National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

Canada

UNIVERSITY OF ALBERTA

PORCUPINE POPULATIONS AND WINTER FEEDING DAMAGE IN THINNED AND UNTHINNED SECOND-GROWTH STANDS

BY

John Andrew Krebs

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of

the requirements for the degree of MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

Edmonton, Alberta

SPRING 1994

National Library
of Canada

Bibliothèque nationale
du Canada

Acquisitions and
Bibliographic Services Branch

Direction des acquisitions et
des services bibliographiques

395 Wellington Street
Ottawa, Ontario
K1A 0N4

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

ISBN 0-612-11263-2

Canada

UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR: John Andrew Krebs

TITLE OF THESIS: Porcupine Populations and Winter Feeding Damage in Thinned and Unthinned Second-Growth Stands

DEGREE: Master of Science (M.Sc.)

YEAR THIS DEGREE GRANTED: Spring 1994

John Krebs

John Andrew Krebs

Department of Zoology
University of Alberta
Edmonton, Alberta
CANADA, T6G 2E9

April 19, 1994

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled PORCUPINE POPULATIONS AND WINTER FEEDING DAMAGE IN THINNED AND UNTHINNED SECOND-GROWTH STANDS submitted by JOHN ANDREW KREBS in partial fulfillment of the requirements for the degree of Master of Science.

Dr Stan A. Boutin

Dr Susan J. Hannon

Mark R.T. Dale

Dr Mark R.T. Dale

Jan O Murie

Dr Jan O. Murie

April 12, 1994

ABSTRACT

Incidence of winter feeding damage and density, survival, movements and feeding preferences of porcupines (*Erethizon dorsatum*) were examined in thinned and unthinned (control) second-growth stands of mixed western hemlock (*Tsuga heterophylla*) and amabilis fir (*Abies amabilis*) in northwestern British Columbia from May 1989 to May 1991. The stands examined were naturally regenerated after clearcut logging and were 28 - 34 years old at the time of the study. I sought to test the prediction that porcupine feeding damage and population density are positively affected by stand thinning.

Annual rates of damage and stem girdling to western hemlock were significantly greater in thinned stands (damage: 8.4%; girdling: 2.7%) than controls (damage: 5.2%; girdling: 1.5%). Damage and girdling rates to amablis fir were lower and did not vary between treatments. Frequency of tree mortality did not differ significantly between treatments but tended to be greater in controls, possibly due to reduced live crown lengths of trees in those stands. Porcupine damage reduced two-year diameter growth of hemlock trees, especially those in control stands.

Based on tallies of 1803 trees, porcupines preferred western hemlock over amabilis fir, large diameter trees over small diameter trees, and previously damaged trees over undamaged trees. Preferences did not vary between treatments. Species preference was not related to diameter growth, as rates did not differ between species and damage rates did. Within species however, diameter preferences may have reflected a preference for faster-growing trees, as growth was positively related to diameter.

The amount of feeding in individual western hemlock trees varied over 3 orders of magnitude (0.003 to > 3.0 m^2), but was significantly greater (1.3 to 2.0 times) in thinned stands than in controls, after controlling for tree diameter. These data suggest an inverse relationship between tree density and degree of use of feeding trees. The distribution of damage within trees was non-random. Porcupines removed the greatest amount of bark from the middle third of feeding trees and this pattern did not vary between treatments.

Repeated censuses of porcupines within one thinned and one control site yielded identical density estimates (9 porcupines km^{-2}) using a maximum likelihood closed population estimator.

Winter survival rates of 42 radio-collared porcupines were significantly lower than summer rates in both years but did not vary between years or sexes. The most common cause of death for adult porcupine was predation by wolverine and to a lesser extent, coyote. Using a life table approach, incorporating the annual survival rates obtained in this study, I illustrate that porcupine populations are likely decreasing within the study area.

Home range sizes tended to be larger in the thinned site and larger for males than females; however differences were not statistically significant. Daily movement distances in winter did not vary between stand types or in relation to foot sinking depth.

I examined feeding behaviour of 12 porcupines by snow tracking. Porcupines in the thinned site fed on a greater number of tree species, used foliage more often and bark less often than their control site counterparts. For bark feeding, western hemlock was the most commonly consumed species within both sites, while foliage feeding primarily occurred in amabilis fir and sitka spruce (*Picea sitchensis*). Repeated use of trees was more frequent in the thinned than control site.

I conclude that stand thinning may result in increased damage rates but this was not due to a numerical response by porcupines. Projections of current girdling rates into the future suggest thinned sites will become non-merchantable in 17 - 32 years.

In the future, stand thinning should be directed at the densest stands (>5000 stems/ha.) and should favour amabilis fir as crop trees. The preferential use of previously damaged trees by porcupines suggests leaving these "sacrifice trees" to deflect damage away from undamaged crop trees. Additional information is needed on juvenile production and mortality as well as predator activity from a cross-section of stand ages to assess wheter porcupine populations are undergoing a widespread decline or decreasing locally due to improved habitat suitability for predators associated with stand aging.

ACKNOWLEDGEMENTS

I am grateful to Tom Sullivan for providing me with the opportunity to undertake this project. Many people assisted me in the field; Andrea Lawson, Martin Geertsema, Martin Sterner, Ken Cripps, Richard Biel and last but certainly not least, Jeff Shatford. Field work was not always pleasant, and I truly appreciate their efforts.

Stan Boutin, Walt Klenner, Tom Sullivan and Jim Pojar all contributed their time to review my initial proposals and to field review the progress of my project.

Many people assisted me with advice and discussions during the write-up stage of this project. Stan Boutin, Rich Moses and my father, Charley Krebs, each red-inked various drafts and identified weakness in the various chapters. Rich Moses and Faye Smith graciously allowed me to use their vehicles and board at their house at various times. I thank my supervisory committee; Drs Stan Boutin, Susan Hannon and Mark Dale for their suggestions and patience throughout my graduate program.

Financial Support was provided through a contract with the B.C. Ministry of Forests, South Moresby Replacement Fund, a BAR grant from the Circumpolar Institute at the University of Alberta and through Skeena Cellulose Inc.

Thanks also goes to my family and children (Bryce, Theo, Stephanie) who tolerated my frequent absences and unknowingly provided much needed inspiration and a touch of reality throughout my endeavor. I thank both my parents for fostering my interest and curiousity in the great outdoors. Finally, to my partner and two-thirds soul mate, Pat Wray, I am wholly thankful of the support and love you have given me through good and bad times.

TABLE OF CONTENTS

CHAPTER **PAGE**

2 WINTER FEEDING BY PORCUPINES IN THINNED AND UNTHINNED SECOND GROWTH STANDS

3 INFLUENCE OF STAND THINNING ON DENSITY, SURVIVAL, MOVEMENTS AND FEEDING BEHAVIOUR OF PORCUPINES

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

CHAPTER 1

GENERAL INTRODUCTION

Plant-herbivore interactions have attracted considerable interest from ecologists and land managers. Feeding by herbivores can dramatically influence plant communities (Crawley 1983), and conversely, plant density and nutritional quality influence herbivore demography and functional response (Cole and Batzli 1979; Batzli et al. 1981). In a study on the effects of vole (*Microtus pennsylvanicus*) density and population fluctuations on seedling survival and recruitment in the eastern U.S., Ostfeld and Canham (1993) suggest that peak populations of voles can delay succession, create habitat patchiness and alter relative abundances of invading tree species through their choice of palatable plants. These authors viewed the population dynamics of voles as a "keystone process" in old-field succession. Land managers are becoming increasingly aware of the dynamic relationship between plant and herbivore communities and are now attempting to develop more realistic management policies reflecting this awareness.

In British Columbia, much crown land is managed for timber production. Until recently, management emphasis was on maximizing rates of tree growth, assuming no interaction with herbivores. The long (80 year) rotation period between seedling establishment and harvest suggests that even a small percentage of annual damage (i.e. <1%) could dramatically affect stand structure, density and timber volume at harvest (Sullivan and Cheng 1989). It is becoming increasingly obvious that many herbivores have the potential to adversely affect timber production: e.g. (voles (*Microtus spp.*; Bucyanayandi et al. 1990, Sullivan 1993); red squirrels (*Tamiascirus hudsonicus*; Sullivan et al. 1993); porcupines (*Erethizon dorsatum*; Sullivan et al. 1986); bears (*Ursus spp.*; Sullivan 1991; black-tailed deer (*Odocoileus hemionus columbianus*; T.P. Sullivan, *personal communication*). All these problems have reinforced the need for herbivores to be considered in forest land management decisions.

Winter feeding by porcupines on coniferous trees has been identified as a threat to tree survival and growth in Minnesota (scotch pine, *Pinus sylvestris*; Rudolf 1949), Oregon (Ponderosa pine *Pinus ponderosa*; Storm and Halvorson 1967), Utah (lodgepole pine *Pinus contorta*; Daniel and Barnes 1958), Idaho (ponderosa pine; Curtis and Wilson 1953) and more recently, in northwestern British Columbia and southeast Alaska (western hemlock, sitka spruce; Sullivan et al. 1986; MacHutcheon 1990; Eglitis and Hennon 1986). Porcupines strip off the outer bark to feed on the underlying cambium and phloem tissues (Dodge 1982). Partially-girdled trees may show reduced growth, while stem girdling causes death of the tree above the point of injury (Storm and Halvorson 1967). Annual rate of new (current year only) and cumulative (i.e. total to date of assessment) damage for unthinned stands in the Khuzymateen Inlet was 5.1% and 52.7% respectively in 1984-85 (Sullivan et al. 1986) and for thinned stands in southeast Alaska was reported to be 9.5% and 41.1% respectively in 1985-86 (Eglitis and Hennon 1986). Although no studies have clearly established the factors influencing the presence or absence of porcupine damage within a particular second-growth stand, it is clear that, at least locally, porcupine damage has the potential to influence tree survival and growth, and therefore stand structure.

Manipulation of stand density is a key component of current forest management. Intensive forestry practices such as stand thinning that concentrate growth on relatively few stems, may predispose stands to damage (Sullivan and Cheng 1989), since improved growth and vigour of trees in thinned stands yield larger annual amounts of carbohydrate-rich cambium and phloem tissues (Bannan 1955; Grillos and Smith 1959). In addition, because larger (dominant) trees within young stands tend to have higher growth rates (Kozlowski 1971), these trees may be preferentially selected by porcupines. Although numerous studies have reported porcupines preference for larger, faster growing trees within individual forest stands (Daniel and Barnes 1958; Spencer 1964; Storm and Halvorson 1967, Harder 1979; Sullivan et al. 1986), the prediction that thinning increases porcupine feeding damage rates and population density has not been tested. An appraisal of these parameters in thinned and unthinned (control) stands is required to enable managers to determine appropriate strategies for managing young second-growth stands in northwestern British Columbia. The presence of thinned and unthinned stands of similar disturbance history in the Kalum Valley near Terrace, B.C. provides an excellent opportunity for obtaining such information.

In this thesis, I test the prediction that porcupine feeding damage and population density are positively associated with stand thinning. Examining damage rates and porcupine density simultaneously in the two treatments will allow me to separate differences in damage rates due to numerical response of porcupines from differences resulting from reduced per hectare availability of trees (and no difference in porcupine density). In Chapter 2, I examine the relationship between stand thinning and porcupine damage rates, tree growth and mortality. Factors influencing the selection of feeding trees are also examined. In Chapter 3, I investigate the influence of stand thinning on porcupine density, survival, movements and feeding behaviour. I conclude by discussing my results and their implications for forest management, and identify future research needs.

LITERATURE CITED

Bannan, M.W. 1955. The vascular cambium and radial growth in Thuja occidentalis L. Can. J. Bot. 33:113-138.

Batzli, G.O., Jung, H.G., and Guntespergen, G. 1981. Nutritional ecology of microtine rodents: linear forage-rate curves for brown lemmings. Oikos 37:112-116.

Bucyanayandi, J., J. Bergeron, and J. Menual. 1990. Preference of meadow voles (Microtus pennsyvanicus) for conifer seedlings: chemical components and nutritional quality of bark of damaged and undamaged trees. J. Chem. Ecol. 16: 2569-2579.

Cole, F.R., and G.O. Batzli. 1979. Nutrition and population dynamics of the prairie vole, *Microtus ochrogaster*, in central Illinois. J. Anim. Ecol. 48:455-470.

Crawley, M.J. 1983. Herbivory: The dynamics of Animal-plant interactions. Studies in Ecology Volume 10, Blackwell Scientific Publications. 437pp.

Curtis, J.D., and A.K. Wilson. 1953. Porcupine feeding on ponderosa pine in central Idaho. J. For. 51: 339-341.

Daniel, T.W., and G.H. Barnes. 1958. Thinning a young stand of lodgepole pine. Proc. Soc. Amer. For. pp. 159-163.

Dodge, W.E. 1982. Porcupine. In: Wild Mammals of N.A. Biology, Management and Economics. J.A. Chapman and G.E. Feldhammer (editors). Johns Hopkins University Press, Baltimore, MD. pp 355-366.

Elgitis, A. and P.E. Hennon. 1986. Porcupine damage in Sitka spruce and western hemlock in southeast Alaska. USDA Forest Service Pest Management report, Juneau. 21pp.

Grillos, S.J., and F.H. Smith. 1959. The secondary phloem of Douglas fir. For. Sci. 5:377-388.

Harder, L.D. 1979. Winter feeding by porcupines in montane forests of southern Alberta. Can. Field Nat. 93:405-410.

Kozlowski, T.T. 1971. The Growth and Development of Trees. Academic Press, New York.

MacHutcheon, A. G. 1990. Porcupine feeding damage in second-growth stands of the North Coast Forest District, B.C.: A Summary. B.C. Ministry of Forests, Smithers B.C. 76pp.

Ostfeld, R. S. and C.D. Canham. 1993. Effects of meadow vole population density on tree seedling survival in old fields. Ecology 74: 1792-1801.

Rudolf, P.O. 1949. Pocupine's preference in pine plantations. J. For. 47:207-209.

Spencer, D.A. 1964. Porcupine population fluctuations in past centuries revealed by dendrochronology. J. Appl. Ecol. 1:127-149.

Storm, G.L., and C.H. Halvorsen. 1967. Effect of injury by porcupines on radial growth of ponderosa pine. J. For. 65:740-743.

Sullivan, T.P. 1991. Impact of feeding damage by bears on managed forests of western hemlock-western red cedar in mid-coastal British Columbia. Unpublished manuscript. 25pp.

Sullivan, T.P. 1993. Population dynamics of voles and control of damage in the Prince Rupert Region. Final Report. B.C. Ministry of Forests, Smithers, B.C. 21pp.

Sullivan, T.P., and C. Cheng. 1989. Impact of Porcupine Feeding damage on intensive forest management in the Prince Rupert Forest Region: Problem Analysis. FRDA Report No. 083. 20pp.

Sullivan, T.P.,W.T. Jackson, J. Pojar, and A. Banner. 1986. Impact of feeding damage by the porcupine on western hemlock - Sitka spruce forests of north coastal British Columbia. Can. J. For. Res. 16:642-647.

Sullivan, T.P., and W.E. Klenner. 1993. Influence of diversionary food on red squirrel populations and damage to crop trees in young lodgepole pine forest. Ecol. Appl. 3: 708-718.

Sullivan, T.P., J.A. Krebs, and P. Diggle. 1993. Prediction of stand susceptibility to feeding damage by red squirrels in young lodgepole pine. Can. J. For. Res. *in press*.

Sullivan, T.P. and D. S. Sullivan. 1982. Influence of fertilization on feeding attacks to lodgepole pine by snowshoe hares and red squirrels. For. Chron. 58: 263-266.

Sullivan, T.P. and A. Vyse. 1987. Impact of red squirrel feeding damage on spaced stands of lodgepole pine in the Cariboo region of British Columbia. Can J. For. Res. 17: 666-674.

CHAPTER 2

WINTER FEEDING BY PORCUPINES IN THINNED AND UNTHINNED SECOND-GROWTH STANDS

INTRODUCTION

The second-growth forests of the Kalum Valley and elsewhere in northwestern British Columbia are currently being intensively managed for timber production. For dense, young stands, thinning is the preferred treatment for growth enhancement (Johnstone 1985). The expected benefits of this procedure include increased merchantable volume and larger, less variable average log size at maturity than would be achieved without thinning (Assmann 1970). Recently, porcupine damage in second-growth stands has been identified as a threat to tree survival and growth production (Eglitis and Hennon 1986; Sullivan et al. 1986; Sullivan and Cheng 1989; MacHutcheon 1990). Reported annual rates of new (current year only) damage and cumulative (total to date of assessment) damage (5.1%, and 52.7%; Khutzymateen Inlet, B.C. Sullivan et al. 1986), and 9.5% and 41.1% (southeast Alaska, Eglitis and Hennon 1986) clearly establish the potential for porcupine damage to influence stand growth and yield. Porcupines' apparent preference for larger, faster-growing trees (Van Duesen and Myers 1962; Harder 1979; Dodge 1982; Sullivan et al. 1986) suggests that stand thinning may enhance conditions for porcupines. In addition, the high per-hectare-cost ($800-$1500; Bob Wilson, B.C. Ministry of Forests, personal communication) of thinning has underlined the need to assess the effect of this silvicultural practice on porcupine damage rates and associated tree growth. Such information is required to determine if changes in the application of stand thinning treatments are warranted. Although a considerable number of studies have examined the potential impact of porcupine damage on young forest stands (Curtis 1941; Curtis 1944; Rudolf 1949; Storm and Halvorson 1967; Eglitis and Hennon 1986; Sullivan et al.1986), none have evaluated the influence of stand thinning on damage. In addition, the impact of porcupines on the stands examined in these studies has been inferred by the percentage of trees damaged; however where tree density among stands varies widely, similar percentages would reflect very different absolute (i.e. number trees damaged per hectare) amounts of damage. It is therefore important to not only assess percentage differences among sites, but also to relate these back to absolute numbers. Also, because tree density may influence the amount of feeding per tree damaged (see Cowie, 1977; Stephens and Krebs, 1986), which may in turn influence tree growth (Storm and Halvorson 1967), an assessment of within-tree use is also needed.

In this chapter I examine the influence of stand thinning on porcupine damage from the stand perspective. Specifically, I investigate the effect of stand thinning on 1) incidence of damage and associated tree mortality, 2) selection and degree of use of feeding trees, and 3) growth of damaged and undamaged trees.

STUDY AREA

This study was carried out in the Kalum Valley (54 36' N, 128 42' E), 15 km. north of Terrace, British Columbia (Figure 2-1). The entire area is within the Coastal Western Hemlock biogeoclimatic zone (Krajina 1969). Dominant tree species include western hemlock (*Tsuga heterophylla*), amabilis fir (*Abies amabilis*) Sitka spruce (*Picea sitchensis*) and western red cedar (*Thuja plicata*). Understory species include *Vaccinium membranaceum, Vaccinium ovalifolium, Menziesia ferriginea, Oplopanax horridus* and *Sambucus racemosa* (see Standish et al. 1987 for a detailed description of zone vegetation characteristics). Extensive logging in the 1950's and 1960's has resulted in the development of large tracts of naturally regenerated, even-aged second growth stands composed of western hemlock and amabilis fir. Stand tending activities (spacing, pruning) have been carried out on approximately 10,000 hectares, and thousands more are scheduled for this treatment in the future.

Four 100 hectare sites were chosen for the study; two thinned stands (treatment), and two unthinned (control) stands. All sites were of similar age and species composition (Table 2-1). Site selection was not random, but was constrained by the availability of sufficiently large homogeneous units. The surrounding habitat matrix of all sites was similar; being comprised of a mosaic of thinned and unthinned stands of similar or younger age. Remnant patches of old-growth forest were present within or adjacent to all sites. Detailed forest cover maps depicting the landscape context of each site are included in Appendix 2-A.

The distribution of tree diameters differed markedly between thinned and control sites (Figure 2-2). Control sites had a preponderance of small diameter stems of both species whereas thinned sites had a less skewed distribution, a situation typical of this silvicultural practice (Johnstone 1985; Assmann 1970). The effects of thinning are clear in this regard; a large numbers of intermediate or suppressed stems are removed, favouring the co-dominant and dominant trees that remain. The diameter of hemlock trees did not differ significantly between control sites (Table 2-1; Mann Whitney U-test: U = 18904, p = 0.213, n = 412) but amabilis fir diameters did (Table 2-1; U = 14998, p = 0.04, n = 371). In thinned sites diameters of both species differed significantly (Table 2-1; hemlock: U = 10269, $p \leq 0.001$, n = 370; amabilis fir: U = 24570, $p \leq 0.001$, n = 617).

TABLE 2-1. Stand information for thinned and unthinned study sites established in the Kalum Valley near Terrace, B.C. in 1989. Logging, thinning dates and stand age were taken from Forest Cover maps (1:20,000). Diameter (DBH), species composition, density and BAF were summarized from variable radius damage plots established on each site.

SITE	YR. LOGGED	YR. THIN	AGE	DBH (cm)	% H[a]	% AF[a]	% S[a]	BAF[c]	STEMS /ha[b]
ALICE (Control)	1954-66	N/A	22-34	H: 16.9 AF: 18.3	47.3	52.7	0	5.0625	2495
BEAR (Control)	1958	N/A	30	H: 17.9 AF: 20.0	62.8	35.7	1.5	3.0625	1499
OTTO (Thinned)	1960	1984	28	H: 20.8 AF: 23.5	39.3	59.6	1.1	1.5625	566
QUILL (Thinned)	1958	1980-84	30	H: 26.7 AF: 30.4	49.6	49.1	1.3	3.0625	537

[a] AF = amabilis fir, H = western hemlock, S = Sitka spruce
[b] stems per hectare >=7.5cm DBH
[c] Basal area factor used for variable radius plots (see Methods for an explanation)

METHODS

Variable Radius Plots

On each 100 hectare site, a 100 x 100m grid pattern was surveyed and marked to aid in navigating through the dense forest and as potential locations for establishing porcupine damage plots. A total of two hundred variable radius plots were established at randomly drawn grid points within the four study sites; fifty-five plots in each low density site and forty-five plots in each high density site. A greater number of plots were needed in the low density sites to obtain equal sample sizes of western hemlock trees, the main food species, on each site. Plots were established between June and August 1989. Plots were re-visited annually in the spring (May through June) of 1990 and 1991 to assess new damage and change in tree diameter (growth).

