. 1967. Reproduction and duration of placental scars in the prairie vole and eastern vole. J. Mammal. 48:287-292.

Coventry, A.P. 1937. Notes on the breeding of some Cricetidae in Ontario. J. Mammal. 18:489-496.

Criddle, S. 1932. The red-backed vole *(Clethrionomys gapperi loringi* Bailey*)* in southern Manitoba. Can. Field-Nat. 46:178-181.

Criddle, S. 1956. Drummond's vole in Manitoba. Can. Field-Nat. 70:78-84.

Davis, D.W. 1969. The behaviour and population dynamics of the red squirrel *(Tamiasciurus hudsonicus)* in Saskatchewan. Ph.D. Thesis. Univ. Arkansas, Fayetteville. Cited in Rusch and Reeder (1978).

de Vos, A. 1964. Food utilization of snowshoe hares on Manitoulin Island, Ontario. J. Forest. 62:238-244.

Dice, L.R. 1921. Notes on the mammals of interior Alaska. J. Mammal. 2:20-28.

Dodds, D.G. 1960. Food competition and range relationships of moose and snowshoe hares in Newfoundland. J. Wildl. Manage. 24:52-60.

Dodds, D.G. 1965. Reproduction and productivity of snowshoe hares in Newfoundland. J. Wildl. Manage. 29:303-315.

Dolbeer, R.A. 1973. Reproduction in the red squirrel *(Tamiasciurus hudsonicus)* in Colorado. J. Mammal. 54:536-540.

Dolbeer, R.A. and W.R. Clark. 1975. Population ecology of snowshoe hares in the central Rocky Mountains. J. Wildl. Manage. 39:535-549.

Dowding, E.S. 1955. *Endogone* in Canadian rodents. Mycologia. 47:51-57.

Drickhamer, L.C. 1970. Seed preferences in wild caught *Peromyscus maniculatus bairdii* and *Peromyscus leucopus noveboracensis*. J. Mammal. 51:191-194.

Dunmire, W.W. 1960. An altitudinal survey of reproduction in *Peromyscus maniculatus*. Ecology. 41:174-182.

Dyke, G.R. 1971. Food and cover of fluctuating populations of northern cricetids. Ph.D. Thesis. Univ. of Alberta, Edmonton. 245 p.

Eadie, W.R. 1953. Response of *Microtus* to vegetative cover. J. Mammal. 34:263-264.

Elliott, P.W. 1969. Dynamics and regulation of a *Clethrionomys* population in central Alberta. Ph.D. Thesis. Univ. of Alberta, Edmonton. 97 p.

Elton, C.S. 1942. Voles, mice and lemmings. Clarendon Press, Oxford. 496 p.

Evans, J. 1974. Pesticides and forest wildlife in the Pacific northwest. Pages 205-219 *in* H.C. Black, ed. Wildlife and forest management in the Pacific northwest. School of Forestry, Oregon State Univ., Corvallis.

Everett, R.L., R.O. Meeuwig and R. Stevens. 1978. Deer mouse preference for seed of commonly planted species, indigenous weed seed and sacrifice foods. J. Range Manage. 31:70-73.

Evernden, L.N. and W.A. Fuller. 1972. Light alteration caused by snow and its importance to subnivean rodents. Can. J. Zool. 50:1023-1032.

Fairbairn, D.J. 1977a. The spring decline in deer mice: death or dispersal? Can. J. Zool. 55:84-92.

Fairbairn, D.J. 1977b. Why breed early? A study of reproductive tactics in *Peromyscus*. Can. J. Zool. 55:862-871.

Fairbairn, D.J. 1978. Dispersal of deer mice, *Peromyscus maniculatus*. Oecologia (Berl.). 32:171-193.

Findley, J.S. 1951. Habitat preferences of four species of *Microtus* in Jackson Hole, Wyoming. J. Mammal. 32:118-120.

Findley, J.S. 1954. Competition as a possible limiting factor in the distribution of *Microtus*. Ecology. 35:418-420.

Findley, J.S. and N.C. Negus. 1953. Notes on mammals of the Gothin region, Gunnison County, Colorado. J. Mammal. 35:235-239.

Fisch, G.G. and E.J. Dimock II. 1978. Shoot clipping by Douglas squirrels in regenerating Douglas fir. J. Wildl. Manage. 42:415-418.

Fisher, R.L. 1968. An ecological study of the red-backed vole, *Clethrionomys gapperi gapperi* (Vigors) in central New York. Ph.D. Thesis. Cornell University, Ithaca. Diss. Abstracts. 69:5757.

Fitzwater, W.D. Jr. 1941. The red squirrel: territorialism, activity, census methods. M.Sc. Thesis. N.Y. State College Forest. Syracuse. Cited *in* Rusch and Reeder (1978).

Fordham, R.H. 1971. Field populations of deermice with supplemental food. Ecology. 52:138-146.

Frischknecht, N.C. 1965. Deermice on crested wheatgrass range. J. Mammal. 46:529-530.

Fuller, W.A. 1969. Changes in numbers of three species of small rodents near Great Slave Lake, N.W.T., Canada, 1964-1967, and their significance for general population theory. Ann. Zool. Fenn. 6:34-55.

Fuller, W.A. 1977a. Demography of a subarctic population of *Clethrionomys gapperi:* numbers and survival. Can. J. Zool. 55:42-51.

Fuller, W.A. 1977b. Demography of a subarctic population of *Clethrionomys gapperi:* size and growth. Can. J. Zool. 55:415-425.

Fuller, W.A., L.L. Stebbins and G.R. Dyke. 1969. Overwintering of small mammals near Great Slave Lake, northern Canada. Arctic. 22:34-55.

Gashwiler, J.S. 1959. Small mammal study in west-central Oregon. J. Mammal. 40:128-138.

Gashwiler, J.S. 1969. Deer mouse repopulation on a poisoned Douglas-fir clearcut. J. Forest. 67:494-497.

Gashwiler, J.S. 1970. Plant and mammal changes on a clearcut in west Oregon. Ecology. 51:1018-1026.

Gessell, S.P. and G.H. Orians. 1967. Rodent damage to fertilized Pacific silver fir in western Washington. Ecology. 48:694-697.

Getz, L.L. 1960. A population study of the vole, *Microtus pennsylvanicus*. Amer. Midland Nat. 64:392-405.

Getz, L.L. 1968. Influence of water balance and microclimate on the local distribution of the redback vole and white-footed mouse. Ecology. 49:276-286.

Goin, O.B. 1943. A study of individual variation in *Microtus pennsylvanicus*. J. Mammal. 24:212-223.

Golley, F.B. 1961. Interaction of natality, mortality and movement during one annual cycle in a *Microtus* population. Am. Midl. Nat. 66:152-159.

Gordon, K. 1936. Territorial behaviour and social dominance among Sciuridae. J. Mammal. 17:171-172.

Grant, P.R. 1969. Experimental studies of competitive interaction in a two-species system. I. *Microtus* and *Clethrionomys* species in enclosures. Can. J. Zool. 47:1059-1082.

Grant, P.R. 1970. Experimental studies of competitive interaction in a two-species system. II. the behaviour of *Microtus*, *Peromyscus* and *Clethrionomys* species. Anim. Behav. 18:411-426.

Grant, P.R. 1971a. The habitat preference of *Microtus pennsylvanicus* and its relevance to the distribution of this species on islands. J. Mammal. 52:351-361.

Grant, P.R. 1971b. Experimental studies of competitive interaction in a two species system. III. *Microtus* and *Peromyscus* species in enclosures. J. Anim. Ecol. 40:323-350.

Grant, P.R. 1972. Interspecific competition among rodents. Ann. Rev. Ecol. Syst. 3:79-106.

Grant, P.R. 1978. Dispersal in relation to carrying capacity. Proc. Nat. Acad. Sci. (U.S.A.). 75:2854-2858.

Green, J.E. 1978a. Interim report on small mammal populations and related tree damage in the AOSERP study area, October and November, 1977. Prep. for the Alberta Oil Sands Environmental Research Program by LGL Ltd., environmental research associates. AOSERP Project VE 7.1.1. 38 p.

Green, J.E. 1978b. Techniques for the control of small mammal damage to plants: a review. Prep. for the Alberta Oil Sands Environmental Research Program by LGL Ltd., environmental research associates. AOSERP Report 38. 111 p.

Green, J.E. 1979. Baseline states of small mammal populations in the AOSERP study area. Interim Report II. Prep. for the Alberta Oil Sands Environmental Research Program by LGL Ltd., environmental research associates. AOSERP Project LS 7.1.2.

Green, R.G. and C.A. Evans. 1940a. Studies on a population cycle of snowshoe hares on the Lake Alexander area. I. Gross annual censuses 1932-9. J. Wildl. Manage. 4:220-238.

Green, R.G. and C.A. Evans. 1940b. Studies on a population cycle of snowshoe hares on the Lake Alexander area. II. Mortality according to age groups and seasons. J. Wildl. Manage. 4:267-278.

Green, R.G. and C.A. Evans. 1940c. Studies on a population cycle of snowshoe hares on the Lake Alexander area. III. Effect of reproduction and mortality of young hares on the cycle. J. Wildl. Manage. 4:347-358.

Gunderson, H.L. 1950. A study of some small mammal populations at Cedar Creek forest, Anoka County, Minnesota. Univ. Minn., Museum Nat. Hist. 4:1-49.

Gunderson, H.L. 1959. Red-backed vole habitat studies in central Minnesota. J. Mammal. 40:405-412.

Halvorson, C.H. 1964. Red squirrel ecology in the montane forests of the northern Rocky Mountains. Intermountain Forest and Range Experimental Station. Annual progress report, Missoula, Montana. Cited *in* Rusch and Reeder (1978).

Hamilton, W.J. Jr. 1937a. Growth and life span of the field mouse. Am. Nat. 71:500-507.

Hamilton, W.J. Jr. 1937b. The biology of the microtine cycles. J. Agric. Res. 54:779-790.

Hamilton, W.J. Jr. 1939. Observations on the life history of the red squirrel. Am. Midl. Nat. 22:732-745.

Hamilton, W.J. Jr. 1940. Life and habits of field mice. Sci. Monthly. 50:425-434.

Hamilton, W.J. Jr. 1941a. The food of small forest mammals in the eastern United States. J. Mammal. 22:250-263.

Hamilton, W.J. Jr. 1941b. Reproduction of the field mouse *Microtus pennsylvanicus* (Ord.). Cornell Univ., Agr. Exp. Sta. Mem. 237. 33 p.

Hansen, L. and G.O. Batzli. 1978. The influence of food availability on the white-footed mouse: populations in isolated wood lots. Can. J. Zool. 56:2530-2541.

Hansen, R.M. and J.T. Flinders. 1969. Food habits of North American hares. Colo. State Univ., Range Sci. Dep., Sci. Ser. No. 1. 17 p. Cited *in* Wolff (1978).

Hansson, L. 1971. Small mammal food, feeding and population dynamics. Oikos. 22:183-198.

Hansson, L. 1973a. Habitat, food and population dynamics of the field vole, *Microtus agrestis* L., in south Sweden. Viltrevy. 8:265-273.

Hansson, L. 1973b. Fatty substances as attractants for *Microtus agrestis* and other small mammals. Oikos. 24:417-421.

Hansson, L. 1975. Effects of habitat manipulation on small rodent populations. Pages 163-173 *in* L. Hansson and B. Nilsson eds. Biocontrol of rodents. Swedish Natural Science Research Council, Stockholm.

Harris, V.T. 1953. Ecological relationships of meadow voles and rice rats in tidal marshes. J. Mammal. 34:479-487.

Hart, A.C. 1936. Red squirrel damage to pine and spruce plantations. J. Forest. 34:729-730.

Hasler, J.F. 1975. A review of reproduction and sexual maturation in microtine rodents. Biologist. 57:52-86.

Hatt, R.T. 1929. The Red squirrel: its life history and habits, with special reference to the Adirondacks of New York and the Harvard Forest. Rossevelt Wildl. Annals. 2:10-146.

Hatt, R.T. 1943. The Pine squirrel in Colorado. J. Mammal. 24:311-345.

Hays, H.A. 1958. The distribution and movement of small mammals in central Oaklahoma. J. Mammal. 39:235-244.

Healey, M.C. 1967. Aggression and self-regulation of population size in deermice. Ecology. 48:377-392.

Hodgson, J.R. 1972. Local distribution of *Microtus montanus* and *Microtus pennsylvanicus* in southwestern Montana. J. Mammal. 53:487-499.

Hoffman, R.S. 1958. The role of reproduction and mortality in population fluctuations of voles *(Microtus)*. Ecol. Monogr. 28:78-109.

Hoffman, R.S. 1960. The small mammal components of six climax plant associations in eastern Washington and northern Idaho. Ecology. 41:371-372.

Holter, J.B., G. Tyler and T. Walski. 1974. Nutrition of the snowshoe hare *(Lepus americanus)*. Can. J. Zool. 52:1553-1558.

Hooven, E.F. 1969. The influence of forest succession on populations of small mammals in western Oregon. Pages 30-34 *in* H.C. Black, ed. Wildlife and reforestation in the Pacific northwest. School of Forestry, Oreg. State Univ., Corvallis.

Hooven, E.F. 1973. Effects of vegetation changes on small forest mammals. Pages 75-97 *in* R.K. Hermann and D.P. Lavender, eds. Even-age management. School of Forestry, Oreg. State Univ., Corvallis.

Hooven, E.F. and H.C. Black. 1976. Effects of some clearcutting practices on small mammal populations in western Oregon. Northwest Sci. 50:189-208.