For each site, a specific basal area factor (BAF) was chosen so as to sample 7-11 trees per plot. At each sample point, a relascope (Bitterlich 1984) was used to determine if individual trees were in or out of the plots. Variable radius plots skew sampling effort toward larger (and usually rarer) diameter trees because BAF, tree diameter and distance from sampling point determine which trees are "in" or out of the plot. In this way, a large diameter tree relatively far away from the sampling point may be considered "in" the plot where a small diameter tree at the same location would be "out". This approach reduces the time-consuming task of tallying small diameter stems which numerically dominate naturally regenerating stands (Kozlowski 1971). The systematic bias exacted by variable radius plots can be corrected for using the following formula (from Bitterlich 1984):

$$\text{Tree Density} = \frac{B}{P} \sum \frac{n_i}{\pi r^2} \qquad \{\text{Formula 1}\}$$

where:

n= number of trees in a particular diameter class

B = Basal Area Factor used during sampling

r = midpoint diameter of diameter class in meters

P = number of plots established

Tree Measurements and Porcupine Damage

Trees determined to be in the plots were tagged with a numbered metal tag at breast height (1.30 m). Measurements taken included: diameter at breast height (DBH), species, height and presence, age, and extent of porcupine damage. Tree DBH was taken with a metal diameter tape to the nearest millimeter, height data were calculated using a 30 meter nylon tape and Sunnto ® clinometer. The precision of this method is considered to be ± 0.3 meters (Watts 1983). Porcupine damage was distinguished from other potential sources of scarring (e.g. moose, stem abrasions etc.) by the prominent transverse tooth marks (0.3 - 0.5 cm wide) on the exposed sapwood and the presence of bark chips and droppings at the tree base. Porcupine damage was classed as new (from the previous winter) or old (greater than one winter old), based on the colour of the exposed sapwood (new = yellow, old = brown) and presence of new cambial growth surrounding the wounds. The position of the damage within the tree was classed as 1 = lower third of tree, 2 = middle third of tree, and 3 = top third of tree. The proportion of circumference girdled was measured by dividing the width of the widest wound by the total circumference of the tree at that point. The area of bark removed was measured using two methods based on the extent of damage. For trees showing small amounts of damage I directly measured areas by climbing the tree and obtaining length and width measurements on individual feeding wounds. For trees with extensive feeding, I estimated the area exposed by measuring top (C_T; in meters) and bottom circumference (C_B; in meters) of the affected section, the height of the cylinder (h; in meters) and applying a visual estimate of percent of bark removed (r) in 5% increments. In this way the total area of sapwood exposed can then be calculated by:

$$\text{Area exposed } (m^2) = \frac{(C_T + C_B)}{2}\, h\, r \qquad \{\text{Formula } 2\}$$

Statistical Analysis

Analyses consider western hemlock (hemlock) and amabilis fir **only** as these species constitute more than 98% of all trees tallied within all sites (Table 2-1).

Rates of Porcupine Damage

Because the variable-radius plots systematically biased the sampling toward larger stems, I had to back-transform frequencies to reflect the actual proportion damaged prior to analysis. To do this I first calculated the proportion damaged by substituting damaged trees only into formula {1}, and then multiplied the proportion by the total number of trees tallied to determine the adjusted frequencies. In most cases, the back-transformed frequencies were lower than the unadjusted counts, indicating transformation was conservative.

To compare rates of damage to hemlock between thinned and control sites, I constructed a three-way log-linear model (variables: damage [yes or no], treatment [thinned or control], year [1989,1990,1991]) with sites pooled within treatments. A similar analysis was not possible for amabilis fir damage, due to low (< 5) cell frequencies, consequently I pooled years and tested for frequency differences between treatments with a 2 x 2 G test of independance. G tests were also used to compare rates of stem girdling and cumulative damage frequency for each species.

Tree Mortality

I compared mortality rates of western hemlock trees between treatment types for a two-year interval (June 1989-June 1991) using a 2 x 2 G-test of independence. Sites and years had to be pooled to maintain sufficient sample sizes. There were insufficient data to compare mortality rates of amabilis fir between treatments.

Diameter growth of undamaged and damaged trees

I used ANCOVA, controlling for tree diameter to examine the effects of treatment and species on two-year diameter growth of undamaged trees. I ran a separate ANCOVA, controlling for tree diameter, to examine the relationship between two-year diameter growth and the intensity (i.e. amount of girdling, area of bark removed) of porcupine damage within and between thinned and control stands. Only those hemlock trees damaged in 1989 ***only***, and ***not*** re-attacked in subsequent years or in years previous to 1989 were examined in this analysis in order to isolate the potential effect on tree growth. The impact of porcupine damage on amabilis fir growth rates was not examined due to insufficient sample size.

Selection of Feeding Trees by Porcupines

I constructed four logistic regression models (Proc Probit, SAS Institute 1990; Bergerud 1989) to identify factors which separated feeding trees from non feeding trees. I estimated separate models for each year (1989, 1990, 1991) and then combined data with 'year' coded as a dummy variable to test for a year effect. The response variable used was the probability of an individual tree being fed upon (P = 1 [damaged]; P = 0 [not damaged]). Independent variables tested in the model were:

(1) Species (categorical)
(2) Stand type [i.e. thinned or control] (categorical)
(3) Diameter (continuous)
(4) Presence of previous damage (categorical)
(5) Site (categorical)
(6) Year (dummy variable)[combined model only]

I used the Probit procedure within SAS (SAS Institute, 1990) to accommodate the combination of continuous and categorical data. Variables were added in a stepwise fashion; only those which significantly improved model fit (i.e. improvement in G statistic[-2log-likelihood ratio]) were kept, others were dropped.

Amount and Distribution of Feeding within Trees

I used ANCOVA, controlling for tree diameter to determine if porcupines removed larger amounts of cambium from trees in thinned stands than from those in control stands. Logarithmic transformation (Krebs 1989) was used to normalize data prior to analysis. I used only previously undamaged trees to avoid the potentially confounding effect of previous damage and associated partial tree mortality (i.e. dead top). These data were analyzed with sites pooled within treatments to maintain sample sizes greater than or equal to 5 in each group.

To test for differences between treatments in the distribution of damage within damaged trees, I used ANCOVA, controlling for the amount of bark available in each of the three sections. The amount of bark available was calculated by considering each tree as a cylinder with a bottom diameter given by the measured diameter at breast height (DBH) and the top diameter set at 10 mm. The bark areas were then calculated using the following equations:

Section 1 (Bottom)

$$\text{Area} = \frac{D\pi(1 + (0.667/0.99))}{2}\,\frac{H}{3} \qquad \{\text{Formula 3}\}$$

Section 2 (Middle)

$$\text{Area} = \frac{D\pi((0.667/0.99) + (0.333/0.99))}{2}\,\frac{H}{3} \qquad \{\text{Formula 4}\}$$

Section 3 (Top)

$$\text{Area} = \frac{D\pi((0.333/0.99) + 0.01)}{2}\,\frac{H}{3} \qquad \{\text{Formula 5}\}$$

Where: D = Diameter at breast height (in meters)
H = Tree height (in meters)

A top diameter of 10 mm was chosen for two reasons: 1) porcupines are unable to climb above this point as trees would be unable to support them, 2) the leader (top) of hemlock trees droop over at approximately 10 mm in diameter, and therefore tree heights actually measure the height to the droop rather than the outstretched length.

RESULTS

A total of 1803 trees in 200 plots were tagged, measured and appraised for porcupine damage during the study. Over the three seasons of monitoring, 235 western hemlock, 38 amabilis fir and 2 Sitka spruce were fed upon by porcupines and previous damage was present on 257 hemlock, 35 amabilis fir and 3 Sitka spruce. Table 2-2 summarizes the damage rates by site and year. The back-transformed and raw damage and girdling frequencies for hemlock and amabilis fir are presented in Appendix 2-A. In 65 of 72 (90%) cases, the back-transformed frequencies were less than or equal to the raw frequency tallies, suggesting that the transformation (and its potential to enhance frequency differences) was conservative.

Rates of Porcupine Damage

Overall, the rate of new (current year) damage to hemlock trees was significantly higher in thinned (mean [years and sites combined] = 8.35%) than control (mean = 5.18%) stands and varied significantly between years (3-way log-linear model; TREATMENT*DAMAGE: G = 9.15, df = 1, $P < 0.005$; YEAR*DAMAGE; G = 6.98, df = 2, $p < 0.04$; Appendix 2-B). The differences in new damage rates between thinned and control sites was most apparent in 1991 (2.4-fold) and 1990 (1.9-fold) and to a lesser extent, 1989 (1.1 fold; Table 2-2; Appendix 2-B). New damage varied among years likely due to reduced rates in all sites (particularly controls) in 1991 (Table 2-2). Cumulative (total to date, including old [before 1989] and new) damage incidence to hemlock was nearly two times greater in thinned (40.4%, 39.9%) than control (26.5%, 21.9%) stands (G = 23.85, df = 1, $p < 0.001$; Table 2-2; Appendix 2-B). Average annual rate of girdling in hemlock was 2.8% for thinned and 1.5% for control sites. Sparse cell frequencies prevented a three-way log-linear analysis of stem-girdling rates (Appendix 2-A), however, pooled data from all years showed a similar trend to above comparisons with significantly higher proportion of new (G = 4.55, df = 1, p = 0.033) and cumulative (thinned =19.8%, control = 12.2%; G = 9.54, df = 1, p = 0.002) girdling in the thinned treatment (Table 2-2, Appendix 2-B).

In contrast to hemlock, new damage rates to amabilis fir were markedly lower overall, and did not vary significantly (p's all >0.29) between thinned and control treatments (Table 2-2, Appendix 2-B). Average annual rates of damage and girdling in amabilis fir were 1.4% and 0.6% in thinned sites, and 0.8% and 0.3% in controls respectively. Cumulative damage and girdling to amabilis fir averaged 3.7% and 2.5% in thinned sites, and 3.4% and 1.4% in controls respectively.

In summary, new and cumulative damage and girdling rates in hemlock were greater in thinned than control sites. Similar comparisons in amabilis fir revealed no significant differences between treatments.

TABLE 2-2. Percent of trees damaged by porcupines by year and tree species for two thinned and two unthinned (control) second growth forest stands near Terrace B.C., 1989-1991 as determined by variable radius plots. Percent of trees stem-girdled is indicated in parentheses. Cumulative damage represents totals to 1991, including old (before 1989) damage.

			1989		1990		1991		CUMULATIVE		
SITE	N (H)	N (AF)	H	AF	H	AF	H	AF	H	AF	Total[a]
Alice (Control)	165	199	8.1(3.3)	0.1(0.0)	2.6(0.0)	0.3(0.3)	3.4(0.5)	0.0(0.0)	**26.5(14.5)**	**1.5(0.6)**	**13.4(7.2)**
Bear (Control)	247	172	7.3(2.0)	1.6(0.3)	7.1(1.6)	0.8(0.0)	2.6(1.4)	2.1(1.3)	**21.9(9.9)**	**5.4(2.3)**	**16.7(7.5)**
Otto (Thinned)	189	361	9.9(3.7)	1.4(0.7)	7.9(2.9)	0.5(0.0)	7.6(1.6)	0.4(0.4)	**40.4(18.5)**	**2.4(1.1)**	**17.5(8.1)**
Quill (Thinned)	181	256	7.4(2.3)	1.7(1.4)	10.6(4.5)	3.0(1.2)	6.7(1.4)	1.2(0.2)	**39.9(21.2)**	**5.0(3.9)**	**22.5(12.6)**

[a] Cumulative damage (%), species combined

Tree Mortality

Porcupine feeding damage does not necessarily result in tree mortality. Of 157 western hemlock trees fed upon in 1989 and 1990 only 13 died. Although the probability of tree mortality of porcupine-damaged trees was two times greater in control (9 of 83; 10.8%) than thinned sites (4 of 74; 5.4%) over the two-year period, the difference was not significant ($G = 1.57$, $df = 1$, $p = 0.210$). The low probability of mortality for individual trees would necessitate a much larger sample of trees or a longer time interval to detect differences. Only one amabilis fir died of 26 damaged within the same two-year time period.

Diameter growth of undamaged and damaged trees

Diameter growth of undamaged hemlock and amabilis fir varied significantly with treatment ($F_{1,821} = 46.47$, $p < 0.001$) and individual tree diameter ($F_{1,821} = 55.77$, $p < 0.001$), but not between species ($F_{1,821} = 2.41$, $p > 0.12$; Interactions all n.s., $p > 0.5$). Larger diameter trees grew faster than smaller diameter trees, and trees in thinned stands grew faster than those in unthinned sites (Figure 2-3).

In damaged hemlock trees, diameter growth varied with the proportion of the tree circumference girdled ($F_{1,19} = 37.38$, $p < 0.001$), but not with the area of bark removed ($F_{1,19} = 0.74$, $p = 0.40$) or diameter ($F_{1,19} = 0.1$, $p > 0.8$). Slopes of the regression lines varied weakly between treatments ($F_{1,19} = 3.822$, $p = 0.068$) Tree growth decreased with increasing girdling, especially in control sites (Figure 2-4). Some trees actually shrank after sustaining extensive porcupine damage, presumably due to dessication through the exposed sapwood.

Selection of Feeding Trees by Porcupines

The logistic regression models estimated on damaged versus undamaged trees clearly shows that porcupines are non-random feeders (Appendix 2-C). The strongest factor influencing the choice of feeding trees was species ($p<0.001$ in all years; Table 2-3; Figure 2-5). Over 80% of damaged trees were western hemlock despite this species comprising only 34 -59 % of the tallied stems. The presence of previous damage (Figure 2-6) and tree diameter (Figure 2-7) influenced feeding tree selection in two of three years (Table 2-3). Previously damaged trees were between 3.7 and 5.2 times more likely to be fed upon than trees without previous damage (Figure 2-6). Porcupines prefer large diameter trees as shown in Figure 2-7. Because tree growth varied with stand type and diameter (see Diameter Growth section), selection for larger trees within a stand results in the selection of the faster growing trees. Although preference for larger trees could indirectly result in the preference for previously damaged trees (or vice-versa), the inclusion of both variables in the 1990 and combined model indicates that preference for previously damaged trees ocurrs in addition to preference for larger diameter trees. A significant site effect was also present in two of three years (Table 2-3). The site effect is likely a result of the low frequency of damage detected in the 'Alice' control site in 1990 and 1991. There was no improvement to the model with the addition of the treatment variable; porcupines appeared to show similar preferences in both thinned and control stands within years (Table 2-3).

Amount and Distribution of Feeding within Trees

Porcupines tended to feed more extensively on hemlock trees within thinned stands than in controls. First-time attacks to hemlock trees in thinned stands resulted in significantly more bark removed than in control stands after controlling for tree diameter (ANCOVA: log-tranformed bark area, $F_{1,109} = 3.62$, $p = 0.06$; Year, $F_{2,109} = 5.04$, $p = 0.008$; diameter, $F_{1,109} = 9.78$, $p = 0.002$; interactions all $p > 0.2$; Figure 2-8). The differences in the amount of feeding between treatments were most apparent in 1989 and 1990 when feeding amounts for thinned trees averaged 1.9 and 2.0 times those for the controls, respectively (Figure 2-8). A significant year effect was detected in the analysis, likely a result of the reduced feeding amounts and lower sample sizes for control trees in 1991 (Figure 2-8).

The amount (area) of feeding in individual trees varied over 3 orders of magnitude (0.002 to 3.430 m^2; Figure 2-9). A possible explanation for the wide variation in the amount of feeding among individual trees is the potential existence of "sampling" of trees by porcupines. Trees may be "sampled" and either be found to be suitable for extensive feeding (resulting in a large amount of feeding) or they would be rejected as unsuitable and not be fed upon further (resulting in a small amount of feeding). Based on Figure 2-9, "sampling" of trees by porcupines occurs in both thinned and control stands.

Porcupines preferentially fed in the middle section of hemlock trees ($F_{2,109} = 25.56$, $p < 0.001$) as is clearly shown in Figure 2-10. Distribution of feeding was unaffected by treatment (i.e. [treatment*tree section], and [treatment*area available*tree section] terms non-significant, p's >0.30) or bark availability ($F_{1,109} = 0.85$, $p = 0.36$); however porcupines fed more per tree in thinned sites ($F_{1,109} = 6.84$, $p = 0.009$). The area of bark removed from the middle section averaged > 2.4 times that measured in the top or bottom sections in all cases (Figure 2-10). Although trees were more extensively damaged in thinned stands, the pattern of feeding with respect to tree section was similar in both thinned and control sites, as shown in Figure 2-10.

TABLE 2-3. Results from four logistic regression models estimated on damaged versus undamaged trees for 1989 (N = 1770), 1990 (N = 1768), 1991 (N = 1756) and all years combined (N = 5294). The best fit model for each run is indicated in bold face. Variables tested include: tree species, presence of previous damage, tree diameter, treatment (thinned or control), site, and year (combined analysis only).

Variables added	-2 log likelihood	Difference (G^2)	Df	P
1989				
Null model	-913.3			
Species	-716.9	196.4	1	<0.001
Species, Prev. (Best Model)	**-691.3**	**25.6**	**1**	**<0.001**
Species, Prev, Diameter	-690.24	1.06	1	N.S.
Species, Prev., Treatment	-688.3	3.0	1	N.S.
Species, Prev., Site	-687.34	3.96	3	N.S.
1990				
Null model	-757.4			
Species	-684.14	73.26	1	<0.001
Species, Prev.	-663.76	20.38	1	<0.001
Species, Prev, Diameter	-652.32	11.44	1	<0.005
Species, Prev., Diameter, Treatment	-651.86	0.46	1	N.S.
Species, Prev., Diameter, Site (Best Model)	**-640.84**	**11.48**	**3**	**<0.01**
1991				
Null model	-569.4			
Species	-518.64	50.76	1	<0.001
Species, Diameter	-507.26	11.38	1	<0.005
Species, Diameter, Prev.	-504.9	2.36	1	N.S.
Species, Diameter, Treatment	-504.98	2.28	1	N.S.
Species, Diameter, Site (Best Model)	**-497.9**	**9.36**	**3**	**<0.025**
YEARS COMBINED				
Null Model	-2150.9			
Species	-1931.3	219.6	1	<0.001
Species, Prev.	-1885.5	45.8	1	<0.001
Species, Prev., Diameter	-1867.4	18.1	1	<0.001
Species, Prev, Diameter, Treatment	-1866.1	1.3	1	N.S.
Species, Prev., Diameter, Year	-1853.3	14.1	2	<0.001
Species, Prev., Diameter, Year, Site (Best Model)	**-1839.1**	**14.1**	**3**	**<0.004**

DISCUSSION

Stand thinning appears to result in increased rates of porcupine damage to western hemlock, but not to amabilis fir. Differences between thinned and control stands in cumulative frequency of hemlock damage and girdling are the most striking; to date, 40.4% and 39.9% of hemlock have been damaged and 18.5% and 21.2% girdled in thinned stands whereas only 26.5% and 21.9% have been damaged and 14.5% and 9.9% girdled in control sites. Similar studies of red squirrel feeding damage in thinned and unthinned lodgepole pine (Sullivan and Sullivan 1982; Sullivan and Moses 1986; Sullivan and Vyse 1987) have demonstrated equivocal conclusions on damage incidence, with results varying between years and sites. Anecdotal evidence from studies of porcupine damage in the U.S. (e.g. Curtis 1941; Daniel and Barnes 1958) suggested a positive association between thinning and damage but they did not provide statistical tests to support their claims.

Comparisons of damage percentages (or the frequencies from which they are derived) among treatments of differing tree density are useful and essential if one wishes to evaluate the potential stand-level impacts of damage among treatments. However, because each tree in a thinned stand represents a greater fraction of the stand total than a single tree in a denser, unthinned stand, the increased damage incidence may not be the result of increased feeding activity (or density) of porcupines, but merely an artifact of using percentages to describe damage incidence. To illustrate the point further, I converted the cumulative total damage percentages for control and thinned stands (from Table 2-2) into number of damaged stems per hectare with the following results:

Site	% Damaged	# damaged per hectare
Alice (control)	13.4	334
Bear (control)	16.7	250
Otto (thinned)	17.5	99
Quill (thinned)	22.5	121

In absolute (number damaged trees per hectare) terms, damage appears greater in controls rather than thinned sites, the reverse of the damage percentages. Clearly, when interpreting differences, increased damage percentages from stands of lower density does not necessarily imply increased feeding activity or density of porcupines (see also Chapter 3).

Because girdled trees survive if live branches are present below the point of injury (Storm and Halvorsen 1967; Sullivan et al. 1986), it follows that trees with more extensive live crowns should have a greater chance of surviving a girdling injury. Further, because stand density is negatively correlated with live crown length (Kozlowski 1971), a higher mortality rate should be expected for damaged trees within control stands. Mortality rates of porcupine-damaged trees were extremely low and although they tended to be higher in control stands, frequency did not differ significantly between treatments. Based on observed differences, the power (Sitt 1992) of this test was only 0.24 indicating a weak ability to reject the null hypothesis of no difference. A longer monitoring interval or a larger sample of damaged trees would be required to test adequately for differences.

Damaged trees showed reduced diameter growth in response to increased girdling, especially in control stands. Although I used a linear model to fit the data, it is generally thought that a threshold in the amount of girdling exists, above which, diameter growth is affected (60%; Cerezke 1974; Sullivan and Vyse 1987). The small sample size of damaged trees suitable for comparison within each treatment precluded determination of any such threshhold in my dataset. The recognition that growth is affected by increasing girdling has important implications for stand thinning, since reductions in growth accompanying damage may obviate growth benefits gained from the treatment, especially since rates of damage with respect to the stand are higher.

If porcupines chose feeding trees randomly, the characteristics of damaged trees should not have differed from undamaged trees. Similarly, if stand density did not influence feeding preferences, there should not have been differences in feeding rates on trees in thinned and those in control stands. In this study, porcupines were 5 to 8 times more likely to feed on hemlock than amabilis fir, similar to findings by Eglitis and Hennon (1986), Sullivan et al. (1986) and MacHutcheon (1990) in the Alaska Panhandle and North-Coastal B.C. Elsewhere porcupines have been demonstrated to prefer a variety of deciduous and coniferous trees (Krefting et al. 1962; Speer and Dilworth 1978; Roze 1984; Tenneson and Oring 1985; Hendricks and Allard 1988), or to show no species preferences (Harder 1979; 1980). Roze (1984) suggested that porcupines exhibit preferences for the numerically most abundant tree species in its foraging area. However, this is clearly not an adequate explanation of the species preference found in the present study since western hemlock (preferred) was present in similar or lower numbers compared with amabilis fir (not preferred) within the study sites. Equally unsatisfactory is the hypothesis that tree growth rates explain species preferences (Harder 1979: Sullivan et al. 1986) since growth rates did not vary between species. Because abundance (encounter rate), handling time and digestible energy content determine the profitability of an item to a forager (Stevens and Krebs 1986), it follows that in this study (where abundance of the two species is roughly equal), variation in the latter two factors may explain the observed species preference. Measurements of bark thickness and toughness as well as a nutritional and plant defense chemical profile of cambium from both species would be required to evaluate the importance of these factors in explaining the observed feeding preference.

Although species preference does not appear to be related to tree growth rates, selection by porcupines of the larger trees (Rudolph 1949; Sullivan et al. 1986, Harder 1979; Daniel and Barnes 1958; Krefting et al. 1962) within a species reflects selection for faster-growing trees since tree diameter and growth rate are positively correlated. This suggests a hierarchy of feeding tree selection by porcupines; initially porcupines choose the species and secondarily choose larger diameter trees within that species.

The apparent preference for previously damaged trees by porcupines has been reported by Curtis (1941), Shapiro (1949) and Spencer (1964); however, goodness of fit statistics were not applied to their data. Conversely, Harder (1977), and Curtis and Wilson (1953) concluded that use of trees was independent of whether or not they had been previously damaged. However, Harder's data is equivocal since 1 of 2 sites showed significant preference for previously damaged trees (Harder 1977: Tables 24 & 25) and Curtis and Wilson (1953) provide no data to enable an assessment of their claim. A plausible explanation for repeated feeding in individual trees is provided by Spencer (1964). He suggests that removal of the cambium and outer phloem layer results in a "damming" of nutrients (photosynthate) above the feeding scar thereby elevating the food quality of the bark (cambium, phloem) distal to the original wound. Baldwin (1934) experimentally girdled several species of eastern hardwoods and found sugar content doubled or tripled above the scars one year following girdling, and indicated anecdotally that porcupines took advantage of the increased nutrients. Porcupines in this study may have responded in a similar fashion to increased nutrients available above the scars of previously damaged trees. In cases of stem girdling, food quality may be enhanced for a short period of time (1-2 years) after the original feeding attack, after which time the portion of the tree distal to the girdling dies (Spencer 1964; Sullivan et al. 1986).