Hornfeldt, B. 1978. Synchronous population fluctuations in voles, small game, owls and tuluaremia in northern Sweden. Oecologia (Berl.). 32:141-152.

Hosie, R.C. 1973. Native trees of Canada. 7th ed., Department of the Environment. Can. Forest Serv. 380 p.

Hosley, N.W. 1928. Red squirrel damage to coniferous plantations and its relation to changing food habits. Ecology. 9:43-48.

Howard, W.E. 1949. Dispersal, amount of inbreeding and longevity in a local population of prairie deermice on the George Reserve, southern Michigan. Contr. Lab. Vert-Biol., Univ. Mich. No. 43. 50 p.

Howard, W.E. 1950. Wildlife depredations in broadcast seeding of burned brushlands. J. Range Manage. 3:291-298.

Howell, A.B. 1923. Periodic fluctuations in the numbers of small mammals. J. Mammal. 4:149-155.

Innes, D.G.L. 1978. A reexamination of litter size in some North American microtines. Can. J. Zool. 56:1488-1496.

Iverson, S.L., R.W. Seabloom and J.M. Hnatiuk. 1967. Small mammal distributions across the prairie-forest transition of Minnesota and North Dakota. Am. Midl. Nat. 78:188-197.

Iverson, S.L. and B.N. Turner. 1972. Winter coexistance of *Clethrionomys gapperi* and *Microtus pennsylvanicus* in a grassland habitat. Am. Midl. Nat. 88:440-445.

Iverson, S.L. and B.N. Turner. 1976. Small mammal radioecology: natural reproductive patterns of seven species. Atomic Energy of Canada Ltd. AECL-5393. 53 p.

Jameson, E.W. Jr. 1952. Food of deer mice, *Peromyscus maniculatus* and *P. boylei,* in the northern Sierra Nevada, California. J. Mammal. 33:50-60.

Jameson, E.W. Jr. 1953. Reproduction of deer mice *(Peromyscus maniculatus* and *P. boylei)* in the Sierra Nevada, California. J. Mammal. 34:44-58.

Jameson, E.W. Jr. 1955. Some factors affecting fluctuations of *Microtus* and *Peromyscus*. J. Mammal. 36:206-209.

Johnson, H.M. 1951. Preliminary ecological studies of microclimates inhabited by small Arctic and subarctic mammals. Proc. Alaska. Sci. Conf. 2:125-131.

Jokela, J.J. and R.W. Lorenz. 1959. Mouse injury to forest planting in the prairie region of Illinois. J. Forest. 57:21-25.

Keith, L.B. 1963. Wildlife's ten year cycle. Univ. of Wisconsin Press, Madison. 201 p.

Keith, L.B. 1972. Snowshoe hare populations and forest regeneration in northern Alberta. Prep. for the Alberta Forest Service. Unpublished report. 21 p.

Keith, L.B. 1974. Some features of population dynamics in mammals. Inter. Congr. Game Biol. 11:17-58.

Keith, L.B., O.J. Rongstad and E.C. Meslow. 1966. Regional differences in reproductive traits of the snowshoe hare. Can. J. Zool. 44:953-961.

Keith, L.B. and D.C. Surrendi. 1971. Effects of fire on a snowshoe hare population. J. Wildl. Manage. 35:16-26.

Keith, L.B. and L.A. Windberg. 1978. A demographic analysis of the snowshoe hare cycle. Wildlife Monographs No. 58. 70 p.

Keller, B.L. and C.J. Krebs. 1970. *Microtus* population biology. III. reproductive changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana, 1965-67. Ecol. Monogr. 40:263-294.

Kemp, G.A. and L.B. Keith. 1970. Dynamics and regulation of red squirrel *(Tamiasciurus hudsonicus)* populations. Ecology. 51:763-779.

Klugh, A.B. 1927. Ecology of the red squirrel. J. Mammal. 8:1-32.

Kott, E. and W.L. Robinson. 1963. Seasonal variation in litter size of the meadow vole in southern Ontario. J. Mammal. 44:467-470.

Krasnowski, P.V. 1969. Aspects of red squirrel *(Tamiasciurus hudsonicus)* population ecology in interior Alaska. M.Sc. Thesis. Univ. of Alaska, College. 63 p.

Krebs, C.J. 1970. Genetic and behavioural studies on fluctuating vole populations. Pages 243-256 *in* P.J. den Boer and G.R. Gradwell, eds. Dynamics of populations. Proc. Adv. Study Inst. Dynamics Numbers Popul. (Oosterbeek, 1970).

Krebs, C.J. 1977. Competition between *Microtus pennsylvanicus* and *Microtus ochrogaster*. Am. Midl. Nat. 97:42-49.

Krebs, C.J., B.L. Keller and J.H. Myers. 1971. *Microtus* population densities and soil nutrients in southern Indianna grasslands. Ecology. 52:660-663.

Krebs, C.J., B.L. Keller and R.H. Tamarin. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. Ecology. 50:587-607.

Krebs, C.J. and J.H. Myers. 1974. Population cycles in small mammals. Adv. in Ecol. Res. 8:267-399.

Krebs, C.J. and I. Wingate. 1976. Small mammal communities of the Kluane region, Yukon Territory. Can. Field-Nat. 90:379-389.

Krefting, L.W. and C.E. Ahlgren. 1974. Small mammal and vegetation changes after a fire in a mixed conifer - hardwood forest. Ecology. 55:1391-1398.

Kucera, E. and W.A. Fuller. 1978. A winter study of small rodents in aspen parkland. J. Mammal. 59:200-204.

Kverno, N.B. 1954. Development of better seed protectants. J. Forest. 52:826-827.

Larsson, T.B. 1975. Damage caused by small rodents in Sweden. Ecol. Bull. 19:47-55.

Larsson, T.B. and L. Hansson. 1977. Vole diet on experimentally managed afforestation areas in northern Sweden. Oikos. 28:242-249.

Lawrence, G.E. 1966. Ecology of vertebrate animals in relation to chapparal fire in the Sierra Nevada foothills. Ecology. 47:278-291.

Layne, J.N. 1954. The biology of the red squirrel *Tamiasciurus hudsonicus loquax* (Bangs) in central New York. Ecol. Monogr. 24:227-267.

Layne, J.N. 1968. Ontogeny. Pages 148-253 *in* J.A. King ed. Biology of *Peromyscus* (Rodentia). Am. Soc. Mammal. Spec. Publ. No. 2.

Lindlof, B., E. Lindstrom and A. Pearson. 1974. Nutrient content in relation to food preferred by mountain hare. J. Wildl. Manage. 38:875-879.

Lindsey, G.D., R.M. Anthony and J. Evans. 1974. Mestranol as a repellent to protect Douglas-fir seed from deer mice. Proc. Vert. Pest Conf. 6:272-279.

Linduska, J.P. 1950. Ecology and land-use relationships of small mammals on a Michigan farm. Michigan Department of Conservation. Game Division Publication, Lansing. Cited *in* Rusch and Reeder (1978).

Littlefield, E.W., W.J. Schoomaker and D.B. Cook. 1946. Field mouse damage to coniferous plantations. J. Forest. 44:745-749.

LoBue, J. and R.M. Darnell. 1959. Effect of habitat disturbance on a small mammal population. J. Mammal. 40:425-436.

Lovejoy, D.A. 1975. The effect of logging on small mammal populations in New England northern hardwoods. Univ. Conn., Occassional Papers, Biol. Sci. Series. 2:269-291.

Lutz, H.J. 1956. Damage to paper birch by red squirrels in Alaska. J. Forest. 54:31-33.

MacLulich, D.A. 1937. Fluctuations in the numbers of the varying hare *(Lepus americanus)*. Univ. Toronto Studies, Biol. Ser. No. 43. 136 p.

Martell, A.M. and A. Radvanyi. 1976. Changes in small mammal populations after clearcutting of northern Ontario black spruce forest. Can. Field-Nat. 91:41-46.

M'Closkey, R.T. 1975. Habitat succession and rodent distribution. J. Mammal. 56:950-955.

Merritt, J.F. and J.M. Merritt. 1978. Population ecology and energy relationships of *Clethrionomys gapperi* in a Colorado subalpine forest. J. Mammal. 59:576-598.

Meslow, E.C. and L.B. Keith. 1968. Demographic parameters of a snowshoe hare population. J. Wildl. Manage. 32:812-834.

Meslow, E.C. and L.B. Keith. 1971. A correlation analysis of weather versus snowshoe hare population parameters. J. Wildl. Manage. 35:1-15.

Millar, J.S. 1970a. Variations in fecundity of the red squirrel *Tamiasciurus hudsonicus* (Erxleben). Can. J. Zool. 48:1055-1058.

Millar, J.S. 1970b. The breeding season and reproductive cycle of the western red squirrel. Can. J. Zool. 48:471-473.

Miller, D.H. and L.L. Getz. 1972. Factors influencing the local distribution of the redback vole *Clethrionomys gapperi* in New England. Occas. Pap. Biol. Ser., Univ. Conn. 2:115-138.

Miller, D.H. and L.L. Getz. 1973. Factors influencing the local distribution of the redback vole in New England. II. vegetation cover, soil moisture, and debris cover. Occas. Pap. Biol. Ser., Univ. Conn. 2:159-180.

Miller, D.H. and L.L. Getz. 1977. Comparisons of population dynamics of *Peromyscus* and *Clethrionomys* in New England. J. Mammal. 58:1-16.

Miller, W.C. 1969. Ecological and ethological isolating mechanisms between *Microtus pennsylvanicus* and *Microtus ochrogaster* at Terre Haute, Indiana. Am. Midl. Nat. 82:140-148.

Modafferi, M.M. 1972. Aspects of reproductive biology of the red squirrel *(Tamiasciurus hudsonicus)* in interior Alaska. M.Sc. Thesis. Univ. of Alaska, College. 80 p.

Moore, A.W. 1940. Wild animal damage to seed and seedlings on cut-over Douglas fir lands of Oregon and Washington. U.S. Dept. Agric., Tech. Bull. No. 706. 28 p.

Morris, R.D. 1969. Competitive exclusion between *Microtus* and *Clethrionomys* in the aspen parkland of Saskatchewan. J. Mammal. 50:291-301.

Morris, R.D. 1970. The effects of endrin on *Microtus* and *Peromyscus*. I. Unenclosed field populations. Can. J. Zool. 48:695-708.

Morris, R.D. 1972. The effects of endrin on *Microtus* and *Peromyscus*. II. Enclosed field populations. Can. J. Zool. 50:885-896.

Morris, R.D. and P.R. Grant. 1972. Experimental studies of competitive interaction in a two-species system. J. Anim. Ecol. 41:275-290.

Moss, E.H. 1967. Flora of Alberta: a manual of flowering plants, conifers, ferns and fern allies found growing without cultivation in the Province of Alberta, Canada. Univ. Toronto Press, Toronto. 546 p.

Mossman, A.S. 1955. Light penetration in relation to small mammal abundance. J. Mammal. 36:564-566.

Murie, O.J. 1927. The Alaska red squirrel providing for the winter. J. Mammal. 8:37-40.

Myers, J.H. and C.J. Krebs. 1971a. Genetic, behavioural and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. Ecol. Monogr. 41:53-78.

Myers, J.H. and C.J. Krebs. 1971b. Sex ratios in open and enclosed vole populations: demographic implications. Am. Nat. 105:325-344.

Newson, J. 1964. Reproduction and prenatal mortality of snowshoe hares on Manitoulin Island, Ontario. Can. J. Zool. 42:987-1005.

Newson, R. and A. de Vos. 1964. Population structure and body weights of snowshoe hares on Manitoulin Island, Ontario. Can. J. Zool. 42:975-986.

Nodler, F.A. 1973. Food habits, vocalizations, and territoriality of Alaskan red squirrels. M.Sc. Thesis. Univ. of Alaska, College. 86 p.

Nord, E.C. 1965. Autecology of bitterbush in California. Ecol. Monogr. 35:307-334.

O'Farrell, T.P. 1965. Home range and ecology of snowshoe hares in interior Alaska. J. Mammal. 46:406-418.

Passof, P.C., R.E. Marsh and W.E. Howard. 1974. Alapha-naphthylthiourea as a conditioning repellent for protecting conifer seed. Proc. Vert. Pest Conf. 6:280-292.

Patric, E.F. 1962. Reproductive characteristics of red-backed mouse during years of differing population densities. J. Mammal. 43:200-205.

Petticrew, B.G. and R.M.F.S. Sadlier. 1974. The ecology of the deer mouse *Peromyscus maniculatus* in a coastal coniferous forest. I. Population dynamics. Can. J. Zool. 52:107-118.

Philip, C.B. 1939. A parasitological reconnaissance in Alaska with particular reference to varying hares. J. Mammal. 20:82-86.

Powell, R.A. 1972. A comparison of populations of boreal red-backed vole *(Clethrionomys gapperi)* in tornado blowdown and standing forest. Can. Field-Nat. 86:377-379.

Price, E. 1967. The effect of reproductive performance on the domestication of the prairie deer mouse. *Peromyscus maniculatus bairdii.* Evolution. 21:762-770.

Pruitt, W.O. Jr. 1957. Observations on the bioclimate of some taiga mammals. Arctic. 10:131-138.

Pruitt, W.O. Jr. and C.V. Lucier. 1958. Winter activity of red squirrels in interior Alaska. J. Mammal. 39:443-444.

Quick, H. 1964. Small mammal populations and ecological variations in an alpine watershed. Processed report to the U.S. Atomic Energy Comm. Cited *in* Merritt and Merritt (1978).