Stand thinning appeared to have no influence on feeding preferences of porcupines in this study. However, once chosen, the amount of use in individual trees varied between treatments. I interpret the increased amount of feeding in hemlock trees within thinned (low density) stands as qualitative support for the marginal value theorem (Charnov 1976) which predicts increased use of food patches (trees in this case) as density of patches decreases. Similar results have been documented for red squirrel and snowshoe hare feeding damage in lodgepole pine (Sullivan and Sullivan 1982). Evidence from frequency distributions of the amount of feeding in individual trees suggests porcupines may "sample" trees to determine food quality (or handling time) prior to intensive feeding. Sampling behaviours are common in generalist herbivores as this permits the continual assessment of food quality in a changing environment (Freeland and Janzen 1974; Crawley 1983; Stephens and Krebs 1986).

Harder (1977) and Sullivan et al. (1986) suggested that the combination of easy accessibility and high food quality probably explain the porcupines' preference for crown (i.e. middle, top sections) feeding. My results concur with this assessment, as porcupines use of the middle third of the tree in relation to bark availability greatly exceeded that of both the bottom and top tree sections.

Stand thinning resulted in increased tree growth rates, increased hemlock damage rates and degree of use by porcupines. From this perspective, thinning has undoubtably enhanced the impact of porcupines on stand productivity. It is unclear however, if the increased damage rates in thinned stands are the result of increased porcupine density or feeding activity or simply related to the greater per-tree-influence of damaged trees on rate estimates in thinned stands. I attempt to discriminate between these two alternatives in the following chapter of this thesis (Chapter 3).

LITERATURE CITED

Assmann, E. 1970. The principles of forest yield study. Pergamon Press. Oxford. 506 pp.

Baldwin, H.I. 1934. Some physiological effects of girdling northern hardwoods. Bull. Torrey bot. Club. 61: 249-257.

Bergerud, W. 1989. Logistic Regression Methods with some Forestry examples. Draft. B.C. Ministry of Forests Research Branch. 59 pp.

Bitterlich, W. 1984. The relascope idea.

Cerezke, H.F. 1974. Effects of partial girdling on growth in lodgepole pine with application to damage by the weevil Hylobius warreni Wood. Can J. For. Res. 4: 312-320.

Charnov, E.L. 1976. Optimal Foraging: The Marginal value theorem. Theor. Pop. Biol. 9: 129-136.

Cowie, R.J. 1977. Optimal Foraging in great tits (*Parus major*). Nature 268:137-139.

Crawley, M.J. 1983. Herbivory: The dynamics of Animal-plant interactions. Studies in Ecology Volume 10, Blackwell Scientific Publications. 437pp.

Curtis, J.D. 1944. Appraisal of porcupine damage. J. Wildl. Manage. 8:88-91.

Curtis, J.D. 1941. The silvicultural significance of the porcupine. J. For. 39:583-594

Curtis, J.D., and A.K. Wilson. 1953. Porcupine feeding on ponderosa pine in central Idaho. J. For. 51: 339-341.

Daniel, T.W., and Barnes, G.H. 1958. Thinning a young stand of lodgepole pine. Proc. Soc. Amer. For. pp. 159-163.

Dodge, W.E. 1982. Porcupine. In: Wild Mammals of N.A. Biology, Management and Economics. J.A. Chapman and G.E. Feldhammer (editors). Johns Hopkins University Press, Baltimore, MD. pp 355-366.

Elgitis, A. and P.E. Hennon. 1986. Porcupine damage in Sitka spruce and western hemlock in southeast Alaska. USDA Forest Service Pest Management report, Juneau. 21pp.

Freeland, W.J. and D.H. Janzen. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. Am. Nat. 108: 269-284.

Harder, L.D. 1977. M.Sc. Thesis, Univ. Alberta, Edmonton, Alberta, Canada.

Harder, L.D. 1979. Winter feeding by porcupines in montane forests of southern Alberta. Can. Field Nat. 93:405-410.

Harder, L.D. 1980. Winter use of montane forests by porcupines in southwestern Alberta: preferences, density effects and temporal changes. Can. J. Zool. 58:13-19.

Hendricks, P., and Allard, H.F. 1988. Winter food habits of prairie porcupines in Montana. Prairie Nat. 20(1):1-6.

Johnstone, W.D. 1985. Thinning lodgepole pine. In Proc. Lodgepole pine, the species and its management. D.M. Baumgartner et al. (Eds). May 8 -10, 1984, Spokane, Wash. and May 14-16, 1984, Vancouver, B.C. Wash. State Univ. Cooperative Extension, pp. 253-262.

Kozlowski, T.T. 1971. The Growth and Development of Trees. Academic Press, New York.

Krajina, V.J. 1969. Ecology of Forest trees in British Columbia. Ecol. West. North Am. 2: 1-147.

Krebs, C.J. 1989. Ecological Methodology. Harper and Row, New York.

Krefting, L.W., J.H. Stoeckeler, R. Bradle, and W.D. Fitzwater. 1962. Porcupine - timber relationships in the Lake States. J. For. 60:325-330.

MacHutchcon, A. G. 1990. Porcupine feeding damage in second-growth stands of the North Coast Forest District, B.C.: A Summary. B.C. Ministry of Forests, Smithers B.C. 76pp.

Roze, U. 1984. Winter foraging by individual porcupines. Can. J. Zool. 62:2425-2428.

Rudolf, P.O. 1949. Pocupine's preference in pine plantations. J. For. 47:207-209.

SAS Institute Inc. 1990. SAS users guide. Version 6 Edition. SAS Institute Inc., Carey, North Carolina.

Shapiro, J. 1949. Ecological and life history notes on the porcupine inthe Adirondacks. J. Mammal. 30: 247-257.

Sitt, V. Contingency tables and log-linear analysis. Biometrics Information Pamphlet # 36, B.C. Ministry of Forests Research Branch, Victoria, B.C.

Speer, R.J., and Dilworth, T.G. 1978. Porcupine winter foods and utilization in central New Brunswick. Can. Field. Nat. 92:271-274.

Spencer, D.A. 1964. Porcupine population fluctuations in past centuries revealed by dendrochronology. J. Appl. Ecol. 1:127-149.

Standish, J.T., S. Haeussler, A. Kokoshke, J. Pojar, D.Holmes, B.M. Geisler, and D. Yole. 1987. A field guide for identification and interpretation of the Coastal Western Hemlock Zone, Northern Drier Maritime Subzone (CWHf), in the Prince Rupert Forest Region. B.C. Ministry of Forests. Land Management Handbook #14, 63 pp.

Stephens, D.W., and Krebs, J.R. 1986. Foraging Theory. Monographs in Behavioural Ecology. Princeton University Press. 247pp.

Storm, G.L., and C.H. Halvorsen. 1967. Effect of injury by porcupines on radial growth of ponderosa pine. J. For. 65:740-743.

Sullivan, T.P., and Cheng, C. 1989. Impact of Porcupine Feeding damage on intensive forest management in the Prince Rupert Forest Region: Problem Analysis. FRDA Report No. 083. 20pp.

Sullivan, T.P.,W.T. Jackson, J. Pojar, and A. Banner. 1986. Impact of feeding damage by the porcupine on western hemlock - Sitka spruce forests of north coastal British Columbia. Can. J. For. Res. 16:642-647.

Sullivan, T.P. and R.A. Moses. 1986. Red squirrel populations in natural and managed stans of lodgepole pine. J. Wildl. Manage. 50: 595-601.

Sullivan, T.P. and D. S. Sullivan. 1982. Influence of fertilization on feeding attacks to lodgepole pine by snowshoe hares and red squirrels. For. Chron. 58: 263-266.

Sullivan, T.P. and A. Vyse. 1987. Impact of red squirrel feeding damage on spaced stands of lodgepole pine in the Cariboo region of British Columbia. Can J. For. Res. 17: 666-674.

Tenneson, C., and Oring, L.W. 1985. Winter food preferences of porcupines. J. Wildl. Manage. 49:28-33.

Van Deusen, J.L. and C.A. Myers. 1962. Porcupine damage in immature stands of ponderosa pine in the Black Hills. J. For. 60: 811-813.

Watts, S.B. 1983. Forestry Handbook for British Columbia. The Forestry Undergraduate Society, University of B.C.

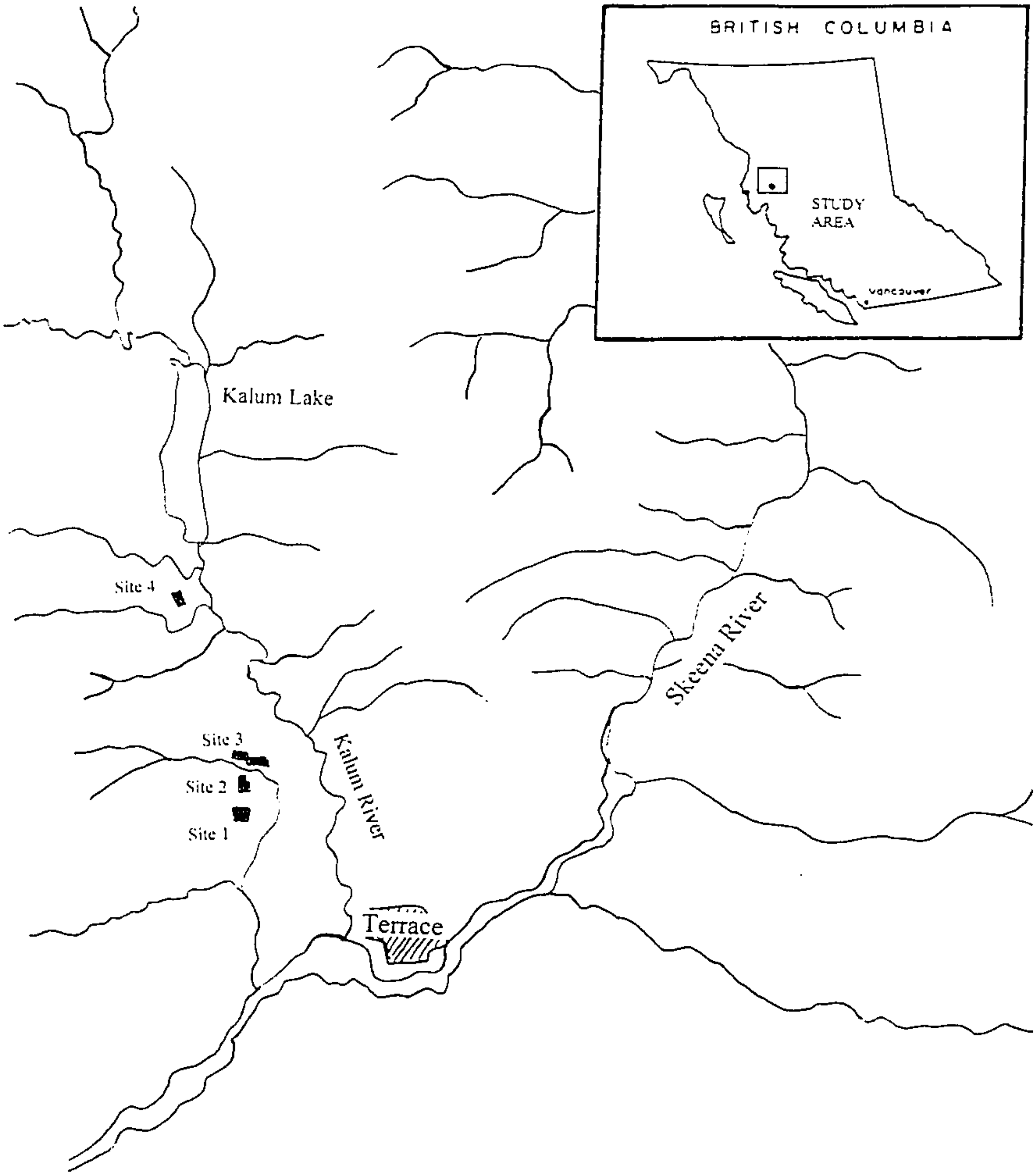


Figure 2-1. Location of two thinned (Site 1 (Otto); Site 3 (Quill)) and two control (Site 2 (Bear); Site 4 (Alice)) study sites near Terrace B.C. Sites are 100 hectares in size.

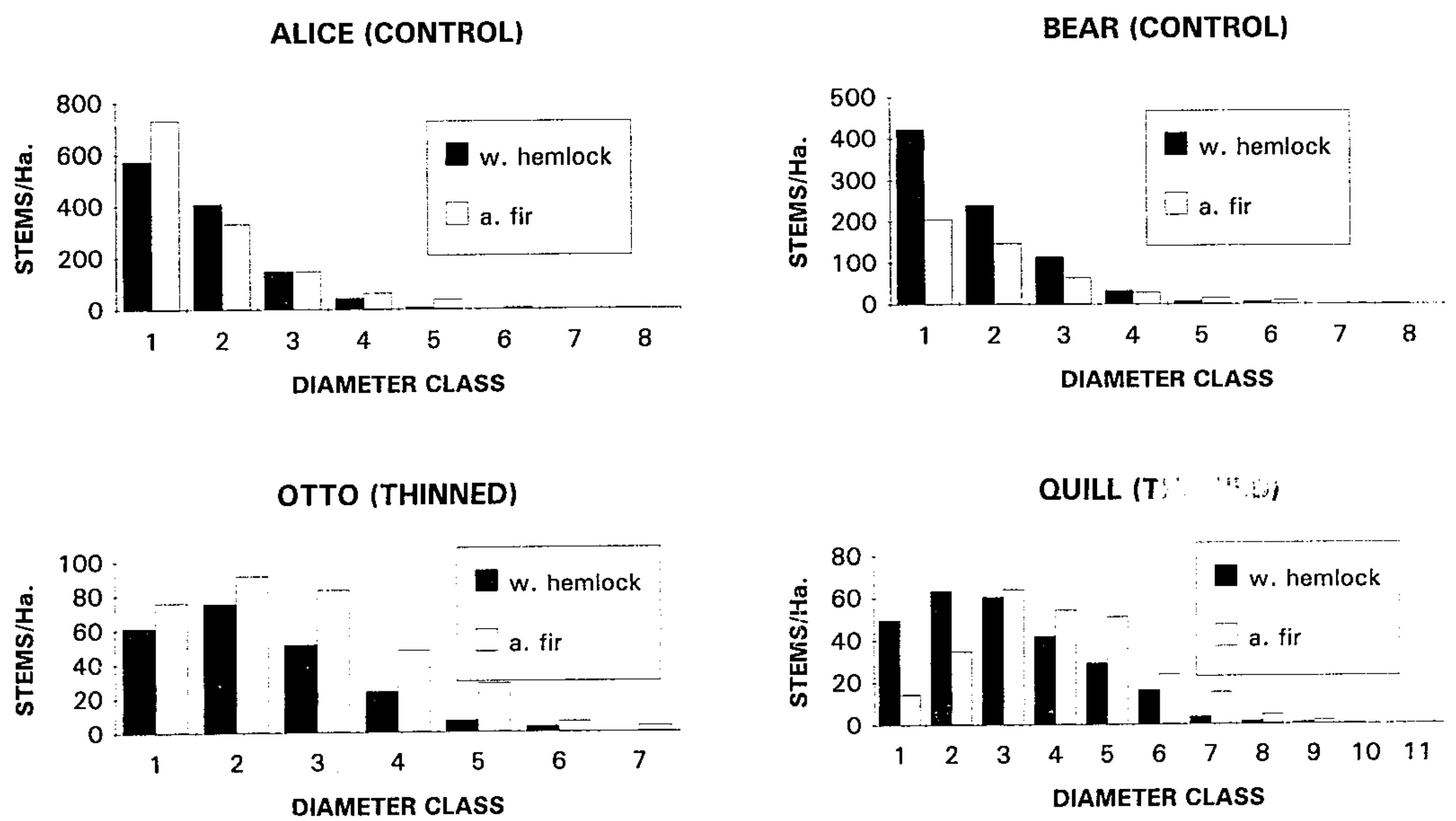


Figure 2-2 Diameter distributions of western hemlock and amabilis fir trees within thinned and control study sites near Terrace B.C. based on variable radius plot tallies

Diameter class	1	2	3	4	5	6	7	8	9
cm range	7.5-12.4	12.5-17.4	17.5-22.4	22.5-27.4	27.5-32.4	32.5-37.4	37.5-42.4	42.5-47.4	47.5-52.4

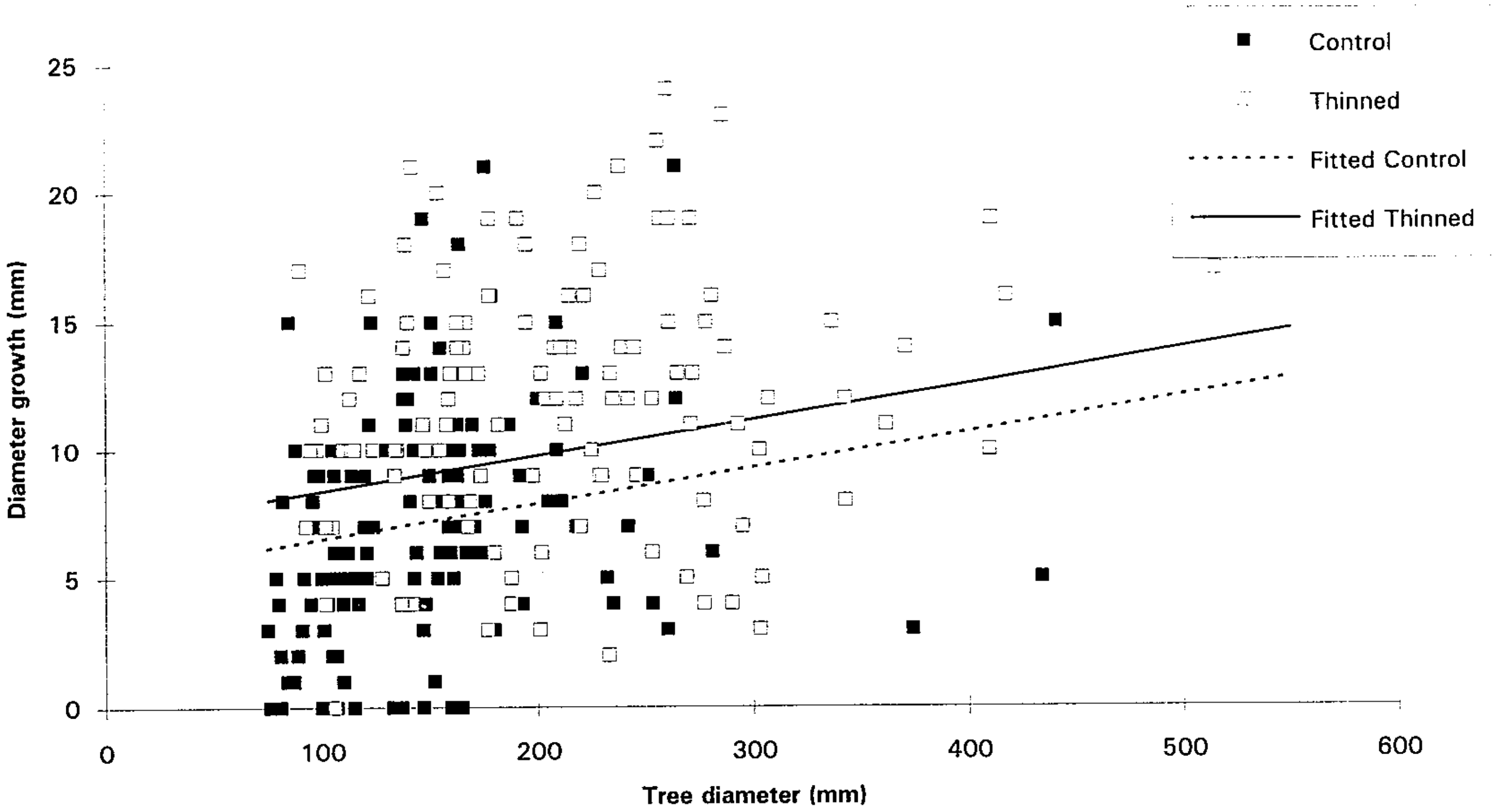


Figure 2-3 Two-year diameter growth of undamaged trees as a function of tree diameter and treatment (thinned, control). ANCOVA : (Treatment, $p < 0.001$; Diameter, $p < 0.001$; Species, $p > 0.12$; Interactions $p > 0.5$). For clarity, values for hemlock only are presented in the above figure.

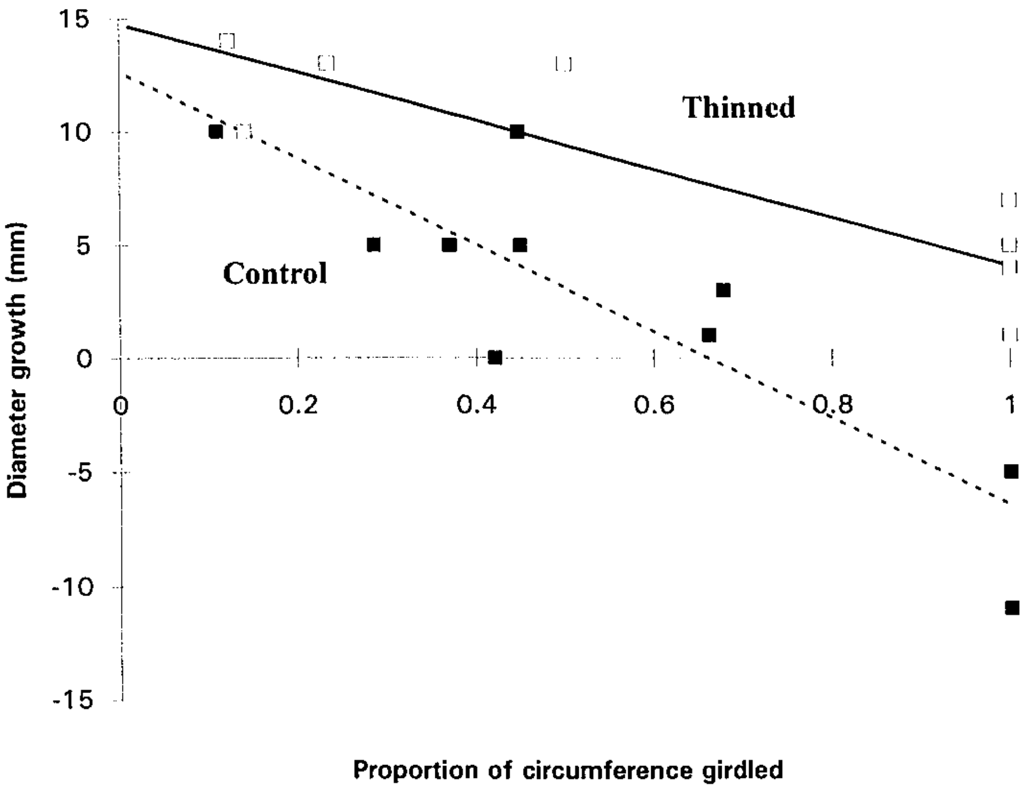


Figure 2-4. Influence of treatment and proportion of tree circumference girdled on hemlock diameter growth. Growth varied significantly with proportion of tree circumference girdled ($p < 0.001$) but not with tree diameter or area of bark removed (p's > 0.39). There was a marginally significant difference in regression slopes between treatments ($p = 0.068$).

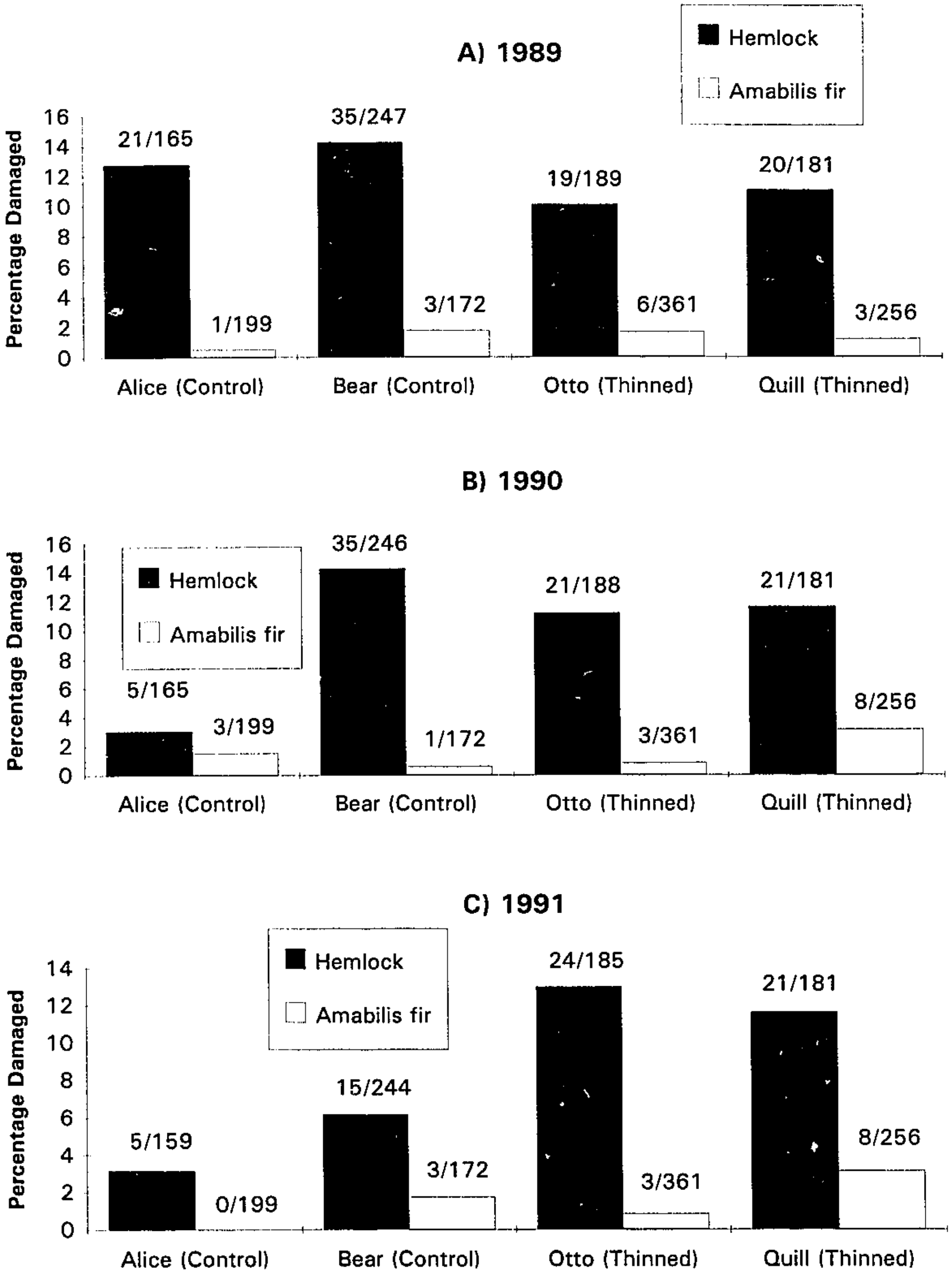


Figure 2-5. Percentage of available hemlock and amabilis fir trees damaged by porcupines within each site summarized by year. A) 1989, B) 1990, C) 1991. Sample sizes are indicated above each bar.

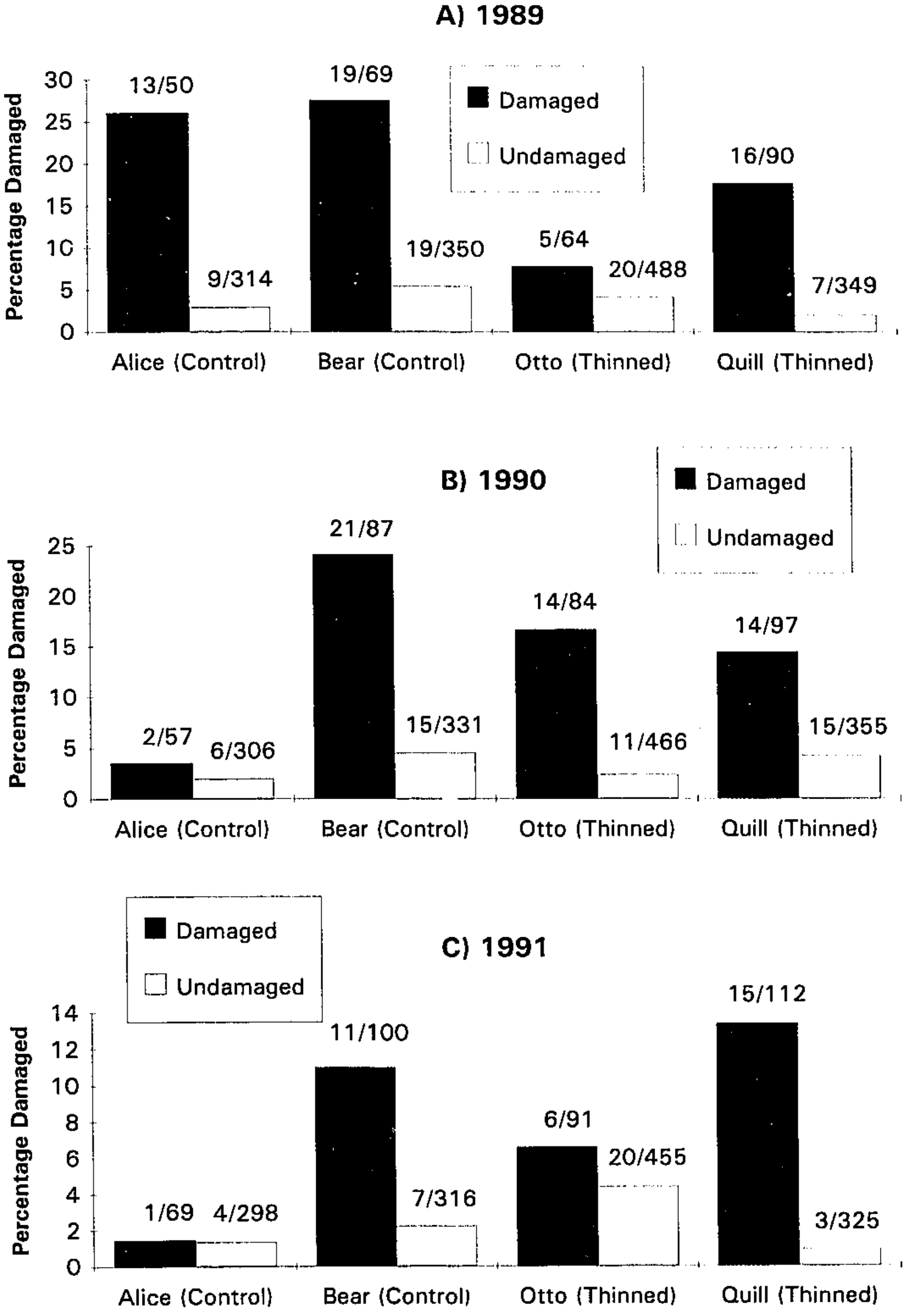


Figure 2-6 Percentage of trees damaged by porcupines that were previously damaged or previously undamaged, summarized by site and year. A) 1989, B) 1990, C) 1991. Sample size indicated above each bar.

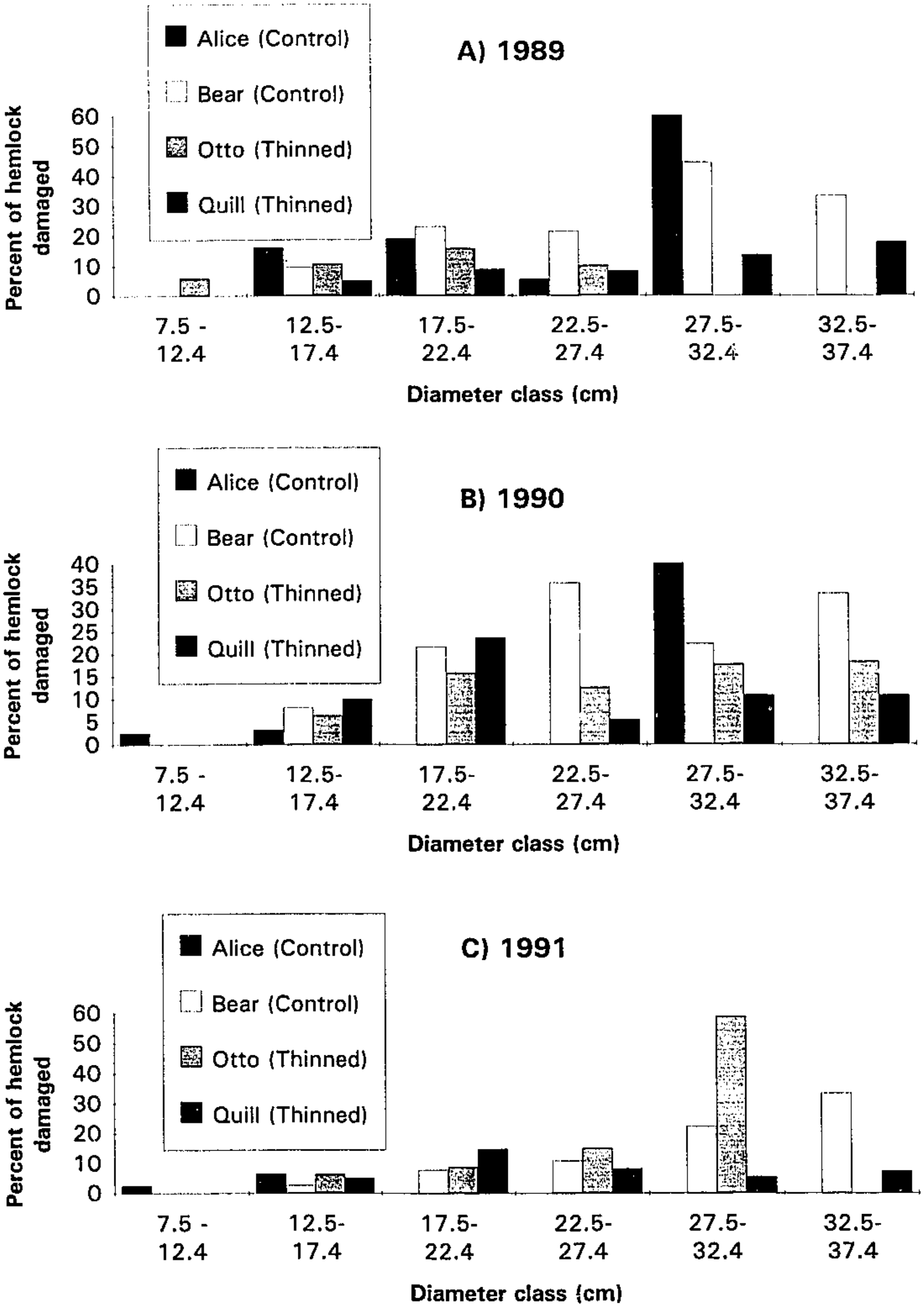


Figure 2-7 Percentage of hemlock trees in each diameter class damaged by porcupines in each site, summarized by year. A) 1989, B) 1990, C) 1991.

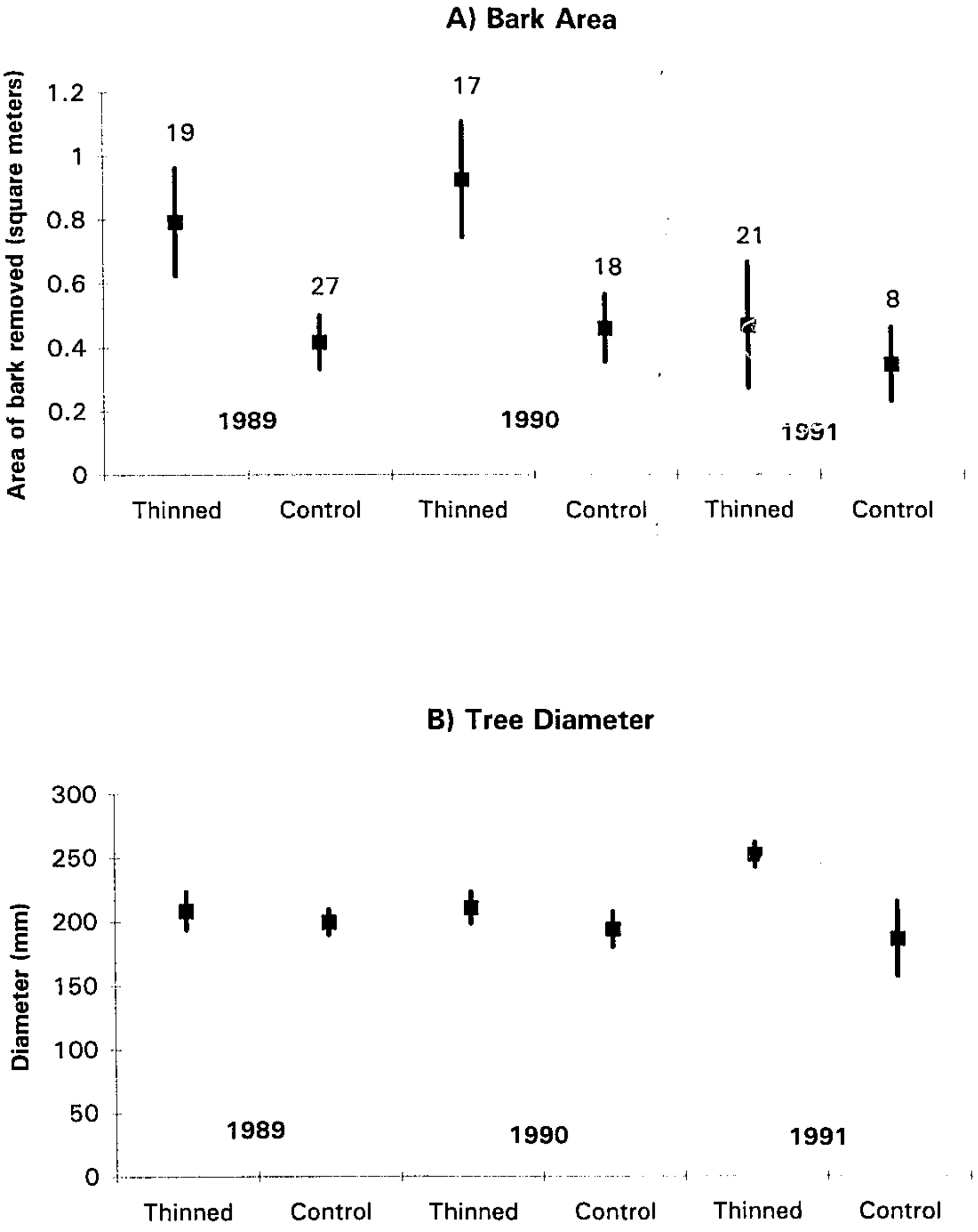


Figure 2-8 A) Mean area (+/- SE) of bark removed by porcupines in first-time attacks of hemlock trees in thinned and control stands near Terrace, B.C., 1989-1991. Sample size is indicated above each bar.
B) Mean diameter (+/- SE) of first-time attacked hemlock trees in thinned and control stands near Terrace, B.C., 1989-1991. Sample size is identical to A)

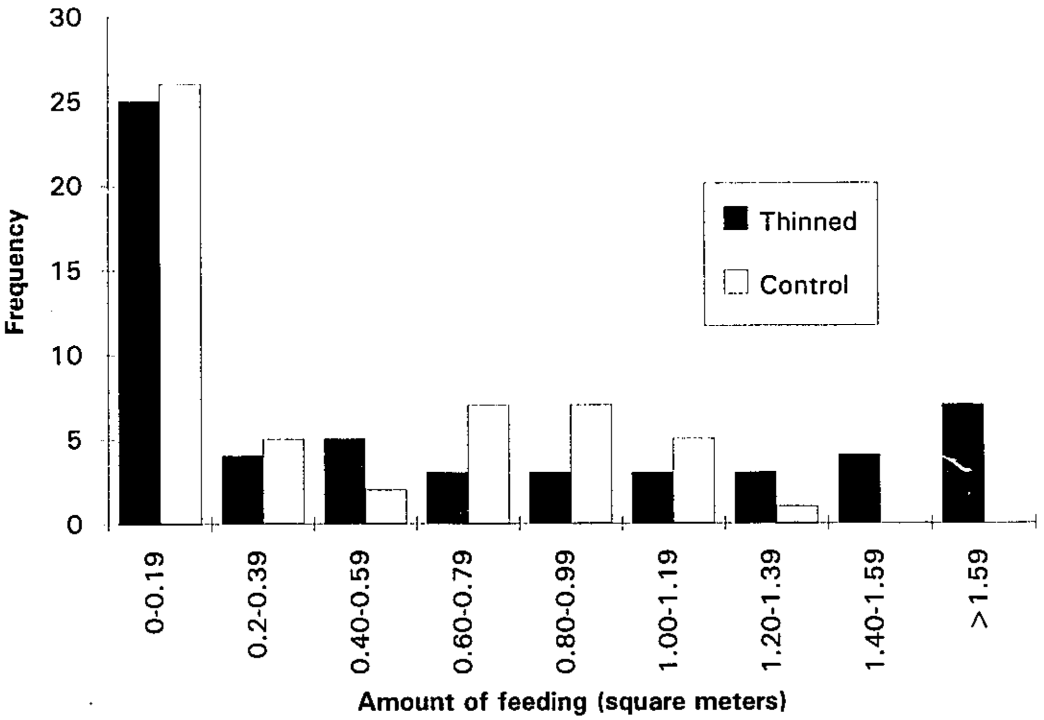


Figure 2-9. Frequency distribution of amount of feeding in first-time atttacked hemlock trees in thinned and control stands near Terrace B.C. Shape of the distribution necessitated a logarithmic transformation to normalize data.

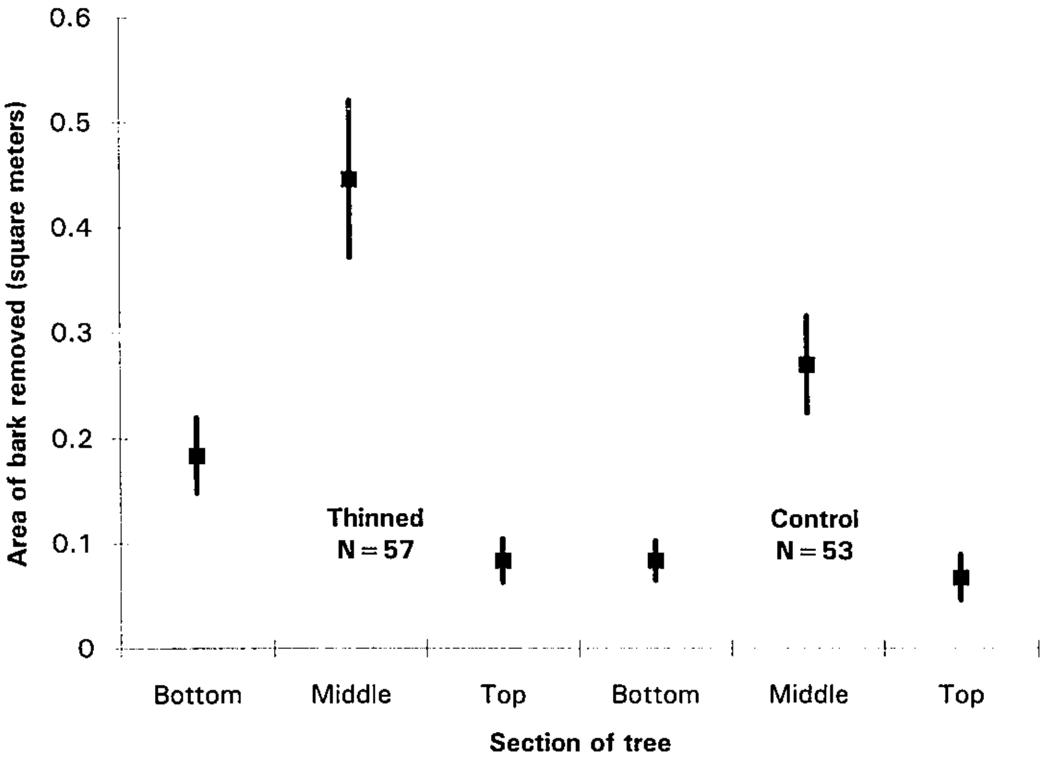


Figure 2-10. Mean (+/- SE) area of bark removed by porcupines from first-time attacked hemlock trees by tree section (Bottom, Middle, Top) and treatment (thinned, control). Untransformed data is presented. Differences between sectionsand treatments were significant (both p's < 0.01; see text for explanation).

CHAPTER 3

INFLUENCE OF STAND THINNING ON DENSITY, SURVIVAL, MOVEMENTS AND FEEDING BEHAVIOUR OF PORCUPINES

INTRODUCTION

Winter feeding damage in coniferous trees by porcupines has been identified as a threat to tree growth and survival in second growth stands in northwestern British Columbia (Sullivan and Cheng 1989; MacHutcheon 1990; Sullivan et al. 1986). Recent reviews of porcupine damage (Sullivan and Cheng 1989; MacHutcheon 1990) have speculated that the increasing area of second growth stands, mild winters and the absence (or low populations) of predators have contributed to the increase in porcupine numbers and damage. Current forest management philosophy promotes the application of growth-enhancing treatments such as thinning to second growth stands. To date more than $70 million have been invested in thinning and reforestation programs in the Kalum and Kitimat Valleys (north and south of Terrace B.C.) alone. However, the porcupines' widely reported preference for faster-growing dominant and co-dominant trees (Harder 1979; Sullivan et al. 1986) suggests that thinning of juvenile stands to improve growth of remaining crop trees has the potential to exacerbate the porcupine damage problem by providing "high quality", easily accessible, winter food (Van Duesen and Myers 1962; Dodge 1982; Sullivan et al. 1986; Sullivan and Cheng 1989). This "food quality" hypothesis predicts the density of porcupines and incidence of porcupine damage to be greater in thinned than control stands (Sullivan and Cheng 1989). Alternatively, the more open thinned stands may represent areas of high predation risk, avoided by porcupines (Sweitzer and Berger 1992).

In addition to the effects on tree growth brought about by thinning, the decrease in tree density also results in an alteration of the distribution and abundance of potential feeding trees for porcupines. Because feeding rates, patch use, and preferences can be affected by changes in prey density and distribution (Cowie 1977; Stephens and Krebs 1986), an examination of the feeding behaviour of individual porcupines within thinned and unthinned stands in addition to density estimation is necessary to evaluate the response of porcupines to stand thinning.

In this chapter I attempt to test the prediction that thinning increases porcupine density. In addition, I combine population and individual-level investigations to examine the influence of stand thinning on survival, home range size, movements and feeding behaviour of porcupines.

STUDY AREA

This study was carried out in the Kalum Valley, 15 km north of Terrace, British Columbia (Figure 3-1). The entire area is within the Coastal Western Hemlock biogeoclimatic zone (Krajina 1969). Dominant tree species include western hemlock (*Tsuga heterophylla*), amabilis fir (*Abies amabilis*) Sitka spruce (*Picea sitchensis*) and western red cedar (*Thuja plicata*). Understory species include *Vaccinium membranacium*, *Vaccinium ovalofolium*, *Menziesia ferriginea*, *Oplopanax horridus* and *Sambucus racemosa* (see Standish et al.1984, for a detailed description of zone vegetation characteristics). Extensive logging in the 1950's and 1960's has resulted in the development of large tracts of naturally regenerated, even-aged second growth stands composed of western hemlock and amabilis fir. Stand tending activities (spacing, pruning) have been carried out on approximately 10,000 hectares, and thousands more are scheduled for this treatment in the future (Sullivan and Cheng 1989).