Radvanyi, A. 1970a. Small mammals and regeneration of white spruce forests in western Alberta. Ecology. 51:1102-1105.

Radvanyi, A. 1970b. A new coating treatment for coniferous seeds. Forest. Chron. 46:406-408.

Radvanyi, A. 1973. Seed loss to small mammals and birds. Pages 67-75 *in* J.H. Cayford, ed. Direct seeding symposium. Department of the Environment. Can. Forest Serv., Publ. No. 1339.

Radvanyi, A. 1974. Small mammal census and control on a hardwood plantation. Proc. Vert. Pest Conf. 6:9-19.

Radvanyi, A. 1976. Continued monitoring of the harmful small mammal problem in the Alberta oil sands reclamation and afforestation program. Progress Report. Fisheries and Environment Canada. Can. Wildl. Serv. 126 p.

Radvanyi, A. 1978. The return of the rodents -- year three in the assessment of harmful small mammals in the Alberta oil sands reclamation and afforestation program. Final Report. Fisheries and Environment Canada. Can. Wildl. Serv. 82 p.

Radwan, M.A. 1969. Protection of coniferous seeds from rodents. Pages 52-54 *in* H.C. Black, ed. Wildlife and reforestation in the Pacific northwest. School of Forestry, Oreg. State Univ., Corvallis.

Radwan, M.A. 1970. Destruction of conifer seed and methods of protection. Proc. Vert. Pest Conf. 4:77-82.

Redfield, J.A. 1976. Distribution, abundance, size, and genetic variation of *Peromyscus maniculatus* on the Gulf Islands of British Columbia. Can. J. Zool. 54:463-474.

Reige, D.A. 1976. Red squirrel ecology and coexistance with gray squirrels in northern Wisconsin mixed forests. M.Sc. Thesis. University of Wisconsin, Madison. 171 p.

Richens, V.B. 1974. Numbers and habitat affinities of small mammals in northwestern Maine. Can. Field-Nat. 88:191-196.

Rickard, W.H. 1960. Distribution of small mammals in relation to climax vegetation patterns in eastern Washington and northern Idaho. Ecology. 41:99-106.

Rolan, R.G. and H.T. Gier. 1967. Correlation of embryo and placental scar counts of *Peromyscus maniculatus* and *Microtus ochrogaster*. J. Mammal. 48:317-319.

Rowan, W. and L.B. Keith. 1956. Reproductive potential and sex ratios of snowshoe hares in northern Alberta. Can. J. Zool. 34:273-281.

Rowe, J.S. 1952. Squirrel damage to white spruce. Canada Department of Northern Affairs and National Resources. Div. Forest Research. Silviculture Leaflet No. 61. 2 p.

Rusch, D.A. and W.G. Reeder. 1978. Population ecology of Alberta red squirrels. Ecology. 59:400-420.

Sadlier, R.M.F.S. 1965. The relationship between agonistic behaviour and population changes in deer mice, *Peromyscus maniculatus* (Wagner). J. Anim. Ecol. 34:331-352.

Sadlier, R.M.F.S. 1974. The ecology of the deer mouse *Peromyscus maniculatus* in a coastal coniferous forest. II. reproduction. Can. J. Zool. 52:119-131.

Sadlier, R.M.F.S., K.D. Casperson and J. Harling. 1973. Intake and requirements of energy and protein for the breeding of wild deer mice, *Peromyscus maniculatus*. J. Reprod. Fert. Suppl. 19:237-252.

Sartz, R.S. 1970. Mouse damage to young plantations in southwestern Wisconsin. J. Forest. 68:88-89.

Schaffer, W.M. and R.H. Tamarin. 1973. Changing reproductive rates and population cycles in lemmings and voles. Evolution. 27:111-124.

Scheffer, T.H. 1924. Notes on breeding of *Peromyscus*. J. Mammal. 5:258-260.

Searing, G.F. 1975. Aggressive behaviour and population regulation of red squirrels *(Tamiasciurus hudsonicus)* in interior Alaska. M.Sc. Thesis. University of Alaska, College. 99 p.

Searing, G.F. 1979. Distribution, abundance and habitat associations of beaver, muskrat, mink and river otters in the AOSERP study area, northeastern Alberta. Prep. for the Alberta Oil Sands Environmental Research Program by LGL Limited, environmental research associates. LS 23.1.

Seton, E.T. 1909. Life histories of northern animals. Volume I. Charles Scribner's Sons. New York. Cited *in* Rusch and Reeder (1978).

Severaid, J.H. 1945. Breeding potential and artificial propagation of the snowshoe hare. J. Wildl. Manage. 9:290-295.

Sheppe, W. 1963. Population structure of the deer mouse *Peromyscus*, in the Pacific northwest. J. Mammal. 44:180-185.

Sheppe, W. 1967. Habitat restriction by competitive exclusion in the mice *Peromyscus* and *Mus*. Can. Field-Nat. 81:81-98.

Sims, H.P. and C.H. Buckner. 1973. The effect of clear-cutting and burning of *Pinus banksiana* forests on the populations of small mammals in southeastern Manitoba. Amer. Midl. Nat. 90:228-231.

Smith, C.C. 1968. The adaptive nature of social organization in the genus of three squirrels *Tamiasciurus*. Ecol. Monogr. 38:31-63.

Smith, C.C. 1970. The coevolution of pine squirrels *(Tamiasciurus)* and conifers. Ecol. Monogr. 40:349-371.

Smith, D.A. and J.B. Foster. 1957. Notes on small mammals of Churchill, Manitoba. J. Mammal. 38:98-115.

Smith, M.C. 1968. Red squirrel responses to spruce cone failure in interior Alaska. J. Wildl. Manage. 32:305-317.

Soper, J.D. 1942. Mammals of Wood Buffalo Park, northern Alberta and District of Mackenzie. J. Mammal. 23:119-145.

Spencer, D.A. 1954. Rodents and direct seeding. J. Forest. 52:824-826.

Spencer, A.W. and H.W. Steinhoff. 1968. An explanation of geographic variation in litter size. J. Mammal. 49:281-286.

Stebbins, L.L. 1976. Overwintering of the red-backed vole at Edmonton, Alberta, Canada. J. Mammal. 57:551-561.

Streubel, D.P. 1968. Food storing and related behaviour of red squirrels *(Tamiasciurus hudsonicus)* in interior Alaska. M.Sc. Thesis. Univ. of Alaska, College. 56 p.

Sullivan, T.P. 1977. Demography and dispersal in island and mainland populations of the deer mouse, *Peromyscus maniculatus*. Ecology. 58:964-978.

Sullivan, T.P. 1978a. Conifer seed predation by the deer mouse: a problem in reforestation. Ph.D. Thesis. Univ. of B.C., Vancouver. 181 p.

Sullivan, T.P. 1978b. Biological control of conifer seed damage by the deer mouse *(Peromyscus maniculatus)*. Proc. Vert. Pest Conf. 8:237-250.

Sullivan, T.P. 1978c. Lack of caching of direct-seeded Douglas fir seeds by deer mice. Can. J. Zool. 56:1214-1216.

Svihla, A. 1930. Breeding habits and young of the red-backed mouse, *Evotomys*. Papers Mich. Acad. Sci., Arts and Letters 11:485-490. Cited *in* Banfield (1977).

Svihla, A. 1932. A comparative life history study of mice of the genus *Peromyscus*. Misc. Publ. Mus. Zool. Univ. Mich. 24:1-39. Cited *in* Beer *et al.* (1957).

Taitt, M. 1978. The dynamics of *Peromyscus maniculatus austerus* and *Microtus townsendii* with supplementary food. Ph.D. Thesis. Univ. of B.C., Vancouver. 162 p.

Tamarin, R.H. 1977. Demography of the beach vole *(Microtus breweri)* and the meadow vole *(Microtus pennsylvanicus)* in southeastern Massachusetts. Ecology. 58:1310-1321.

Telfer, E.S. 1972. Browse selection by deer and hares. J. Wildl. Manage. 36:1344-1349.

Terman, C.R. 1968. Population dynamics. Pages 412-450 *in* J.A. King ed., Biology of *Peromyscus* (Rodentia). Am. Soc. Mammal., Spec. Publ. No. 2.

Terman, C.R. and J.F. Sassaman. 1967. Sex ratio in deer mouse populations. J. Mammal. 48:589-597.

Tevis, L. 1956a. Responses of small mammal populations to logging of Douglas fir. J. Mammal. 37:189-196.

Tevis, L. 1956b. Effect of a slash burn on forest mice. J. Wildl. Manage. 20:405-409.

Thompson, D.Q. 1965. Food preferences of the meadow vole *(Microtus pennsylvanicus)* in relation to habitat affinities. Am. Midl. Nat. 74:76-85.

Todd, A. 1976. Analysis of fur production records for registered traplines in the AOSERP area, 1970-75. Unpubl. Rep., Alberta Recreation, Parks and Wildlife, Fish and Wildl. Div., Edmonton. 15 p.

Townsend, M.T. 1935. Studies on some of the small mammals of central New York. Rossevelt Wildl. Ann. No. 4. Cited *in* Innes (1978).

Trapp, G.R. 1962. Snowshoe hares in Alaska. II. home range and ecology during an early population increase. M.Sc. Thesis. University of Alaska, College. 137 p.

Turner, B.N. and S.L. Iverson. 1973. The annual cycle of aggression in male *Microtus pennsylvanicus* and its relation to population parameters. Ecology. 54:967-981.

Turner, B.N., M.P. Perrin and S.L. Iverson. 1975. Winter coexistance of voles in spruce forest: relevance of seasonal changes in aggression. Can. J. Zool. 53:1004-1011.

Vaughan, T.A. 1969. Reproduction and population densities in a montane small mammal fauna. Univ. Kansas. Mus. Hist. Misc. Publ. 51:51-74.

Verts, B.J. 1957. The population and distribution of two species of *Peromyscus* on some Illinois strip-mined land. J. Mammal. 38:53-59.

Von Althen, F.W. 1971. Mouse damage in an 8-year old plantation. Forest. Chron. 47:160-161.

Wagg, J.W.B. 1963. Notes on the food habits of small mammals of the white spruce forest. Forestry Chronicle 39:436-445.

Webb, W.L. 1937. Notes on the sex ratio of the snowshoe rabbit. J. Mammal. 18:343-347.

Wecker, S.C. 1963. The role of early experience in habitat selection by the prairie deer mouse *Peromyscus maniculatus bairdii*. Ecol. Monogr. 33:307-325.

West, S.D. 1977. Mid-winter aggregation in the northern red-backed vole, *Clethrionomys rutilus*. Can. J. Zool. 55(9):1404-1409.

Westworth, D.A. and D.L. Skinner. 1978. A study of small mammal populations on Syncrude Lease No. 17. Prep. for Syncrude Canada Ltd. by D.A. Westworth and Associates, environmental analysts. 57 p.

Whitaker, J.O. Jr. 1962. *Endogone, Hymenogaster* and *Melanogaster* as small mammal foods. Amer. Midl. Nat. 67:152-156.

Whitaker, J.O. Jr. 1966. Food of *Mus musculus, Peromysus maniculatus bairdii* and *Peromyscus leucopus* in Vigo county, Indiana. J. Mammal. 47:473-486.

Williams, A.B. 1936. Composition and dynamics of a beech-maple climax community. Ecol. Monogr. 4:318-408.

Williams, O. 1955. Distribution of mice and shrews in a Colorado montane forest. J. Mammal. 36:221-231.

Williams, O. 1959. Food habits of deer mice. J. Mammal. 40:415-419.

Williams, O. and B.A. Finney. 1964. *Endogone* - food for mice. J. Mammal. 45:265-271.

Windberg, L.A. and L.B. Keith. 1976. Snowshoe hare population response to artificial high densities. J. Mammal. 57:523-553.

Windberg, L.A. and L.B. Keith. 1978. Snowshoe hare populations in woodlot habitat. Can. J. Zool. 56:1071-1080.

Wirtz, W.O. II. and P.G. Pearson. 1960. A preliminary analysis of habitat orientation in *Microtus* and *Pennsylvanicus*. Am. Midl. Nat. 63:131-142.

Wolff, J.O. 1978. Food habits of snowshoe hares in interior Alaska. J. Wildl. Manage. 42:148-153.

Wood, T.J. 1967. Ecology and population dynamics of the red squirrel *(Tamiasciurus hudsonicus)* in Wood Buffalo National Park. M.Sc. Thesis. Univ. of Saskatchewan, Saskatoon. 97 p.

Wood, T.J. and S.A. Munroe. 1977. Dynamics of snowshoe hare populations in the Maritime provinces. Canadian Wildlife Service. Occassional Paper No. 30. 19 p.

Wrigley, R.E. 1969. Ecological notes on the mammals of southern Quebec. Can. Field-Nat. 83:201-211.

Zemanek, M. 1972. Food and feeding habits of rodents in a deciduous forest. Acta Theriol. 17:315-325.

Zimmerman, E.G. 1965. A comparison of habitat and food of two species of *Microtus*. J. Mammal. 46:605-612.

Zirul, D.L. 1970. Ecology of a northern population of the red squirrel, *Tamiasciurus hudsonicus preblei* (Howell). M.Sc. Thesis. Univ. of Alberta, Edmonton. 131 p.

9. APPENDIX

9.1 SCIENTIFIC NAMES AND COMMON NAMES OF PLANTS

Common names of most plants (when provided in the cited reference) were used throughout the text to enhance readability. Common names (as given in the cited reference) and scientific equivalents are provided in this Appendix.