Porcupine movements, density and feeding behaviour were monitored within two of the four 100 hectare sites originally chosen for the study. One thinned site and one unthinned control of similar disturbance history and species composition (Table 3-1) were selected based on their integrity as homogeneous units, and ease of access in winter. Detailed study area maps of both sites can be found in Appendix 2-A.

TABLE 3-1. Stand Characteristics of the two study sites chosen for monitoring of porcupine density, survival, movements and feeding behaviour in the Kalum Valley near Terrace, B.C., winter 1991.

SITE	YR. LOGGED	YR. SPACED	AGE	% H[a]	% AF	% S[a]	STEMS/ha[b]
OTTO (Thinned)	1960	1984	30	39.3	59.6	1.1	566
BEAR (Control)	1958	N/A	32	62.8	35.7	1.5	1499

[a] AF = amabilis fir, H = western hemlock, S = Sitka spruce
[b] stems per hectare >=7.5cm DBH

METHODS

Capture

Porcupines were captured through systematic searches of the study areas in the winter (November 1 - April 30), through opportunistic encounters while carrying out other work (year-round), and from travelling roads within and around the study areas at night in summer (May 1 - October 31) throughout the two-year period. Animals encountered in trees were captured by hand using leather gloves and a large dip-net. Those located in dens were trapped using single door live traps (40 x 40 x100 cm) placed at the den entrance. I used 10:1 ketamine (80mg ml^{-1}) : ace promisine (100mg ml^{-1}) at 0.07ml kg^{-1} to anesthetize captured porcupines. During late winter when animals were in poorer condition (Roze 1989), I reduced the dose to 0.04 ml kg^{-1}. Captured animals were eartagged with Monel # 3 metal ear tags, sexed, weighed to the nearest 0.05 kg using a Pesola spring scale, length of the right hind foot measured (heel to tip of claw, in millimeters) and fitted with mortality-sensitive radio collars. Animals were classed as adults (> 1 year old) or juveniles (< 1 year old) based on body mass (juveniles < 4.0 kg) and pelage colour (juveniles = black; adults = brown to dark brown).

Porcupine Density

Porcupine density was determined on two sites (1 thinned, 1 control) during the winter period using Minta and Mangels' (1989) closed estimator (ie. no immigration, no emigration). This mark-recapture method employs a Monte-Carlo simulation to solve for the number of unmarked individuals in the sample, yielding an asymmetrical 95% maximum likelihood interval. The main advantage of this method is that unlike Petersen estimates, the assumption of equal sightability (catchability) of all individuals is not applicable. The estimate was derived in the following way:

1) Transects were run through the study area at 100m intervals 24 hours after a fresh snowfall, all fresh sign (tracks, feeding) was followed until the animal was located, its mark (collar frequency or unmarked) was then noted

2) The above procedure was carried out three times within a one week period

3) The number and identity of all collared animals within the census area was determined by monitoring their approximate locations (i.e. on or off study area) at the end of each census day.

4) Solve for the number of unmarked animals in the sample using the iterative monte carlo program "Minta" from Minta and Mangel (1989).

Two observers completed the censuses of the two sites between March 12 and April 17, 1991. Petersen estimates and binomial-generated 95% confidence intervals (Seber 1982) are presented for comparison.

Although replication of the density estimates on all sites would clearly be desireable it was not logistically feasible.

Survival Rates

All radio-collared animals were monitored at least twice-weekly during winter field work and weekly during summer work. No monitoring was done between December 1989 and February 1990, during April 1990, and July to December 1990. Mortalities were investigated immediately following detection of the mortality signal. I classed mortalities as: predator (wolverine, coyote, unknown predator), collar-caused, or unknown cause. Predator kills were distinguished from other mortalities by the presence of fresh blood at the kill sites. Wolverine and coyote kills were distinguished from each other, and from unknown predator kills by the presence of tracks in snow. Additionally, the presence of a small (10 cm diameter) entrance hole into the abdomen of the killed porcupine, a characteristic of mustelid kills (Powell 1982), confirmed the distinction between predators. Unknown predator kills were characterized by the lack of snow tracks in crusty snow conditions, or the presence of the tracks of more than one predator at the kill site. When there was no evidence of predation and the neck area had significant open sores I classed the mortality as collar-caused. Unknown mortalities were animals not killed by predators and showed no sign of collar related injuries.

I used the staggered entry (Kaplan-Meier) method as outlined by Pollock et al. (1989) to estimate survival rates. Due to the low mortality rates, particularly during the summer, a thirty day period was chosen as the censoring interval used in survival rate estimation. I subdivided the dataset by year (1989-90; 1990-91), sex (M or F) and season (Winter = November 1 - April 30; Summer = May 1 - October 31) and ran separate analyses on each. I used F-tests (Lee 1980) to compare between groups.

Home range

Home range data were obtained for 13 porcupines (4 control, 9 treatment). An additional collared animal which moved from the control to the treatment site and back again (a one-way distance of 2.2 km) was omitted from the main dataset. For descriptive purposes I have calculated and presented separately, two home ranges for this individual.

Radio-collared animals were located using a handheld antenna at least once per week between January 15 and April 30, 1991. The number of locations varied between individuals (range 13-41, mean = 24.3) due to staggered entry of individuals into the tagged population, predation prior to the end of the period and receiver malfunctions during wet weather. To calculate home range sizes for individual porcupines within the study areas I used the simple minimum convex polygon technique (Mohr 1947). I used a harmonic mean contouring method (Kenward 1987) to identify the number of activity centres within each animals home range.

To test for differences in home range size between treatments and sexes I used ANCOVA, controlling for the number of locations per animal. This procedure allowed an assessment of potential bias due to unequal sample sizes.

Daily Movements, Feeding behaviour

Daily movement distances and feeding site characteristics were determined by snow trailing radio-collared porcupines from present to previous day locations. These data were gathered opportunistically when snow conditions were favourable for the detection of fresh tracks. Feeding sites along the trail were described by: distance from starting point, species, diameter, and type of feeding (bark or foliage). Bark feeding was characterized by the presence of strips of outer bark at the base of the tree and the evidence of exposed sapwood; foliage feeding was characterized by the presence of clipped twigs with needles browsed off, lying at the base of the feeding tree. For each day I estimated the sinking depth of the tracks into the snow by measuring track depths into the snow at 5 locations along the feeding trail. When no movement occured in a 24 hour period the sinking depth was considered to be the depth a 300g diameter tape would sink into the snow when dropped from 15 cm above the snow surface. This was verified through trial and error to correspond closely with porcupine sinking depth. These measurements were taken in untracked snow at least 2m away from the tree trunk (and associated tree-well).

A total of 109 (Thinned = 91 days; Control = 18 days) porcupine-days of snow trailing data were obtained from 12 individual animals. Two additional animals which were represented by a single day of trailing data were dropped entirely from the dataset. In a similar fashion to the home range analysis, I have summarised and presented separately the movement and feeding data from the one animal which moved back and forth between study sites. The relatively low sample size for control site tracking-days reflects the difficulty in trailing porcupines in the denser, unthinned stand. The higher levels of crown closure resulted in less snow penetrating the canopy (resulting in poorly defined tracks), more canopy drip (which obscured tracks) and more frequent tree-to-tree movements all of which contributed to the lower numbers of tracking days in the unthinned site.

I used Nested ANOVA to examine the relationship between distance travelled and stand type, with individual animals as the nested factor within stand type. I ran similar analyses for number of feeding sites used per night, number of species used per night, number of trees used for bark feeding per night and the number of foliage feeding sites used per night. I regressed subsequent versus initial travel distances to examine the independence of observations from sequential days. If subsequent travel distances were inversely or positively related with initial movements, I expected to find a significant regression with negative or positive slope, respectively.

RESULTS

Captures

A total of 42 porcupines (17 females, 25 males) were captured and radio-collared between May 1989 and May 1991. Of these, four were juveniles (< 1 year old); an additional three juveniles were captured and ear-tagged, but were not fitted with radio-collars due to their small size (0.5 - 2.0 kg). Captures totalled 19 (9 M; 10 F) for the thinned site (OTTO) and 23 (16 M: 7 F) for the unthinned control (BEAR). The majority of captures (52%) were made by directly removing porcupines from feeding or resting trees. The remaining animals were captured on roads (21%) within and adjacent to the study areas, in traps (17%) or on the ground (10%). Capture weights of adult porcupines varied between sexes but not between sites (Two-way ANOVA; sex: $F_{1,38} = 12.6$, $p = 0.001$; site: $F_{1,38} = 0.74$, $p = 0.397$; interaction N.S.). Males were 17 - 37% heavier (Thinned: 8.9 ; 1.57 S.D.; Control: 9.95 ; 1.91 S.D.) than females (Thinned: 7.58 ; 1.16 S.D.; Control: 7.24 ; 1.91 S.D.).

Porcupine Density

Porcupine densities were similar on both sites (Thinned: 9 per 100 ha; Control: 9 per 100 ha.; Table 3-2) in 1991. Collared porcupines were more than twice as likely to be detected in the thinned stand than those in the control (Table 3-2). Reduced detectability of porcupines in the control site resulted in a wider maximum likelihood interval of density on that site. Petersen and maximum likelihood estimates [MLE] were similar on both sites, however the confidence intervals were tighter for the MLE of the thinned site and asymmetrical around the mean for both sites. Asymmetrical confidence intervals appear to be more realistic as it was ***known*** that at least 6 and 5 porcupines were present within the thinned and control site respectively, and therefore the lower confidence limits for the Petersen estimates seem conservative (Table 3-2).

On both sites, at least one collared porcupine known to be present was not detected during any of the three census days. Zero detections of animals were due to transects not crossing their feeding trails, or lack of movement by the animal.

TABLE 3-2. Encounter frequency of marked (0, 1, 2 or 3 times) and unmarked porcupines and density estimates [Petersen estimate (95% CI, using Baileys binomial Model); maximum liklihood estimate; (MLE)] per 100 ha for two study sites during the winter of 1991 based on three repeated censuses of each site.

	No. encounters						DENSITY (per 100 Ha.)	
SITE	**0**	**1**	**2**	**3**	**Unmarked**	**Encounter probability[1]**	**Petersen**	**MLE**
Thinned	1	0	3	1	7	0.60	8.9 (5.7-12.1)	9 (8-12)
Control	2	1	1	0	4	0.25	9.3 (4.3-14.3)	9 (7-17)

[1] Probability that any collared animal is detected in a single census

Survival Rates

A total of 13 porcupines died during this study. The most common cause of death was predation (8 deaths), followed by collar-caused mortalities (3 deaths) and unknown (2 deaths). All but one mortality occured during the winter (November 1 - April 30). Predator kills included: 3 by wolverine (*Gulo gulo*), 1 by coyote (*Canis latrans*) and 4 by unknown predators. All deaths classed as unknown predator kills had the appearance of mustelid attacks (entry hole in abdomen, severe facial wounding; Powell 1977;1982); however confirmation as to species of predator was not possible due to lack of tracks (3 of 4) or mixture of marten and wolverine tracks at the kill site (1 of 4). Two mortalities occured during my absences from the field; both were classed as a unknown predator kill as both carcasses were headless (one animal's battered head was retrieved separately nearby) and resembled mustelid kills (entry hole in abdomen). While it is possible that these animals were scavenged rather than depredated, the appearance of the carcasses were consistent with those from confirmed wolverine attacks.

Predator kills were located in the thinned site (2), control site (3), on the road between sites (1) and within residual patches of old-growth forest adjacent to the study sites (2). There was no clear indication that stand thinning influenced predation. In two cases, porcupines which were from the thinned site were killed in openings within adjacent unthinned forest, confounding the ability to calculate separate estimates for thinned and control sites. However, 5 of the 8 predator kills were made in small (<1 ha.) openings within sites, suggesting porcupines may be more vulnerable in open areas, even those of small size.

I attributed the death of three animals to the radio-collars themselves. All three animals had chafing of the skin and infection at the jaw flexure from the sharp-edged backing plate used to close the collar. The two unknown mortalities were likely due to starvation as they both occured in late winter (March) when porcupines are in the poorest condition (Roze 1989). These animals died in their dens, and examination of the carcasses revealed no evidence of collar-caused infection or predation.

TABLE 3-3. Kaplan-Meier estimates of survival for porcupines by year, season and sex. Groups joined by the same last letter were significantly different at $p < 0.05$ using an F-test (Pollock et al. 1989).

GROUP	YEAR[1]	No. present	No. Killed	Survival (95% C.I.)
Year				
1989	-	20	3	0.796 (0.608 - 0.984)
1990	-	35	7	0.652 (0.484 - 0.821)
Season[2]				
Summer	1989	14	0	1.000
Winter	1989	18	3	0.796 (0.608 - 0.984)
Summer	1990	19	1	0.923 (0.798 - 1.000)[b]
Winter	1990	32	6	0.707 (0.539 - 0.874)[b]
Sex				
Male	1989	12	1	0.875 (0.673 - 1.000)
Female	1989	8	2	0.667 (0.329 - 1.000)
Male	1990	22	4	0.700 (0.506 - 0.894)
Female	1990	13	3	0.533 (0.214 - 0.853)

[1] Winter 1989 = Nov. 1989 - April 1990; Winter 1990 = Nov. 1990 - April 1991)

[2] No statisical test performed due to zero variance in summer survival rate.

Seasonal survival rates differed markedly; summer survival was 100% in 1989 and 92% in 1990, winter survival was 80% in 1989 and 71% in 1991 (Table 3-3). Differences in seasonal survival rates were significant for 1990 ($F_{2,12} = 4.97$, $p < 0.05$)

and were not compared due to zero variance in the summer survival rate for 1989. Yearly survival was higher in 1989 (80%) than in 1990 (65%), and males tended to have higher survival (1989: 88%; 1990: 70%) than females (1989: 67%, 1990: 53%) however these differences were not statistically significant (years: $F_{6,14} = 1.46$, $p > 0.10$; sexes [1989]: $F_{2,4} = 2.68$, $p > 0.10$; sexes [1990]: $F_{8,6} = 2.02$, $p > 0.10$; Table 3-3).

Home Range

Mean home range size for 13 porcupines during the winter of 1991 was 8.6 ha. (S.D. = 7.3) using the minimum convex polygon [MCP] method (Table 3-4). Home range sizes tended to be larger in the thinned than control site, and greater among males than females, however these differences were not significant (ANCOVA: Sites: $F_{1,12}= 0.08$, p=0.79; Sexes: $F_{1,12}= 1.2$, p =0.30; Covariate (No. Fixes): F = 0.02, p = 0.91; Table 3-4). Unequal numbers of locations evidently did not bias home range estimates as home range size did not vary with the number of locations (r = 0.24, p =0.379, n = 13). The number of activity centres per animal also did not differ between sites or sexes (Sites: $F_{1,12}= 0.13$, p=0.72; Sexes: $F_{1,12}= 0.91$, p =0.36; Covariate (No. Fixes): F = 2.49, p = 0.15). Home ranges overlapped extensively on both sites within and between sexes.

TABLE 3-4. Mean home range size and number of activity centres for porcupines in second growth forest near Terrace, B.C. during winter 1990-91 summarized by sex and treatment. Areas were calculated by Minimum Convex Polygon method, activity centres were determined by Harmonic Mean Contouring.

MEANS	Number of porcupines	Number of fixes (SD)	Home Range [ha.](SD)	Activity Centres (SD)
Thinned	9	27.7 (10.1)	9.3 (6.7)	1.8 (0.7)
Control	4	16.8 (5.6)	7.1 (9.4)	1.5 (0.6)
Males	7	29.6 (10.4)	11.2 (8.5)	1.7 (0.8)
Females	6	18.2 (5.6)	5.7 (4.6)	1.7 (0.5)
Overall	**13**	**24.3 (10.1)**	**8.6 (7.3)**	**1.7 (0.6)**

Daily movements, Feeding Behaviour

Average daily movements of individual porcupines in winter ranged from 63 - 295 meters (Figure 3-2). Movements did not vary between sites but varied significantly among animals (Table 3-5 ; Figure 3-2). Snow conditions varied widely (sinking depths:

1-100 mm), but did not influence distance moved by porcupines ($r = 0.10$, $n = 110$, $p = 0.342$; Figure 3-3). In addition, there was no relationship between "initial" and "subsequent" movements ($r = 0.28$, $n = 48$, $p > .05$; Figure 3-4), indicating that the observations were independent. Movements of porcupines did not appear to be influenced by thinning (Table 3-5).

The number of feeding sites used per day (Figure 3-5, Table 3-5) did not differ for porcupines feeding within the two stand types. However the number of species (Figure 3-6; Table 3-5), and the number of foliage feeding sites used per day (Figure 3-7; Table 3-5) were significantly greater, and the number of bark feeding sites used, significantly less (Figure 3-8; Table 3-5) for porcupines feeding in the thinned than those in the control site. This is attributable to the frequent inclusion of sitka spruce foliage, amabilis fir foliage and bark in the diets of porcupines within thinned stands (Figure 3-9). Overall, 93 of the 96 foliage feeding sites were tallied in the treatment site. Foliage feeding within hemlock trees was rare and absent in the thinned and control site respectively. Porcupines also fed on the stems of *Sambucus racemosa* nine times within the thinned site.

The frequency of repeated (used more than once) feeding within trees was significantly greater ($G = 3.87$, $df = 1$, $p = 0.049$) in the thinned site (31.4%) than the control (17.4%).

TABLE 3-5: Nested ANOVA Analysis of movements, number of trees damaged, number of species used, number of bark feeding trees used, number of foliage feeding trees used and the area of bark removed per night by porcupines between sites and animals within sites.

Dependant Variable ([var.] night^{-1})	Mean Thinned (SD)	Mean Control (SD)	Independant Variable(s)	N	df	F-ratio	p
Distance (m)	145 (134)	113 (82)	Site	116	1	0.038	0.846
			Animal (Site)		11	1.857	0.06
Number of trees	2.30 (1.3)	2.55 (1.1)	Site	109	1	0.025	0.876
			Animal (Site)		11	2.563	0.009
Number of species	1.6 (0.6)	1.1 (0.3)	Site	109	1	13.312	<0.001
			Animal (Site)		11	5.515	<.001
Number bark feeding trees	1.2 (1.4)	2.38 (1.0)	Site	109	1	13.034	<0.001
			Animal (Site)		11	3.651	<0.001
Number foliage feeding trees	1.1 (0.97)	0.17 (0.24)	Site	109	1	25.622	<0.001
			Animal (Site)		11	3.567	<0.001

DISCUSSION

I found no evidence to suggest that porcupine density was greater in the thinned treatment. Although my estimates of porcupine density within treatments are unreplicated, the similar damage rates and tree density (particularly hemlock; Table 2-1, 2-2) *within* treatments offers some indirect support for the observed similarities in density. My estimates of 9 porcupines per km^2 in both thinned and control stands are similar to those reported by Roze (1984; 10.7 /km^2), Smith (1977; 12.6/km^2) and Curtis (1944; 9.3/ km^2); however their estimates were based on "total enumerations", a technique likely to underestimate density. The finding in this study that not all animals were detectable, even after three censuses, clearly shows the inability to estimate density confidently using a total enumeration method, particularly in dense forest. The use of a mark-resighting method (Minta and Mangel 1989) for estimating porcupine density produced a relatively narrow likelihood interval (i.e. mean +/- 22%) for the thinned stand where detectability of animals was high (0.60); in contrast the denser, control sites yielded much lower probability of detection (0.25) and a wider, assymetrical likelihood interval (i.e. mean + 89%, mean - 22%) . These differences in detectability of porcupines between treatments may account for the perceived increase in porcupine numbers following stand thinning reported by Sullivan and Cheng (1989). In order to improve the precision of the estimate for the unthinned stand, the number of repeated censuses would have to be increased. By bootstrapping (Efron 1982), the possible configurations of the "observed" encounter frequencies across a range of census repetitions, the approximate number of repetitions required to reach a desired level of precision in the population estimate could determined.

The validity of the density estimates obtained however, rests on the adherence to the assumptions. The assumption of demographic closure was not violated for the collared porcupines present during the brief census period as no collared individuals moved on or off the 100 ha. sites. However, movement in and out of the sites did occur over the winter period, indicating closure was only temporary. Despite this, bias is unlikely as there is no reason to expect different movement patterns of marked and unmarked porcupines in and around the study sites. The assumption of equal probability of initial capture is difficult to examine rigorously. However because porcupines were captured opportunistically during all times of the year using a variety of methods and no attractants were used, I believe this assumption was not violated. The assumption of independance between initial and subsequent "capture" is also reasonable as the animals were encountered on systematic searches of the study sites and "re-capturing" was done visually without disturbing or handling.

Although it is clearly desirable to minimize potential edge effects by using as large a study site as possible, the 100 ha. sites used in this study were sufficient for obtaining reasonable estimates. In addition, because study site selection was constrained by the silvicultural history of the second growth stands, larger, homogenous sites were not available.

The maximum likelihood method developed by Minta and Mangel (1989), has also been recently applied to estimate grizzly bear (*Ursus horribilis*) densities with photo-recapture data (Mace et al. *in press*). Use of the maximum likelihood estimate was preferred over Petersen estimates because the former method avoids the assumption of equal catchability (Mace et al. *in press*). Clearly, this method offers advantages over traditional Petersen estimates and will likely be used with increasing frequency in the future.

I was unable to evaluate rigorously the importance of stand thinning to porcupine survival because only 5 of the 8 predator kill sites could be ascribed simply to thinned or control sites. The calculation of separate survival rates for thinned and unthinned stands was not possible since data were confounded by animals inhabiting the thinned site being killed in adjacent unthinned stands. Nonetheless, the fact that 5 of 8 predation mortalities were in small (< 1 ha.), sparsely treed openings within stands suggests that vulnerability may be greater in more open habitats. In Nevada grassland-shrub habitat, Sweitzer and Berger (1992) concluded that porcupines forage in a risk-sensitive manner, avoiding open habitats unless nutritionally stressed. Although the stand density of the thinned site (566 stems/ha) was much less than the control site (1499 stems/ha), thinned stands may only become "risky" for porcupines when tree densities are much lower (i.e.100-200 stems/ha), approximating those of the sparsely treed openings.

At present, there are no published data on causes and rates of porcupine mortality in the literature. My data suggest predation to be the primary source of adult mortality and the wolverine to be the main predator. In the field, wolverine tracks following those of a porcupine and the presence of wolverine bedding sites beneath porcupine feeding trees suggest that wolverine actively pursued porcupine. I sighted a wolverine on two occasions and also chanced upon the kill of an uncollared porcupine by a wolverine. Marten (*Martes americana*) and coyote were also present on the site; however, marten (although abundant) were not observed pursuing porcupines and although a coyote did kill one porcupine, sign was rarely noted within the study sites. Fisher (*Martes pennanti*) are widely touted as the main predator of porcupines (Cook and Hamilton 1957; Dodge

1982; Earle and Kramm 1982; Powell 1982; Roze 1989) and have been suggested to limit porcupine density (Earle 1978). However, the evidence for this was purely correlational as those studies only examined prey (porcupine) density in the presence and absence of fisher to draw their conclusions. In my study area, fisher have not been trapped, or fisher sign noted over the past 30 years (Otto Lindstrom: trapper, *personal communication*). Based on these observations, I suggest that wolverine constitute the main predator of adult porcupines in the present study system and were likely responsible for those predation mortalities classed as unknown.

In order to explore the impacts of the estimated survival rates on the potential for population growth (r), I constructed a simple life table using published data on age at first reproduction (2 years; Dodge 1982), litter size (1 porcupette; Earle 1978; Dodge 1982) and the sex ratio (1:1; Earle 1978), and set emigration = immigration. I specified a wide range of values for adult and juvenile survival and solved iteratively for r, the intrinsic rate of increase using the formula: (from Lotka 1907)

$\Sigma e^{-rx} l_x b_x = 1$, where

r = intrinsic rate of increase
lx = age-specific survival rate (specified [0.40 - 1.00 per year])
bx = age-specific birth rate of female offspring (assumed to be constant (0.5 females per year per female greater than or equal to 2 years old) for this example)
x = age

Figure 3-10 graphically presents the results of this analysis. Clearly, for porcupine populations to increase (r positive), both adult and juvenile survival must be very high (>=0.75 per year). The adult survival rates calculated for porcupine in this study suggest that the population is probably declining. The assumptions used in the preceeding analysis were probably more likely to overestimate r values than underestimate them as it is unlikely that all females (>= 2 years old) reproduced each year. Through repeated locations and/or physical examinations (May - July), I found in 1989 only 5 of 7 and in 1990 only 2 of 3 females to be lactating or with young accompanying them. Similarly, Smith (1977) calculated an adult female : young ratio of 0.58 in August, suggesting that juvenile mortality is high or females do not reproduce each year. At the estimated adult survival rates, the population could only increase through immigration and/or sex ratio adjustment of the young produced. Additional data on juvenile production and survival, as well as dispersal and immigration will be needed to determine if populations are declining.

The home range size estimates generated from this study correspond with those of Roze (1989) and Smith (1979) who reported an average winter home range size of 7.4 ha. and 6.0 ha respectively. A study by Craig and Keller (1986), in scrub-desert habitat yielded an average winter home range size of only 0.07 ha.; however, in their study only two animals were monitored over a short time period. My data suggest that home range size and daily movement distances are not sensitive to stand thinning

There were several differences in feeding behaviour of porcupines between the two stand types. Porcupines in thinned stands fed on a greater number of species per night and consumed amabilis fir and spruce foliage more frequently than those in the control site. These behavioural differences may indicate a relaxation of feeding preferences of porcupines within the thinned stand or possibly, food quality differences between sites.

The marked difference in the frequency of foliage feeding between the thinned and control site appears strong, but a note of caution should be raised: owing to the poor detectability of snow tracks beneath the canopy in the control site, only 18 snow trailing days from 3 male porcupines represent the control site data. An examination of the feeding data from the porcupine from which I gathered snow trailing data from both sites, provides support for the reported pattern of foliage feeding; in the thinned stand this animal fed at 10 of 38 sites, while in the control site only 3 of 24 was recorded. The possibility of bias from obtaining data only from males seems unlikely given the wide within-sex variation in behaviour of porcupines in the thinned stand.

Numerous studies have reported increased damage by small mammals in conjunction with growth-enhancing treatments such as thinning (Daniel and Barnes 1958; Sullivan and Vyse 1987; Sullivan and Klenner 1993) and fertilization (Sullivan and Sullivan 1982). However, the relationship between animal density and damage incidence among treatments has always led to equivocal results; animal density does not correlate directly with the percentage of trees damaged (Sullivan and Moses 1986). I suggest the reason for this is twofold; (1) stand density influences the availability and therefore selection of food items (the ratio of bark to foliage feeding in this case), and (2) stand density influences the intensity of feeding within trees (Chapter 2), resulting in different use (damage) rates for animals in different treatments. Comparisons of damage rates between treatments are appropriate for evaluating stand-level impacts; however to examine the relationship among animal density, damage rates and treatment, damage rates must be expressed in the same absolute (per hectare) terms. Further, because treatment (thinning) influence rates and selection of feeding trees by individual porcupines, a simple relationship between porcupine density and per-hectare damage is not indicated. Given that the density of porcupines did not differ between stand types, the number of trees damaged *per hectare* should have been equal if porcupines damaged the trees at the same rate in both stand types. This was clearly not the case, porcupines damaged fewer trees on a *per hectare* basis in thinned stands than in controls. More frequent repeated feeding in trees within (this Chapter) and among years (Chapter 2) and the increased frequency of foliage feeding (which was not detected in damage assessment plots) within thinned stands may explain these differences.

LITERATURE CITED

Brander, R.B. 1973. Life history notes on the porcupine in a hardwood hemlock forest in upper Michigan. Michigan Acad. 5:425-433.

Cook, D.B., and W.J. Hamilton. 1957. The forest, the fisher and the porcupine. J. For. 55: 719-722.

Cowie, R.J. 1977. Optimal Foraging in great tits (*Parus major*). Nature 268:137-139.

Craig, E.H., and Keller, B.L. 1986. Movements and home range of porcupines (*Erethizon dorsatum*) in Idaho shrub desert. Can. Field Nat. 100(2):167-173.

Curtis, J.D. 1944. Appraisal of porcupine damage. J. Wildl. Manage. 8:88-91.

Daniel, T.W., and Barnes, G.H. 1958. Thinning a young stand of lodgepole pine. Proc. Soc. Amer. For. pp. 159-163.

Dodge, W.E. 1982. Porcupine. In: Wild Mammals of N.A. Biology, Management and Economics. J.A. Chapman and G.E. Feldhammer (editors). Johns Hopkins University Press, Baltimore, MD. pp 355-366.

Earle, R.D. 1978. The fisher-porcupine relationship in upper Michigan. MSc. thesis. Michigan Technical University. 114 pp.

Earle, R.D. and K.R. Kramm. 1982. Correlation between fisher and porcupine abundance in Upper Michigan. Am. Midl. Nat. 107:244-249.

Efron, B. 1982. The jackknife, the bootstrap, and other resampling plans. Society of Industrial and Aplied Mathematics, Philadelphia.

Elgitis, A. and P.E. Hennon. 1986. Porcupine damage in Sitka spruce and western hemlock in southeast Alaska. USDA Forest Service Pest Management report, Juneau. 21pp.

Harder, L.D. 1979. Winter feeding by porcupines in montane forests of southern Alberta. Can. Field Nat. 93:405-410.

Kenward, R.E. 1987. Wildlife Radio Tagging. Academic Press. San Diego, CA. 222 pp.

Kozlowski, T.T. 1971. The Growth and Development of Trees. Academic Press, New York.

Krajina, V.J. 1969. Ecology of Forest trees in British Columbia. Ecol. West. North Am. 2: 1-147.

Lee, E.T. 1980. Statistical Methods for Survival Analysis. Lifetime Learning Publications, Belmont, California. WA950 L477

Lotka, A.J. 1907. Studies on the mode of growth of material aggregates. American Journal of Science 24: 199-216.

MacHutcheon, A. G. 1990. Porcupine feeding damage in second-growth stands of the North Coast Forest District, B.C.: A Summary. B.C. Ministry of Forests, Smithers B.C. 76pp.

Mace, R.D., S.C. Minta, T.L. Manley, and K.E. Aune. 1993. Use of cameras to sight grizzly bears for estimating population size. J. Wildl. Manage. *in press.*

Minta, S. and Mangel, M. 1989. A simple population estimate based on simulation for capture-recapture and capture-resight data. Ecology. 70(6): 1738-1751.

Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37: 223-249.

Pollock, K.H., S.R. Winterstein, C.M. Bunck, and P.D. Curtis. 1989. Survival Analysis in telemetry studies: the staggered entry design. J. Wildl. Manage. 53:7-15.

Powell, R.A. 1977. Hunting behaviour, ecological energetics and predator-prey community stability of the fisher (*Martes pennanti*). Ph.D thesis. Univ. Chicago.

Powell, R.A. 1982. The fisher: life history, ecology and behaviour. Univ. Minnesota Press. 217pp.

Roze, U. 1989. The North American porcupine. Smithsonian Institute Press.

Roze, U. 1987. Denning and winter range of the porcupine. Can. J. Zool. 65:981-986.

Roze, U. 1984. Winter foraging by individual porcupines. Can. J. Zool. 62:2425-2428.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. 2nd Edition. Charles Griffin & Company. London.

Smith, G.W. 1977. Population characteristics of the porcupine in northeastern Oregon. J. Mammal. 58:674-676.

Smith, G.W. 1979. Movements and home range of the porcupine in northeastern Oregon. Northwest Sci. 53:277-282.

Spencer, D.A. 1964. Porcupine population fluctuations in past centuries revealed by dendrochronology. J. Appl. Ecol. 1:127-149.

Standish, J.T., S. Haeussler, A. Kokoshke, J. Pojar, D.Holmes, B.M. Geisler, and D. Yole. 1987. A field guide for identification and interpretation of the Coastal Western Hemlock Zone, Northern Drier Maritime Subzone (CWHf), in the Prince Rupert Forest Region. B.C. Ministry of Forests. Land Management Handbook #14, 63 pp.

Stephens, D.W., and Krebs, J.R. 1986. Foraging Theory. Monographs in Behavioural Ecology. Princeton University Press. 247pp.

Storm, G.L., and C.H. Halvorsen. 1967. Effect of injury by porcupines on radial growth of ponderosa pine. J. For. 65:740-743.

Sullivan, T.P., and Cheng, C. 1989. Impact of Porcupine Feeding damage on intensive forest management in the Prince Rupert Forest Region: Problem Analysis. FRDA Report No. 083. 20pp.

Sullivan, T.P.,W.T. Jackson, J. Pojar, and A. Banner. 1986. Impact of feeding damage by the porcupine on western hemlock - Sitka spruce forests of north coastal British Columbia. Can. J. For. Res. 16:642-647.

Sullivan, T.P., and W.E. Klenner. 1993. Influence of diversionary food on red squirrel populations and damage to crop trees in young lodgepole pine forest. Ecol. Appl. 3: 708-718.

Sullivan, T.P. and R.A. Moses. 1986. Red squirrel populations in natural and managed stans of lodgepole pine. J. Wildl. Manage. 50: 595-601.

Sullivan, T.P. and D. S. Sullivan. 1982. Influence of fertilization on feeding attacks to lodgepole pine by snowshoe hares and red squirrels. For. Chron. 58: 263-266.

Sweitzer, R.A. and J. Berger. 1992. Size-related effects of predation on habitat use and behavior of porcupines (*Erethizon dorsatum*). Ecology 73:867-875.

Van Deusen, J.L. and C.A. Myers. 1962. Porcupine damage in immature stands of ponderosa pine in the Black Hills. J. For. 60: 811-813.

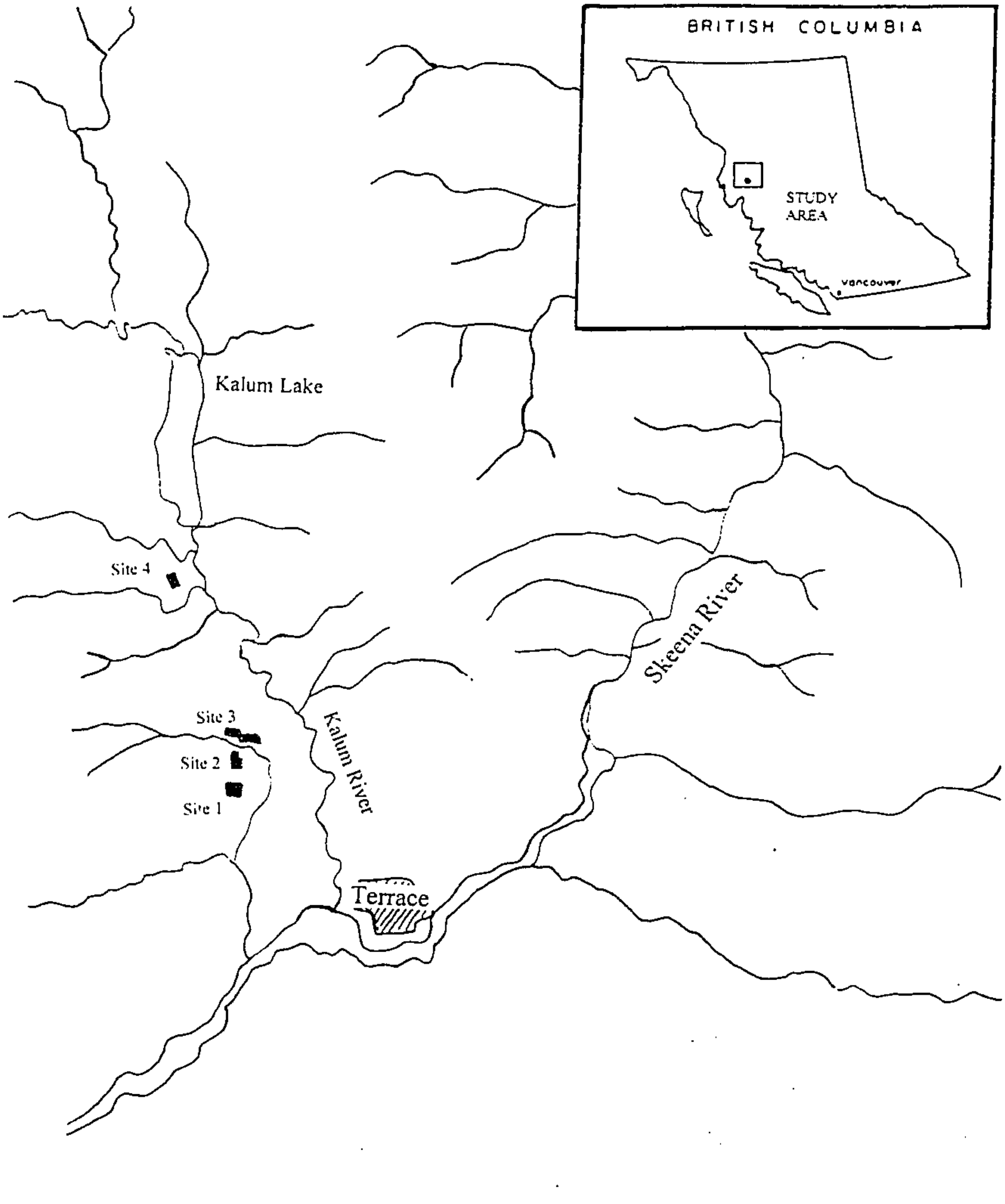


Figure 3-1. Location of thinned (Site 1 [Otto]) and control (Site 2 [Bear]) study sites near Terrace B.C. Sites are 100 hectares in size.

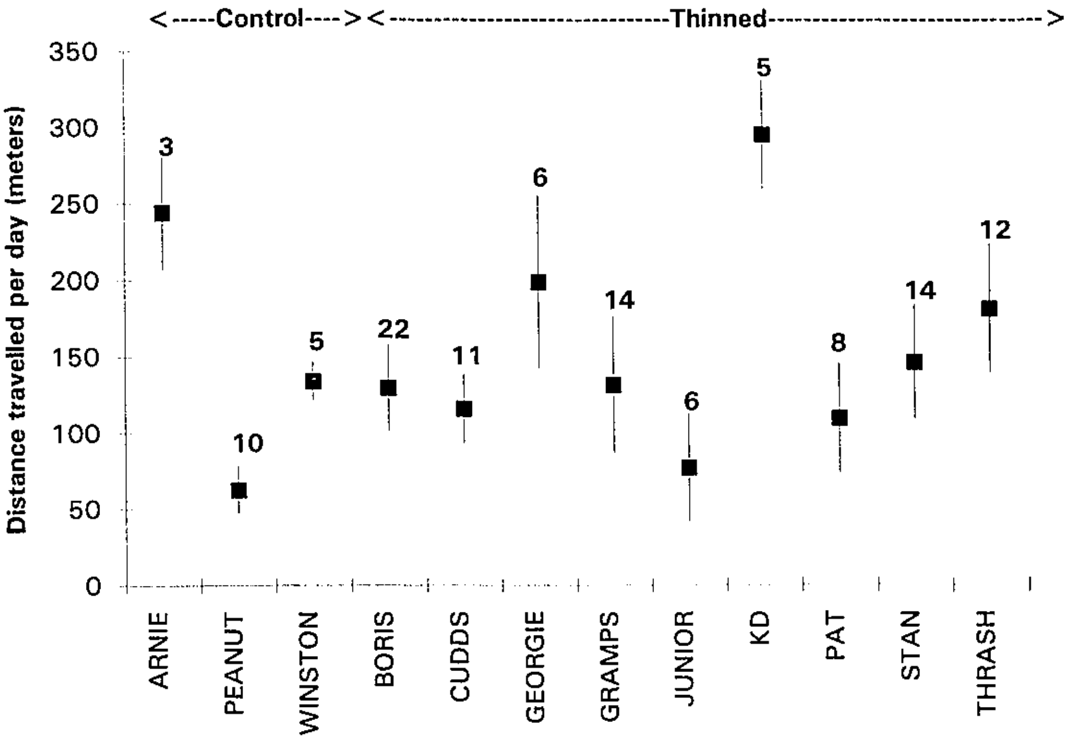


Figure 3-2. Average distance travelled per day for 12 radio-collared porcupines within a thinned and a control stand near Terrace B.C. during winter 1990-91. Bars represent +/-SE, sample size is indicated above each bar.

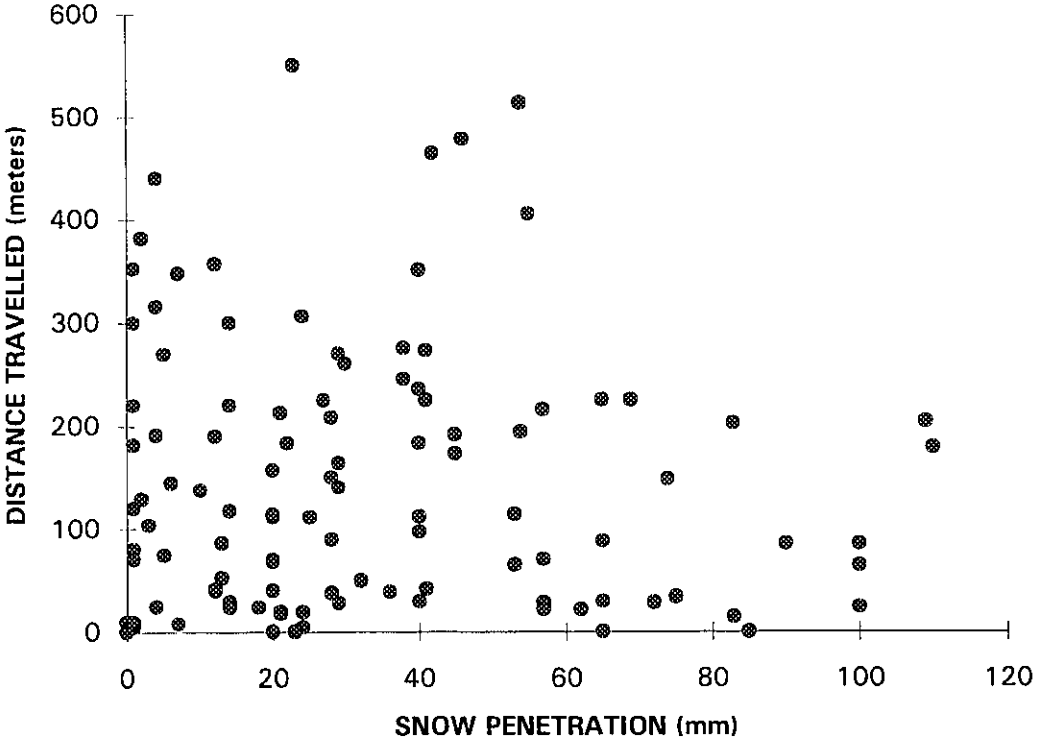


Figure 3-3. Distance travelled over a 24 hr period versus porcupine foot sinking depth for porcupines foraging in second growth stands near Terrace B.C. during winter 1990-91 (r =0.10 , n = 110 , p = 0.34).

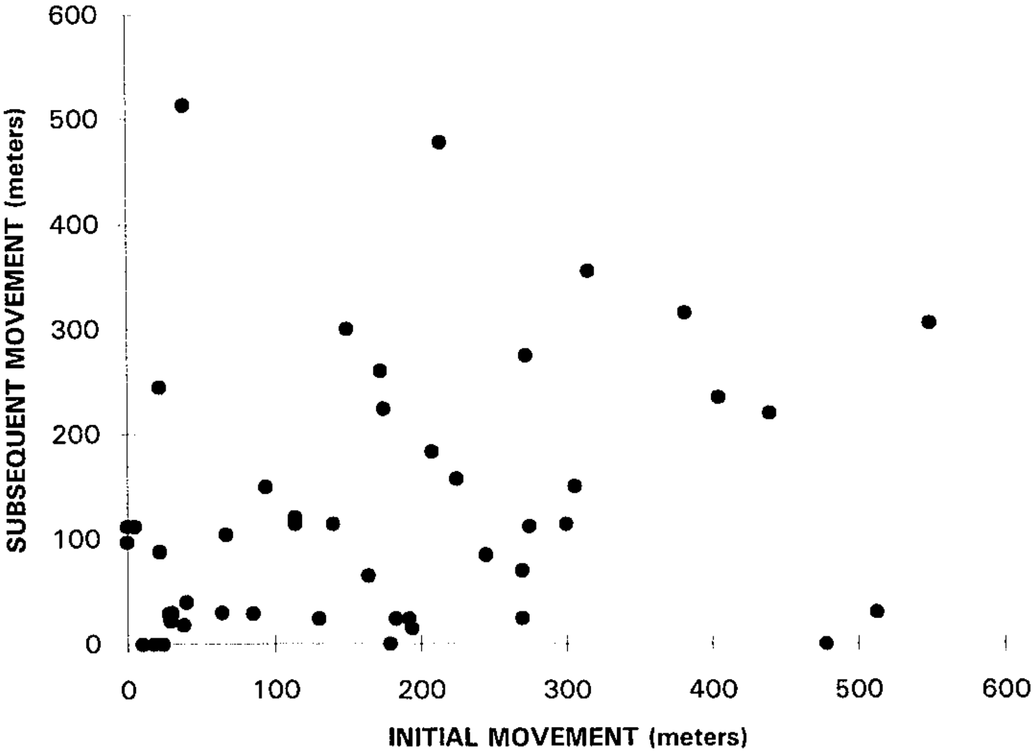


Figure 3-4. Subsequent versus Initial movement distance for porcupines foraging in second growth stands near Terrace B.C. during winter 1990-91 ($r = 0.28$, $n = 48$, $p > 0.05$).