Scientific Name	Common Name
Abies	fir
Abies amabilis	Pacific silver fir
Abies balsamea	balsam fir
Abies lasiocarpa	alpine fir
Acer spp.	maple
Acer glabrum	dwarf maple
Acer circinatum	vine maple
Acer spicatum	mountain maple
Achillea millefolium	common yarrow
Agropyron repens	quack grass
Agropyron trachycaulum	slender wheat grass
Alnus spp.	alder
Alopecurus aequalis	short-awn fox tail
Arctostaphylos uva-ursi	common bearberry
Arnica spp.	arnica
Artemisia spp.	sagebrush
Avena spp.	oats
Balsamorhiza sagittata	balsam-root
Betula spp.	birch
Betula alleghaniensis	yellow birch
Bromus spp.	brome grass
Bromus marginatus	smooth brome grass (brome grass)

Scientific Name	Common Name
Carex spp.	sedge
Corylus spp.	hazelnut (hazel)
Commandra pallida	bastard toad flax
Dactylis glomerata	orchard grass
Dryas drummondi	yellow dryad
Elaeagnus spp.	silverberry
Epilobium spp.	fireweed
Equisetum spp.	horsetails
Fagus grandifolia	beech
Fragaria virginiana	wild strawberry
Fraxinus spp.	ash
Fraxinus lanceolata	green ash
Hordeum spp.	barley
Koeleria cristata	junegrass
Larix decidua	European larch
Larix laricina	larch
Linum spp.	flax
Liriodendron tulipfera	yellow poplar
Maclura pemifera	osage-orange
Malus spp.	crab apple
Medicago spp.	alfalfa
Medicago sativa	medick
Melilotus alba	white clover
Muhlenbergia sobolifera	muhly grass
Ostrya spp.	ironwood
Panicum capillare	witch grass
Phalaris arundinacea	reed canary grass
Phleum pratense	common timothy
Picea abies	Norway spruce
Picea glauca	white spruce
Picea mariana	black spruce

Scientific Name	Common Name
Picea pungens	blue spruce
Pinus spp.	pine
Pinus banksiana	jack pine
Pinus contorta	lodgepole pine
Pinus engelmanii	Engelmann spruce
Pinus flexilis	limber pine
Pinus nigra	austrian pine
Pinus ponderosa	ponderosa pine
Pinus resinosa	red pine
Pinus strobus	white pine
Pinus sylvestris	Scotch pine
Plantago lanceolata	English plaintain or rib grass
Plantanus occidentalis	American sycamore
Poa spp.	bluegrass
Poa compressa	Canada blue grass
Poa pratensis	Kentucky blue grass
Populus deltoides	cottonwood
Populus tremuloides	trembling aspen
Prunus virginiana	chokecherry
Pseudotsuga menziesii	Douglas fir
Quercus macrocarpa	bur oak
Quercus rubra	northern oak
Rosa woodsii	wild rose
Rubus strigosus	raspberry
Rubus urisinus	blackberries
Salix spp.	willow
Shepherdia canadensis	Canadian buffalo-berry
Sphagnum	moss
Spiraea lucida	white spirea
Taraxacum spp.	dandelion
Thuja occidentalis	white cedar

Scientific Name	Common Name
Thuja plicata	western red cedar
Trifolium pratense	red clover
Triticum aestivum	common wheat
Tsuja spp.	hemlock
Ulmus spp.	elm
Viburnum alnifolium	hobblebush
Viburnum trilobum	high-bush cranberry
Vaccinium spp.	blueberry
Vaccinium vitis-idaea	bog cranberry (cow-berry)

10. AOSERP RESEARCH REPORTS

1.		AOSERP First Annual Report, 1975
2.	AF 4.1.1	Walleye and Goldeye Fisheries Investigations in the Peace-Athabasca Delta--1975
3.	HE 1.1.1	Structure of a Traditional Baseline Data System
4.	VE 2.2	A Preliminary Vegetation Survey of the Alberta Oil Sands Environmental Research Program Study Area
5.	HY 3.1	The Evaluation of Wastewaters from an Oil Sand Extraction Plant
6.		Housing for the North--The Stackwall System
7.	AF 3.1.1	A Synopsis of the Physical and Biological Limnology and Fisheries Programs whithin the Alberta Oil Sands Area
8.	AF 1.2.1	The Impact of Saline Waters upon Freshwater Biota (A Literature Review and Bibliography)
9.	ME 3.3	Preliminary Investigations into the Magnitude of Fog Occurrence and Associated Problems in the Oil Sands Area
10.	HE 2.1	Development of a Research Design Related to Archaeological Studies in the Athabasca Oil Sands Area
11.	AF 2.2.1	Life Cycles of Some Common Aquatic Insects of the Athabasca River, Alberta
12.	ME 1.7	Very High Resolution Meteorological Satellite Study of Oil Sands Weather: "A Feasibility Study"
13.	ME 2.3.1	Plume Dispersion Measurements from an Oil Sands Extraction Plant, March 1976
14.		
15.	ME 3.4	A Climatology of Low Level Air Trajectories in the Alberta Oil Sands Area
16.	ME 1.6	The Feasibility of a Weather Radar near Fort McMurray, Alberta
17.	AF 2.1.1	A Survey of Baseline Levels of Contaminants in Aquatic Biota of the AOSERP Study Area
18.	HY 1.1	Interim Compilation of Stream Gauging Data to December 1976 for the Alberta Oil Sands Environmental Research Program
19.	ME 4.1	Calculations of Annual Averaged Sulphur Dioxide Concentrations at Ground Level in the AOSERP Study Area
20.	HY 3.1.1	Characterization of Organic Constituents in Waters and Wastewaters of the Athabasca Oil Sands Mining Area
21.		AOSERP Second Annual Report, 1976-77
22.		Alberta Oil Sands Environmental Research Program Interim Report to 1978 covering the period April 1975 to November 1978
23.	AF 1.1.2	Acute Lethality of Mine Depressurization Water on Trout Perch and Rainbow Trout
24.	ME 1.5.2	Air System Winter Field Study in the AOSERP Study Area, February 1977.
25.	ME 3.5.1	Review of Pollutant Transformation Processes Relevant to the Alberta Oil Sands Area

26.	AF 4.5.1	Interim Report on an Intensive Study of the Fish Fauna of the Muskeg River Watershed of Northeastern Alberta
27.	ME 1.5.1	Meteorology and Air Quality Winter Field Study in the AOSERP Study Area, March 1976
28.	VE 2.1	Interim Report on a Soils Inventory in the Athabasca Oil Sands Area
29.	ME 2.2	An Inventory System for Atmospheric Emissions in the AOSERP Study Area
30.	ME 2.1	Ambient Air Quality in the AOSERP Study Area, 1977
31.	VE 2.3	Ecological Habitat Mapping of the AOSERP Study Area: Phase I
32.		AOSERP Third Annual Report, 1977-78
33.	TF 1.2	Relationships Between Habitats, Forages, and Carrying Capacity of Moose Range in northern Alberta. Part I: Moose Preferences for Habitat Strata and Forages.
34.	HY 2.4	Heavy Metals in Bottom Sediments of the Mainstem Athabasca River System in the AOSERP Study Area
35.	AF 4.9.1	The Effects of Sedimentation on the Aquatic Biota
36.	AF 4.8.1	Fall Fisheries Investigations in the Athabasca and Clearwater Rivers Upstream of Fort McMurray: Volume I
37.	HE 2.2.2	Community Studies: Fort McMurray, Anzac, Fort MacKay
38.	VE 7.1.1	Techniques for the Control of Small Mammals: A Review
39.	ME 1.0	The Climatology of the Alberta Oil Sands Environmental Research Program Study Area
40.	WS 3.3	Mixing Characteristics of the Athabasca River below Fort McMurray - Winter Conditions
41.	AF 3.5.1	Acute and Chronic Toxicity of Vanadium to Fish
42.	TF 1.1.4	Analysis of Fur Production Records for Registered Traplines in the AOSERP Study Area, 1970-75
43.	TF 6.1	A Socioeconomic Evaluation of the Recreational Fish and Wildlife Resources in Alberta, with Particular Reference to the AOSERP Study Area. Volume I: Summary and Conclusions
44.	VE 3.1	Interim Report on Symptomology and Threshold Levels of Air Pollutant Injury to Vegetation, 1975 to 1978
45.	VE 3.3	Interim Report on Physiology and Mechanisms of Air-Borne Pollutant Injury to Vegetation, 1975 to 1978
46.	VE 3.4	Interim Report on Ecological Benchmarking and Biomonitoring for Detection of Air-Borne Pollutant Effects on Vegetation and Soils, 1975 to 1978.
47.	TF 1.1.1	A Visibility Bias Model for Aerial Surveys for Moose on the AOSERP Study Area
48.	HG 1.1	Interim Report on a Hydrogeological Investigation of the Muskeg River Basin, Alberta
49.	WS 1.3.3	The Ecology of Macrobenthic Invertebrate Communities in Hartley Creek, Northeastern Alberta
50.	ME 3.6	Literature Review on Pollution Deposition Processes
51.	HY 1.3	Interim Compilation of 1976 Suspended Sediment Date in the AOSERP Study Area
52.	ME 2.3.2	Plume Dispersion Measurements from an Oil Sands Extraction Plan, June 1977

53.	HY 3.1.2	Baseline States of Organic Constituents in the Athabasca River System Upstream of Fort McMurray
54.	WS 2.3	A Preliminary Study of Chemical and Microbial Characteristics of the Athabasca River in the Athabasca Oil Sands Area of Northeastern Alberta
55.	HY 2.6	Microbial Populations in the Athabasca River
56.	AF 3.2.1	The Acute Toxicity of Saline Groundwater and of Vanadium to Fish and Aquatic Invertebrates
57.	LS 2.3.1	Ecological Habitat Mapping of the AOSERP Study Area (Supplement): Phase I
58.	AF 2.0.2	Interim Report on Ecological Studies on the Lower Trophic Levels of Muskeg Rivers Within the Alberta Oil Sands Environmental Research Program Study Area
59.	TF 3.1	Semi-Aquatic Mammals: Annotated Bibliography
60.	WS 1.1.1	Synthesis of Surface Water Hydrology
61.	AF 4.5.2	An Intensive Study of the Fish Fauna of the Steepbank River Watershed of Northeastern Alberta
62.	TF 5.1	Amphibians and Reptiles in the AOSERP Study Area
63.	ME 3.8.3	Analysis of AOSERP Plume Sigma Data
64.	LS 21.6.1	A Review of the Baseline Data Relevant to the Impacts of Oil Sands Development on Large Mammals in the AOSERP Study Area
65.	LS 21.6.2	A Review of the Baseline Data Relevant to the Impacts of Oil Sands Development on Black Bears in the AOSERP Study Area
66.	AS 4.3.2	An Assessment of the Models LIRAQ and ADPIC for Application to the Athabasca Oil Sands Area
67.	WS 1.3.2	Aquatic Biological Investigations of the Muskeg River Watershed
68.	AS 1.5.3 AS 3.5.2	Air System Summer Field Study in the AOSERP Study Area, June 1977
69.	HS 40.1	Native Employment Patterns in Alberta's Athabasca Oil Sands Region
70.	LS 28.1.2	An Interim Report on the Insectivorous Animals in the AOSERP Study Area
71.	HY 2.2	Lake Acidification Potential in the Alberta Oil Sands Environmental Research Program Study Area
72.	LS 7.1.2	The Ecology of Five Major Species of Small Mammals in the AOSERP Study Area: A Review
73.	LS 23.2	Distribution, Abundance and Habitat Associations of Beavers, Muskrats, Mink and River Otters in the AOSERP Study Area, Northeastern Alberta
74.	AS 4.5	Air Quality Modelling and User Needs
75.	WS 1.3.4	Interim Report on a Comparative Study of Benthic Algal Primary Productivity in the AOSERP Study Area
76.	AF 4.5.1	An Intensive Study of the Fish Fauna of the Muskeg River Watershed of Northeastern Alberta
77.	HS 20.1	Overview of Local Economic Development in the Athabasca Oil Sands Region Since 1961.
78.	LS 22.1.1	Habitat Relationships and Management of Terrestrial Birds in Northeastern Alberta

79.	AF 3.6.1	The Multiple Toxicity of Vanadium, Nickel, and Phenol to Fish.
80.	LS 22.3.1	Biology and Management of Peregrin Falcons (*Falco peregrinus anatum*) in Northeastern Alberta.
81.	LS 22.1.2	Species Distribution and Habitat Relationships of Waterfowl in Northeastern Alberta.
82.	LS 22.2	Breeding Distribution and Behaviour of the White Pelican in the Athabasca Oil Sands Area.
83.	LS 22.2	The Distribution, Foraging Behaviour, and Allied Activities of the White Pelican in the Athabasca Oil Sands Area.
84.	WS 1.6.1	Investigations of the Spring Spawning Fish Populations in the Athabasca and Clearwater Rivers Upstream from Fort McMurray; Volume I.
85.	HY 2.5	An intensive Surface Water Quality Study of the Muskeg River Watershed. Volume I: Water Chemistry.
86.	AS 3.7	An Observational Study of Fog in the AOSERP Study Area.
87.	WS 2.2	Hydrogeological Investigation of Muskeg River Basin, Alberta

These reports are not available upon request. For further information about availability and location of depositories, please contact:

Alberta Oil Sands Environmental Research Program
15th Floor, Oxbridge Place
9820 - 106 Street
Edmonton, Alberta
T5K 2J6