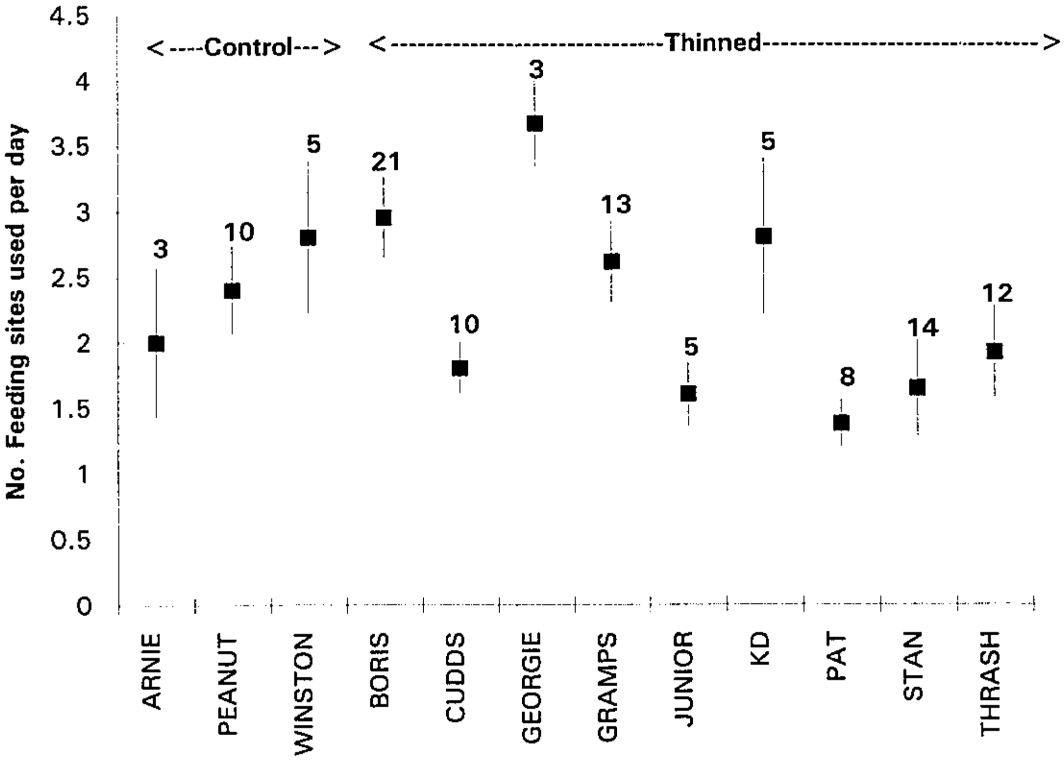


Figure 3-5. Average number of feeding sites used per day for 12 radio-collared porcupines within a thinned and a control stand near Terrace B.C. during winter 1990-91. Bars represent +/-SE, sample size is indicated above each bar.

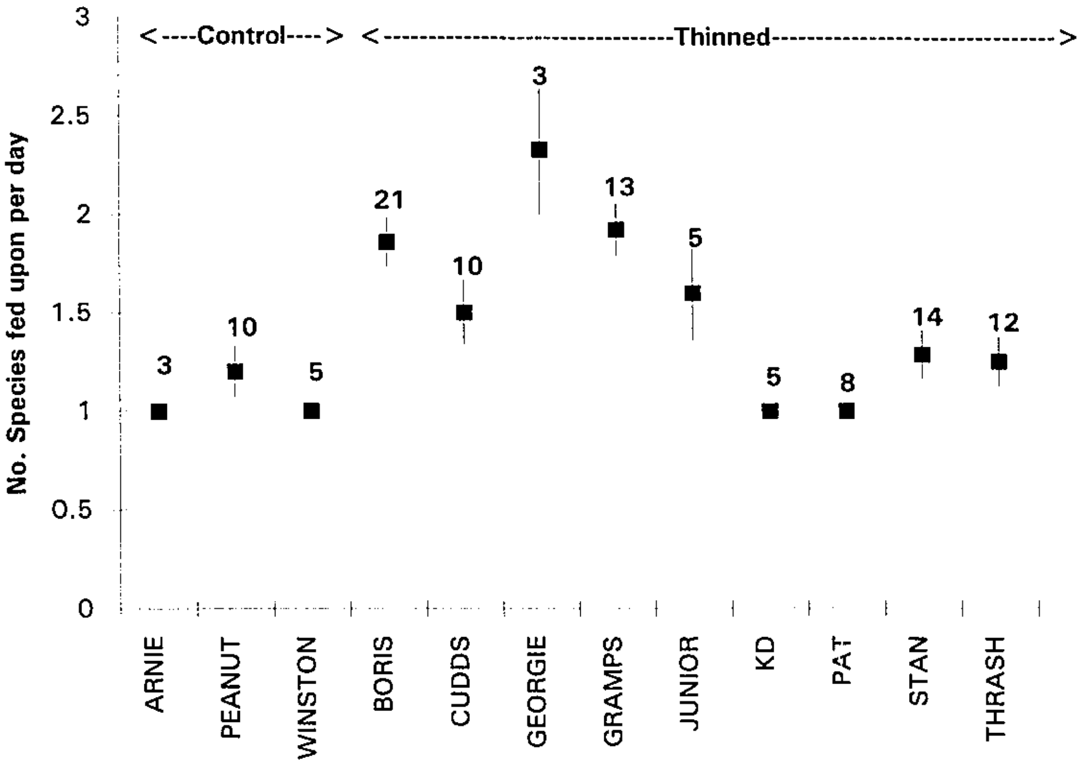


Figure 3-6. Average number of species fed upon per day for 12 radio-collared porcupines within a thinned and a control stand near Terrace B.C. during winter 1990-91. Bars represent +/-SE, sample size is indicated above each bar.

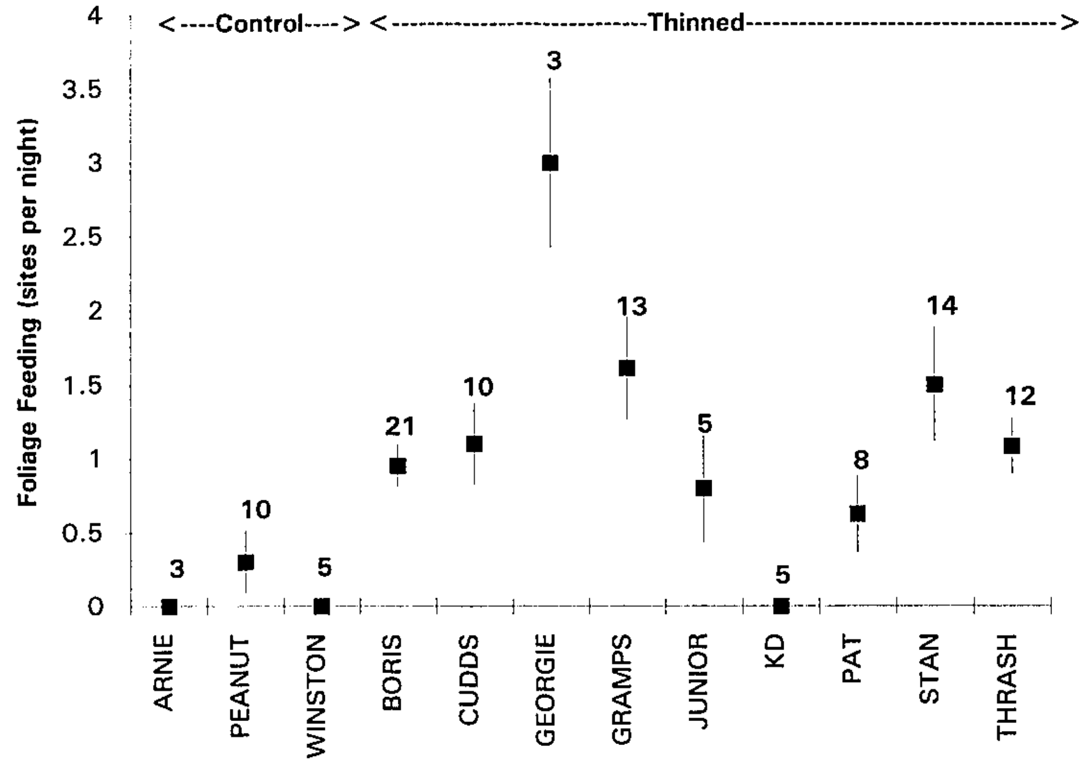


Figure 3-7. Average number of foliage feeding sites used per day for 12 radio-collared porcupines within a thinned and a control stand near Terrace B.C. during winter 1990-91. Bars represent +/- SE, sample size is indicated above each bar.

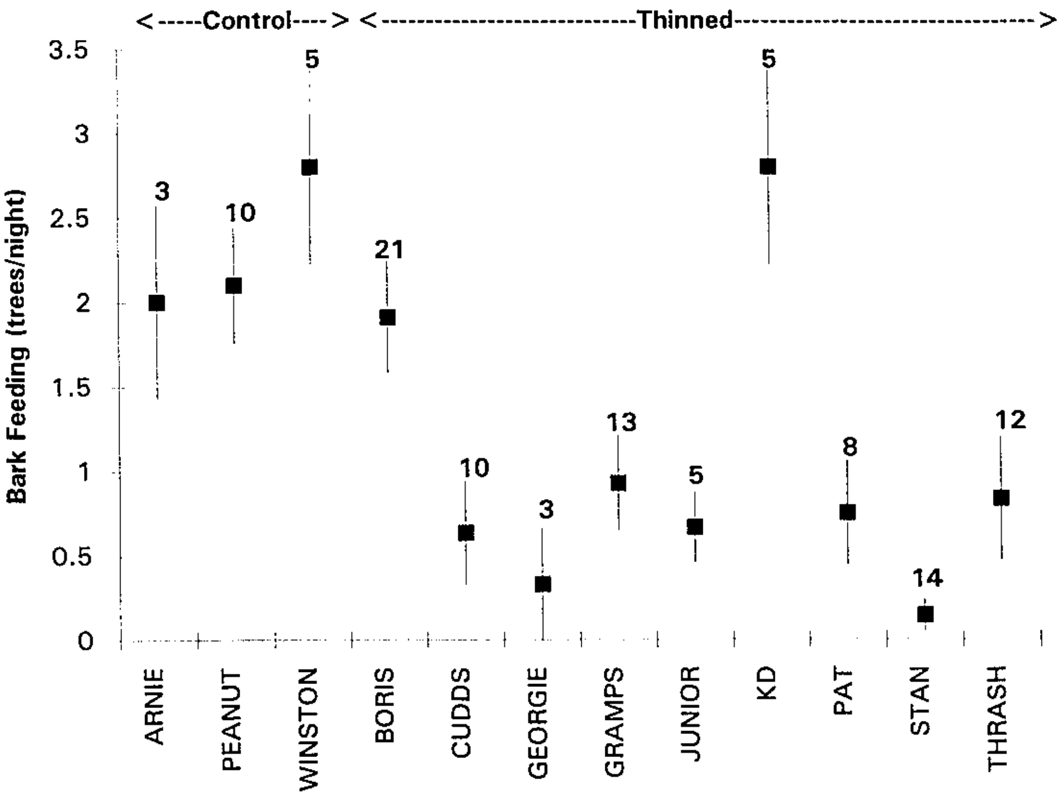


Figure 3-8. Average number of bark feeding sites used per day for 12 radio-collared porcupines within a thinned and a control stand near Terrace B.C. during winter 1990-91. Bars represent +/- SE, sample size is indicated above each bar.

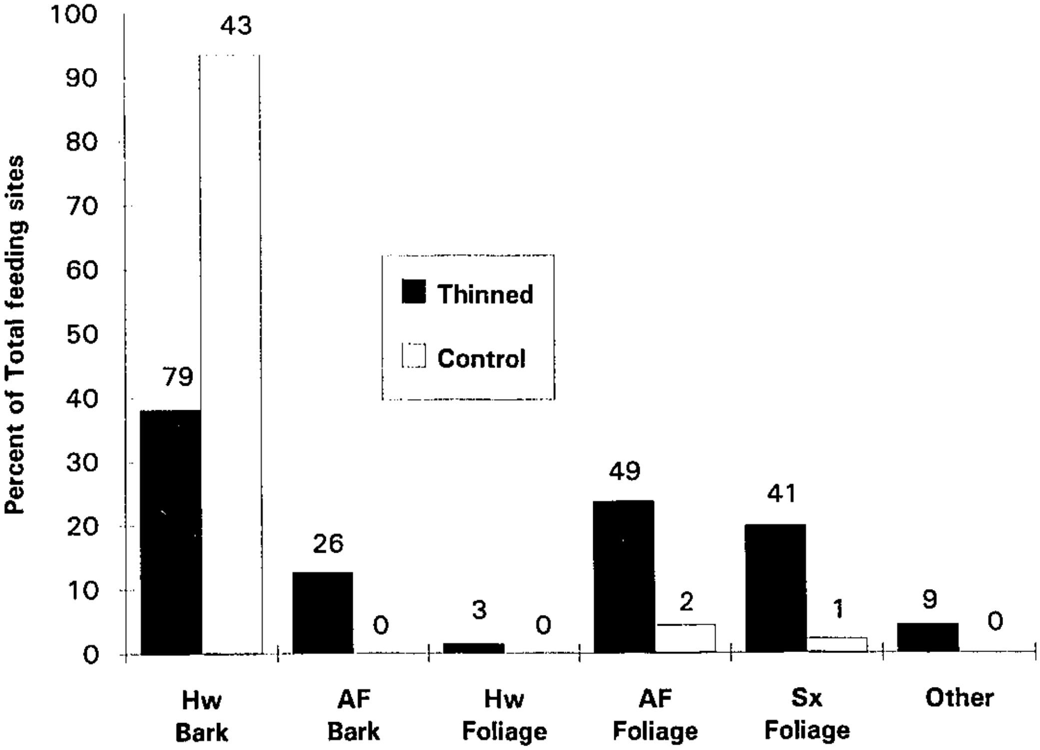


Figure 3-9. Percent frequency of bark and foliage feeding by porcupines in a thinned and a control stand near Terrace, B.C. winter 1990-91. Raw frequencies are indicated above each bar.

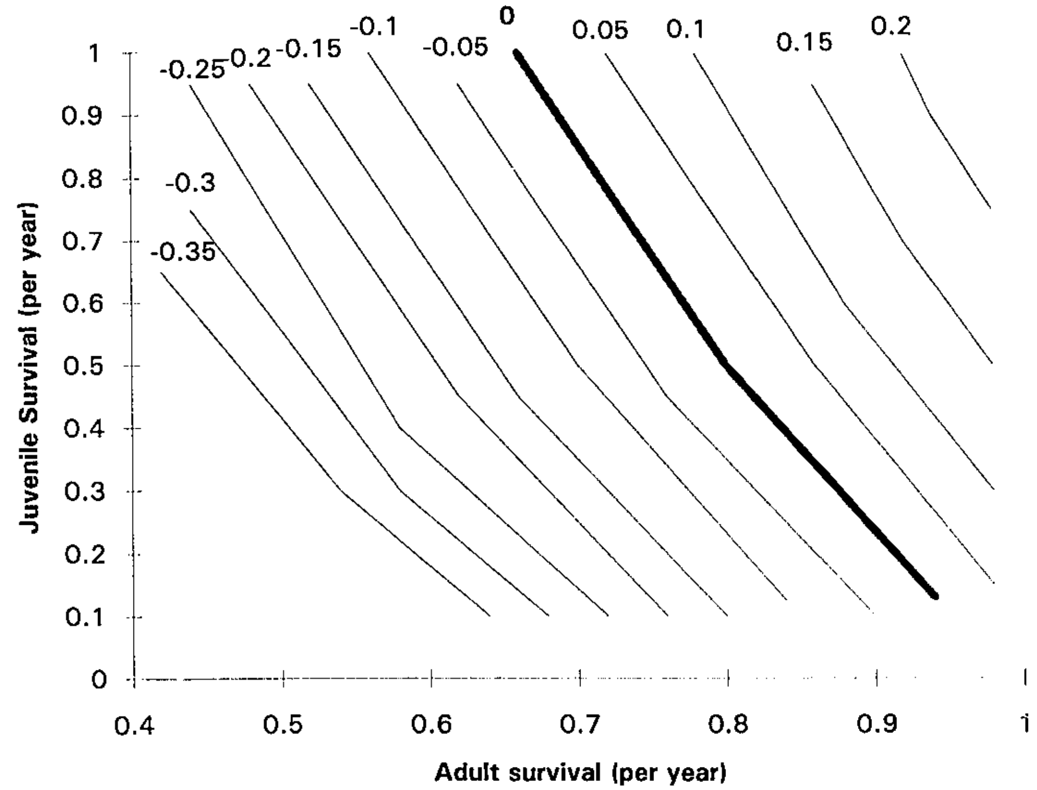


Figure 3-10. Contour plot of predicted r (intrinsic rate of increase) values for a population of porcupines across a range of juvenile and adult survival rates (see text for details on assumptions).

CHAPTER 4

GENERAL DISCUSSION: IMPLICATIONS FOR FOREST MANAGEMENT

The relationship between porcupines, their damage to trees and thinning in second-growth stands can be viewed from two perspectives; the tree population, and porcupine population. When viewed from the tree population perspective, stand thinning appears to have resulted in increased rates of damage (Chapter 2), and therefore increased impact on stand productivity in comparison to unthinned controls. Porcupine populations, on the other hand did not show a positive (or negative) density response to stand thinning (Chapter 3). In fact, on a *per-hectare* or *per-porcupine* basis, damage was less on thinned sites than controls, due to changes in feeding behaviour (Chapter 3). Although foresters are primarily concerned with the damage caused by porcupines and not the animals themselves, in order to develop ecologically-based management recommendations, both animals and damage must be considered.

Impact on Thinned and Unthinned Second-Growth Forests

Stand thinning improves growth of remaining crop trees in relation to their unthinned counterparts. In order to determine if the losses from porcupine damage outweigh the growth benefits in stands such as the ones sampled in this study, survivorship curves of thinned and control stands need to be estimated through a forest rotation (80 years). I have constructed a first approximation of such a model below.

The model depicts the number of ungirdled hemlock and amabilis fir trees remaining through time, given the rates of girdling reported in Table 2-2 . This approach requires acceptance of the assumption that girdled trees will not produce merchantable wood as suggested by Sullivan and Cheng (1989) and MacHutcheon (1990), due to death, heart rot, form defects, or small piece size and can therefore be considered as mortalities. Although a certain amount of tree mortality is expected throughout the life of a stand, if tree density falls below a certain (undefined) level, volume reductions are expected to occur. In the absence of empirical data, I set the minimum at 350 stems per hectare as this represents the minimum stocking required to reach economically viable harvest volume (350 m^3 per ha. @ 1m^3 per tree). The actual growth reduction threshold is likely to be considerably higher (Kevin Derow, *personal communication*).

The results from the projections are shown in Figure 4-1 and 4-2. Both thinned sites decline below the minimum stocking level, 17 (Quill) and 32 (Otto) years from the starting date (1991; Figure 4-1). These differences in time required to reach minimum stocking reflect initial differences in species compositions and species-specific girdling rates. In the control sites, projected stocking density did not fall below the minimum level (Figure 4-2), primarily because of the low girdling rates to amabilis fir (see Table 2-2).

These simple projections demonstrate that *if sustained*, porcupine damage in these thinned sites will likely result in reduced or non-sufficient harvest volumes at maturity. However, a crucial assumption that remains to be tested is that damage continues at the same rate until maturity. Evans and Mathews (1972), Sullivan and Cheng (1989) and MacHutcheon (1990) suggest that stands between 15 and 40 years are most susceptible to porcupine damage. However, the scarcity of stands in the 40-80 year age classes at the present time (MacHutcheon 1990) makes this difficult to test. As second-growth stands established in the 1950's and 1960's (following the onset of widespread logging in the area) progress in age, continued monitoring of damage rates within these, and a cross-section of younger stands, will enable the susceptibility interval to be determined. If damage rates decrease significantly in the older stands and remain high in the younger stands, the decline will signify the upper age limit to the susceptibility. Alternatively, if declines are demonstrated across all stand ages, a larger regional pattern of population fluctuation of porcupines (Spencer 1964; Payette 1987) is indicated. Both of these possible outcomes would influence the accuracy of the damage projections presented in figures 4-1 and 4-2.

Recommendations for Stand Management

The selection and management of tree density is fundamental in determining productivity (i.e. volume at maturity) in second-growth stands. The relatively low densities of trees in the thinned sites examined in this study (537 and 566 stems per ha.), coupled with the present damage rates, will likely result in a net reduction in volume when compared to an unmanaged stand under the same conditions. The degree to which tree density would have to be reduced to create high predation risk habitat (Sweitzer and Berger 1992), unsuitable for use by porcupines is not known. However, it is clearly less than the densities of the thinned study sites which are already too low to realize fully the growth benefits of thinning. The question arises then; should stands be thinned and if so, when, and to what density? The first part of the question is the most difficult since densities, species compositions and ecological attributes vary enourmously between sites.

Accordingly, I suggest a conservative approach to identifying suitable sites (> 5000 stems per hectare) for thinning, and once sites are chosen, employing species selection and "Sacrifice tree" (discussed below) measures to reduce potential impacts of damage.

The second growth stands sampled in this study clearly showed that porcupines exhibit clear feeding preferences for western hemlock and that these preferences were independent of stand treatment. By using less-preferred species (amabilis fir) during reforestation, or favouring this species in thinning programs, it may be possible to reduce the impact of porcupine damage on the resulting juvenile stand. A review of the literature on porcupine feeding preferences suggests that porcupines preferences vary regionally or perhaps even locally in relation to available tree species and their relative profitabilities (Roze 1989). This fact must be considered when attempting to extrapolate results to other areas where species composition and growing conditions vary.

Porcupines preferred to feed in previously damaged trees. The pattern of repeated feeding within and between years suggests that the retention of previously damaged trees during thinning may deflect damage away from "crop" trees and reduce losses. This "Sacrifice tree" prescription could be evaluated in an operational trial by comparing damage rates in thinned, unthinned and "Sacrifice tree" treatments.

Porcupine Populations in Second-Growth Forests

The high rates of predation during winter documented in this study suggest that predators could limit porcupine populations. Because habitat suitability for some predators (mustelids in particular) is linked to mature stand attributes (overhead canopy cover, down woody debris; Steventon and Major 1982; Thompson 1986), the age at which second growth stands become suitable mustelid habitat may correspond to the upper age threshold of susceptibility to damage. An examination of use and kill success of predators and the survival rate of porcupines within those stands recommended for porcupine damage monitoring would enable an evaluation of this prediction. Estimates of juvenile survival would be especially important (and influential on the population growth) as it is likely that juveniles are at risk from a wider variety of predators (marten especially) than adults. The finding in this study that wolverine may be the main predator of adult porcupine suggests that measures to reduce wolverine harvest may be warranted as these animals have low reproductive output and large space requirements (Banci and Harestad 1988). Trappers could be individually or collectively approached to enlist in a voluntary restriction on harvest. To succeed, a large contiguous refuge encompassing several traplines would be required.

SUMMARY OF RECOMMENDATIONS

1) Apply conservative criteria to identify stands suitable for thinning (> 5000 stems/ha.; free from porcupine damage)

2) Monitor porcupine damage across stand ages to determine the interval of susceptibility

3) Determine the activity of predators and the survival rates of juvenile and adult porcupines in relation to stand age to establish if predators limit porcupine numbers and under which circumstances.

4) Field test the species selection and "Sacrifice tree" prescription in an operational trial

5) Attempt to institute and evalute a voluntary restriction on the harvest of wolverine in concert with predator activity study (recommendation #3)

LITERATURE CITED

Banci, V., and A. Harestad. 1988. Reproduction and natality of wolverine (Gulo gulo) in Yukon. Naa. Zool. Fennica 25: 265-270.

Evans, J, and R.P. Matthews. 1972. Porcupine damage survey in western Washington. Washington Forest Protection Association, Seattle, Wash. 14pp.

MacHutcheon, A. G. 1990. Porcupine feeding damage in second-growth stands of the North Coast Forest District, B.C.: A Summary. B.C. Ministry of Forests, Smithers B.C. 76pp.

Payette, S. 1987. Recent porcupine expansion at treeline: a dendroecological analysis. Can J. Zool. 65: 551-557.

Roze, U. 1989. The North American porcupine. Smithsonian Institute Press.

Spencer, D.A. 1964. Porcupine population fluctuations in past centuries revealed by dendrochronology. J. Appl. Ecol. 1:127-149.

Steventon, J.D., and J.T. Major. 1982. Marten use of habitat in a commercially clear-cut forest. J. Wildl. Manage. 46: 175-182.

Sullivan, T.P., and Cheng, C. 1989. Impact of Porcupine Feeding damage on intensive forest management in the Prince Rupert Forest Region: Problem Analysis. FRDA Report No. 083. 20pp.

Sweitzer, R.A. and J. Berger. 1992. Size-related effects of predation on habitat use and behavior of porcupines (*Erethizon dorsatum*). Ecology 73:867-875.

Thompson, I.D. 1986. Diet Choice, hunting behaviour, activity patterns, and ecological energetics of marten in natural and logged areas. Ph. D. Thesis, Queens University, Kingston, Ontario. 179 pp.

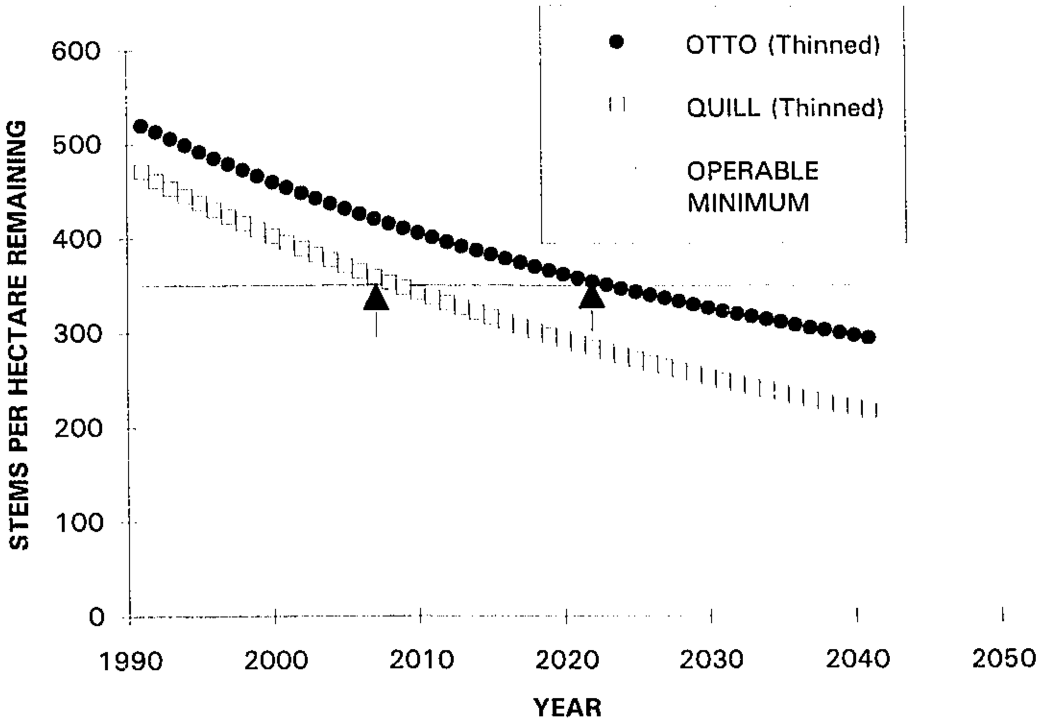


Figure 4-1. Projections of numbers of ungirdled trees remaining on two thinned sites based on current density and girdling rates of trees (species combined). The minimum stocking to produce a merchantable stand at 80 years is indicated by the line at 350 stems per hectare. At present girdling rates, these sites will become non- merchantable at 2008 (Quill) and 2023 (Otto)[see text for details on assumptions].

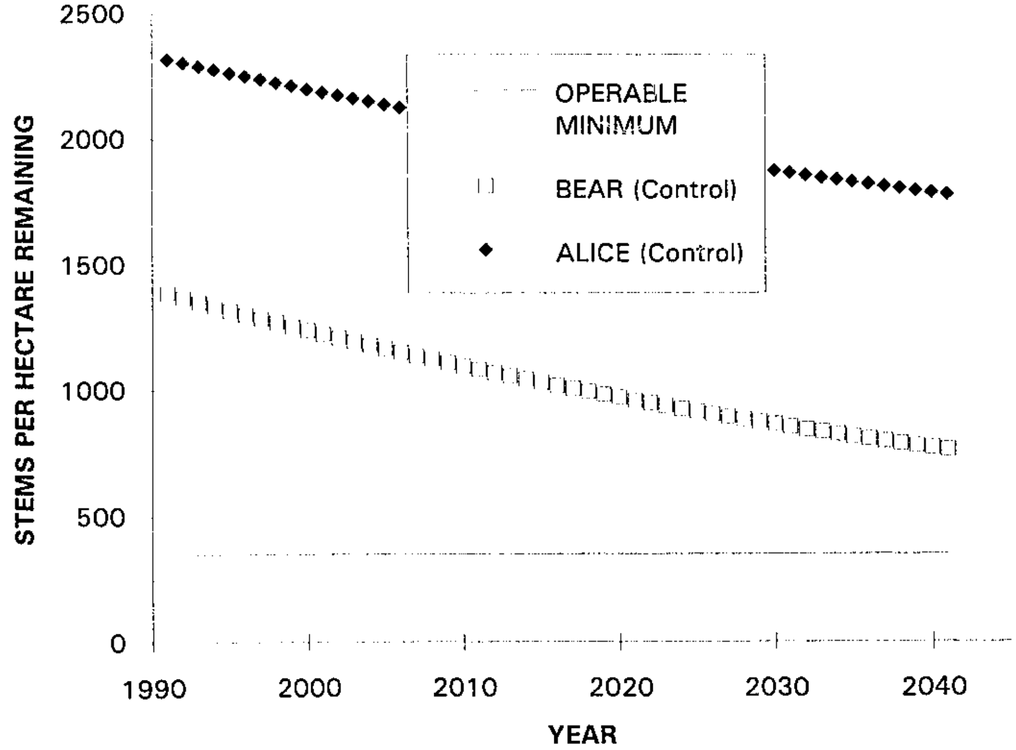


Figure 4-2 Projections of numbers of ungirdled trees remaining on two unthinned sites based on current density and girdling rates of trees (species combined). The minimum stocking to produce a merchantable stand at 80 years is indicated by the line at 350 stems per hectare (see text for detail on assumptions).

APPENDICES

APPENDIX 2-A: Detailed Forest Cover maps depicting the juxtaposition, shape and surrounding habitat matrix of each study site. Maps were reduced from 1: 20000 originals to fit on pages provided. Approximate scale is 1: 26500.

Map Legend

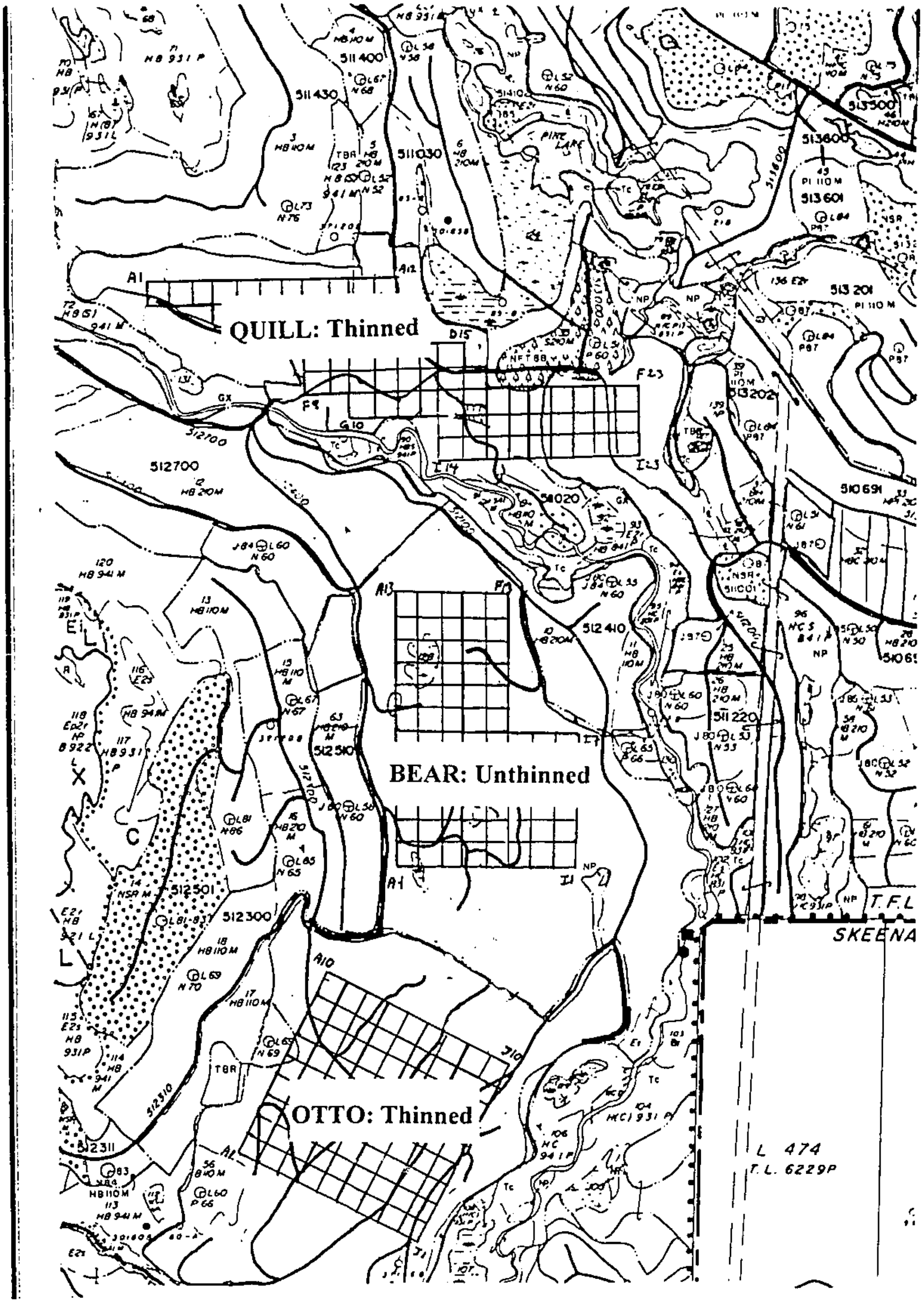
Example Polygon Label:	HB 210 M	H =Hemlock, B = Amabilis fir; 2 = 21-40yrs; 1 = less than 10.4m height; Stocking class 0 = immature; Site class M = medium
Disturbance History	J84 O L54 N54	L54 = Logged 1954; N54 = Naturally regenerated 1954; J80 = Juvenile thinned 1980

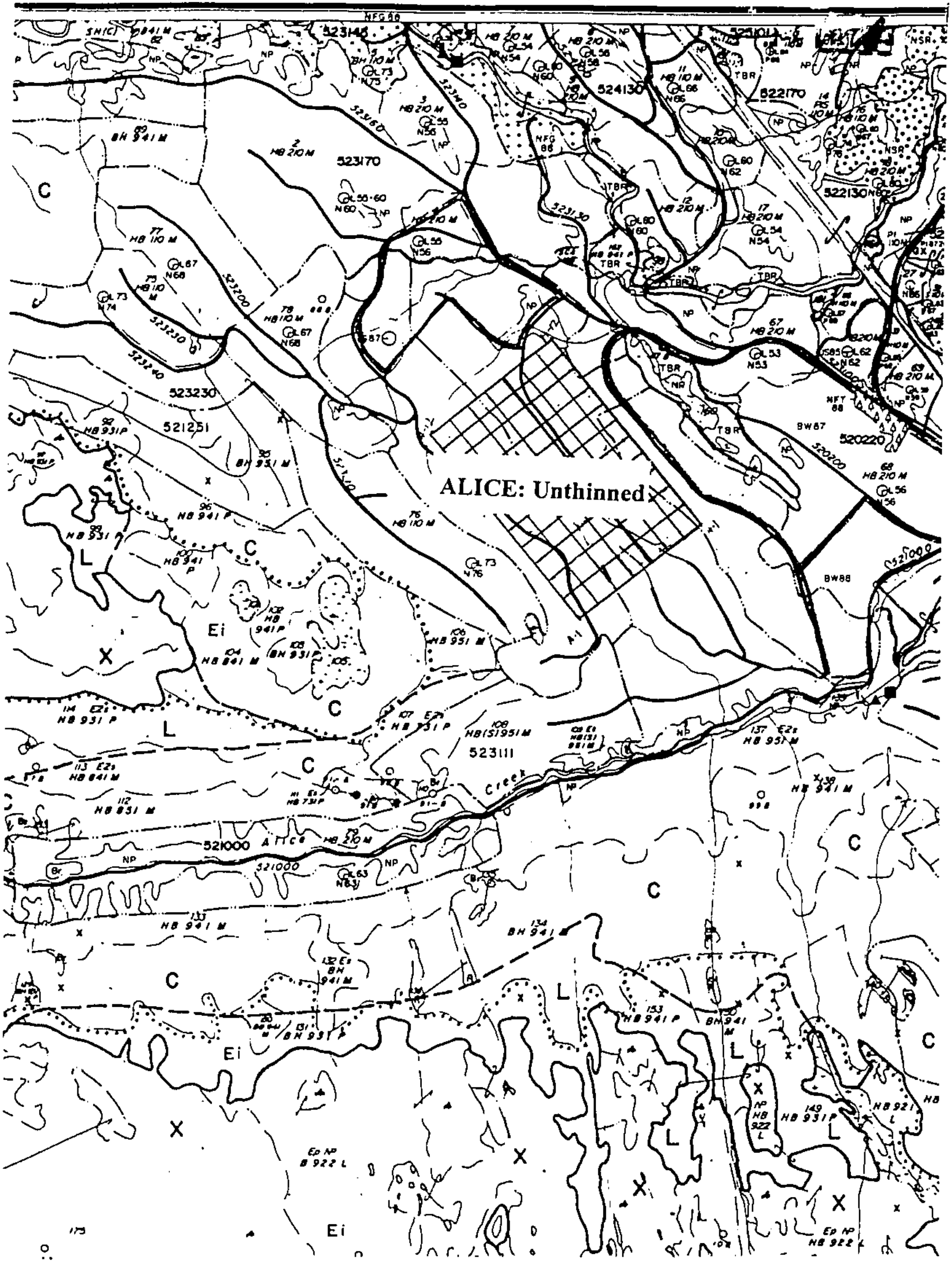
Note:

(1) Polygon Labels for the study sites were removed from the maps to reduce clutter and are presented below.

(2) Age classes 1-7 each represent a 20 year age interval; Age class 8 = 141-250 years; Age class 9 = greater than 250 years (see Watts [1983] for more detailed information).

SITE	Polygon Label	Disturbance History
OTTO (Thinned)	HB 210 M	L60, N60, J84
QUILL (Thinned)	HB 210 M	L58, N60, J80-84
BEAR (Control)	HB 210 M	L58, N60
ALICE (Control)	HB 210 M	L54,57,60, N54,60


QUILL: Thinned
BEAR: Unthinned
OTTO: Thinned
511400
511430
511030
513500
513600
513601
513201
513202
512700
512700
510691
511020
512410
512510
511220
511001
512501
512300
512311
A1
A12
A13
A10
F23
I14
PINE LAKE
NP
TBR
T.F.L
SKEENA
L 474
T.L. 6229P


ALICE: Unthinned
NFG 96
523140
523170
523160
523200
523230
523240
521251
524130
523130
522170
522130
520220
520200
521000
523111
Alice
Creek
BW87
BW88
C
L
X
Ei
NP
TBR

Appendix 2-B: Back-transformed and raw frequency (in parentheses) tallies for porcupine-damaged (A), and girdled (B) trees by yearand tree species for two thinned and two unthinned (control) second growth forest stands near Terrace B.C., 1989-1991, as determined by variable radius plots. Cumulative damage represents totals to 1991, including old (before 1989) damage. Superscripts denote statistical tests as described below table. Where 2 x 2 contingency tests are presented, frequencies have been pooled across years to maintain cell frequencies ≥ 5.

			1989		1990		1991		CUMULATIVE		
SITE	N (H)	N (AF)	H^{a}	AF^{b}	H^{a}	AF^{b}	H^{a}	AF^{b}	H^{c}	AF^{d}	Total
A) DAMAGE											
Alice (Control)	165	199	13(21)	0(1)	4(5)	1(3)	6(5)	0(0)	**44(67)**	**3(10)**	**47(77)**
Bear (Control)	247	172	18(35)	4(3)	17(35)	1(1)	6(15)	4(3)	**54(103)**	**9(11)**	**63(114)**
Otto (Thinned)	189	361	19(19)	5(6)	15(22)	2(3)	14(24)	1(2)	**76(104)**	**9(13)**	**85(117)**
Quill (Thinned)	181	256	13(20)	4(3)	19(21)	8(8)	12(13)	12(5)	**72(98)**	**13(17)**	**85(115)**
B) GIRDLING	**N (H)**	**N (AF)**	**H^{e}**	**AF^{f}**	**H^{e}**	**AF^{f}**	**H^{e}**	**AF^{f}**	**H^{g}**	**AF^{h}**	**Total**
Alice (Control)	165	199	5(8)	0(0)	0(0)	1(3)	1(1)	0(0)	**24(33)**	**1(4)**	**25(37)**
Bear (Control)	247	172	5(10)	1(1)	4(8)	0(0)	3(6)	2(2)	**24(37)**	**4(5)**	**28(42)**
Otto (Thinned)	189	361	7(8)	3(3)	5(7)	0(0)	3(7)	1(2)	**35(42)**	**4(5)**	**39(47)**
Quill (Thinned)	181	256	4(6)	4(2)	8(7)	3(4)	3(3)	1(1)	**38(52)**	**10(12)**	**48(64)**

[a] 3-way log-linear analysis of the influence of treatment and year on back transformed hemlock damage frequency (Treatment: $G = 9.15$, $df = 1$, $p < 0.005$, Year: $G = 6.98$, $df = 2$, $p < 0.04$).

[b] 2 x 2 contingency analysis of the influence of treatment on back-transformed amabilis damage frequencies ($G = 0.77$, $df = 1$, $p = 0.38$).

[c] 2 x 2 contingency analysis of the influence of treatment on back-tranformed hemlock cumulative damage frequencies ($G = 23.85$, $df = 1$, $p < 0.001$).

[d] 2 x 2 contingency analysis of the influence of treatment on back-tranformed amabilis fir cumulative damage frequencies ($G = 0.08$, $df = 1$, $p = 0.78$).

[e] 2 x 2 contingency analysis of the influence of treatment on back-tranformed hemlock girdling frequency ($G = 4.55$, $df = 1$, $p = .033$).

[f] 2 x 2 contingency analysis of the influence of treatment on back-tranformed amabilis fir girdling frequency ($G = 0.80$, $df = 1$, $p = 0.37$).

[g] 2 x 2 contingency analysis of the influence of treatment on back-tranformed hemlock cumulative girdling frequency ($G = 9.54$, $df = 1$, $p = 0.002$).

[h] 2 x 2 contingency analysis of the influence of treatment on back-tranformed amabilis fir cumulative girdling frequency ($G = 1.1$, $df = 1$, $p = 0.30$).

Appendix 2-C. Observed and Expected frequencies for Categorical variables used in logistic regression analysis of damaged versus undamaged trees. A positive value in the DIFF column indicates observed frequency exceeded expected frequency; a negative value implies observed frequency was less than expected frequency.

YEAR	GRID	SPECIES	PREV	DAM	UNDAM	TOTAL	EXP. FREQ.	DIFF.	PROB	PRED. Prob.
1989	ALICE	Balsam	0	0	192	192	9.89	-9.89	0.0000	0.0091
		Hemlock	0	9	113	122	6.29	2.71	0.0738	0.0539
		Balsam	1	1	6	7	0.36	0.64	0.1429	0.0271
		Hemlock	1	12	31	43	2.22	9.78	0.2791	0.1327
	BEAR	Balsam	0	1	164	165	8.50	-7.50	0.0061	0.0183
		Hemlock	0	18	167	185	9.53	8.47	0.0973	0.0997
		Balsam	1	2	5	7	0.36	1.64	0.2857	0.0424
		Hemlock	1	17	45	62	3.19	13.81	0.2742	0.2293
	OTTO	Balsam	0	6	352	358	18.45	-12.45	0.0168	0.0166
		Hemlock	0	14	114	128	6.60	7.40	0.1094	0.0908
		Balsam	1	0	3	3	0.15	-0.15	0.0000	0.0442
		Hemlock	1	5	56	61	3.14	1.86	0.0820	0.1998
	QUILL	Balsam	0	2	246	248	12.78	-10.78	0.0081	0.0158
		Hemlock	0	5	94	99	5.10	-0.10	0.0505	0.0802
		Balsam	1	1	7	8	0.41	0.59	0.1250	0.0424
		Hemlock	1	15	67	82	4.23	10.77	0.1829	0.1919
TOTAL				**108**		**1770**				
1990	ALICE	Balsam	0	3	189	192	9.89	-6.89	0.0156	0.0088
		Hemlock	0	3	111	114	5.87	-2.87	0.0263	0.0462
		Balsam	1	0	7	7	0.36	-0.36	0.0000	0.0234
		Hemlock	1	2	48	50	2.58	-0.58	0.0400	0.1145
	BEAR	Balsam	0	0	164	164	8.45	-8.45	0.0000	0.0158
		Hemlock	0	15	152	167	8.61	6.39	0.0898	0.0858
		Balsam	1	1	7	8	0.41	0.59	0.1250	0.0373
		Hemlock	1	20	59	79	4.07	15.93	0.2532	0.2007
	OTTO	Balsam	0	2	350	352	18.14	-16.14	0.0057	0.0143
		Hemlock	0	9	105	114	5.87	3.13	0.0789	0.0799
		Balsam	1	1	8	9	0.46	0.54	0.1111	0.0344
		Hemlock	1	13	62	75	3.86	9.14	0.1733	0.1717
	QUILL	Balsam	0	7	239	246	12.68	-5.68	0.0285	0.0136
		Hemlock	0	8	86	94	4.84	3.16	0.0851	0.0693
		Balsam	1	1	9	10	0.52	0.48	0.1000	0.0345
		Hemlock	1	13	74	87	4.48	8.52	0.1494	0.1695
TOTAL				**98**		**1768**				

Appendix 2-C
(Continued)

YEAR	GRID	SPECIES	PREV	DAM	UNDAM	TOTAL	EXP. FREQ.	DIFF.	PROB	PRED. Prob.
1991	ALICE	Balsam	0	0	188	188	9.69	-9.69	0.0000	0.005
		Hemlock	0	4	106	110	5.67	-1.67	0.0364	0.0302
		Balsam	1	0	10	10	0.52	-0.52	0.0000	0.0159
		Hemlock	1	1	48	49	2.52	-1.52	0.0204	0.0761
	BEAR	Balsam	0	3	161	164	8.45	-5.45	0.0183	0.0101
		Hemlock	0	4	148	152	7.83	-3.83	0.0263	0.0556
		Balsam	1	0	8	8	0.41	-0.41	0.0000	0.0241
		Hemlock	1	11	81	92	4.74	6.26	0.1196	0.1374
	OTTO	Balsam	0	2	348	350	18.04	-16.04	0.0057	0.0092
		Hemlock	0	18	87	105	5.41	12.59	0.1714	0.052
		Balsam	1	0	11	11	0.57	-0.57	0.0000	0.0228
		Hemlock	1	6	74	80	4.33	1.67	0.0714	0.1175
	QUILL	Balsam	0	0	239	239	12.32	-12.32	0.0000	0.0087
		Hemlock	0	3	83	86	4.43	-1.43	0.0349	0.0464
		Balsam	1	5	12	17	0.88	4.12	0.2941	0.0213
		Hemlock	1	10	85	95	4.90	5.10	0.1053	0.1125
TOTAL				67		1756				