

INFLUENCE OF PRE-COMMERCIAL THINNING OF SECOND GROWTH
CONIFEROUS FORESTS IN NORTHWESTERN BRITISH COLUMBIA ON
PORCUPINE (*ERETHIZON DORSATUM*)
MOVEMENTS, MORTALITY AND FORAGING

by

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A THESIS SUBMITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE STUDIES

(Department of Zoology)

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

October 2001

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ABSTRACT

To determine if pre-commercial thinning to 1200 stems/ha and 400 stems/ha influences movements, mortality rates and foraging behaviour of porcupines (*Erethizon dorsatum*), I monitored 33 radio-collared individuals over 4 winters. The study area consisted of three second-growth conifer stands (20 –25 years of age) located in Shames Valley, near Terrace, British Columbia.

I found that porcupines selected den locations that had a higher than average density of sitka spruce (*Picea sitchensis*) within 10 m of the den compared to the rest of the stand. Once a den site was selected, porcupines foraged in a non-random manner, selecting western hemlock (*Tsuga heterophylla*) > 9.9 cm diameter at breast height. Amabilis fir (*Abies amabilis*) of all stem diameter sizes were avoided during foraging, as were western hemlock and sitka spruce $\leq$ 9.9 cm diameter at breast height.

Throughout the winter months, a single porcupine damaged an average of 0.54 new forage trees per day. A regression analysis revealed a strong relationship ($r^2 = 0.92$) between mid-winter mass of a porcupine and the number of new trees damaged per day.

Porcupines chose the type of den they would use (stump, rock, log or pre-excavated den) based on the level of thermal protection provided. Stump dens and rock dens were used most frequently. Although fourteen of the 20 winter months of the study had average minimum temperatures below the lower critical temperature of the porcupines (-4°C), rock and stump dens provided enough thermal protection to maintain den temperatures above -4°C under most conditions.

In areas thinned to 400 stems/ha, porcupines increased their foraging radius around the den site compared to porcupines in the control area. Porcupines in thinned areas compensated for the increased cost of travel to reach their forage trees by increasing the amount of vascular

tissue removed per forage tree. Porcupines in the thinned areas travelled through deep snow more and in open areas more often compared to control animals, but did not lose more mass or suffer higher predation as a result.

Based on the conceptual model developed from this study, in areas where porcupine feeding damage is a risk, forest managers are advised to avoid thinning to low stem densities and thin to > 1200 stems/ha, or avoid pre-commercial thinning completely.

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ACKNOWLEDGEMENTS

Major funding for this project was provided by Forest Renewal British Columbia. Funding was also provided by Skeena Cellulose Inc., Terrace Woodlands Operations, and Applied Ecosystem Management Ltd.. Logistical support was supplied by BC Ministry of Forests, Kalum Forest District.

I thank Kevin Derow and Kevin Kilpatrick for their help in the initial establishment of this project, and in gaining funding for the project. I also thank Dr. T.P. Sullivan who was a tremendous aid in developing the initial research plan. My supervisor at U.B.C., Dr. C.J. Krebs, and my research committee; Dr. J.N.M. Smith, Dr. J. H. Myers, Dr. L. Gass, and Dr. R. Turkington provided excellent advice, and constructive criticism when required.

I owe a large debt of gratitude to the many people who trudged through snow and rain and up and down mountainsides to help me collect the field data for this project. I thank Martin Bahr, Melinda Bahr, Amanita Coosemans, Wendi Croft, Chad Croft, Melody Dawson, Brendan Delahanty, Mike Hamilton, Claire Jardine, Ken Kranrod, Paula Kranrod, Mike Krisinger, Julie Pylon, Wayne Sheridan, Patty Skinner, Linda Zimmerling, and Ryan Zimmerling for their hard work under extreme conditions.

Thank you does not adequately express the level of love and respect I have for my wife, Linda. When I began this project we were a couple, and now that I have come to the end, we are a family of four. Even through bringing two children into this world, she still found the time and energy to provide me with constant support and encouragement.

FOREWARD

Some sections of Chapter 1 of this thesis have been previously published in the Western Journal of Applied Forestry, and have been reproduced with the permission of the journal. The original publication was: Zimmerling, T.N. and C.D. Croft. 2001. Resource selection by porcupines: Winter den site location and forage tree choices. Western Journal of Applied Forestry 16: 53-57. Todd N. Zimmerling was the primary author undertaking all of the writing for this original manuscript and Chad D. Croft aided in field data collection and data analysis.

~~Todd N. Zimmerling~~

~~Chad D. Croft~~

GENERAL INTRODUCTION

Several species of small mammals, including meadow voles (*Microtus pennsylvanicus*), red squirrels (*Tamiasciurus hudsonicus*), snowshoe hares (*Lepus americanus*) and porcupines (*Erethizon dorsatum*), inflict feeding damage on forest and agricultural crops in North America, Europe and Asia (Van Deusen and Myers 1962; Hansson and Nilsson 1975; Green 1978; Sullivan and Sullivan 1982; Byers 1984; Hansson 1985; Sullivan et al. 1986; Sullivan and Moses 1986a, 1986b; Zimmerling and Zimmerling 1996; Singleton et al. 1999). The impact of these herbivores on their food source can be substantial (Crawley 1983; Ostfeld and Canham 1993, Singleton et al. 1999) and conversely, changes in plant density, nutritional quality or chemistry can have an equally dramatic effect on herbivores (Cole and Batzli 1979; Batzli et al. 1981; Sullivan and Moses 1986a, 1986b; Bryant et al. 1992; Krebs 1994). As a result of the potential impacts of herbivores on forest trees, forest managers have become increasingly interested in the dynamic relationship between plant and herbivore communities and methods by which to manipulate these interactions.

Since the early 1900's porcupines have been considered a pest to commercial forest operations throughout their range (Hunter 1918; Cox 1923; Gabrielson 1928; Hatt 1930; Curtis 1941). As a result, a wide variety of control measures for reducing porcupine feeding damage to commercial forestry plantations have been implemented (Roze 1989). Sullivan and Cheng (1989) provided a review of the methods and examined the practicality of each. There are two broad categories of control strategies: population reduction methods and damage reduction methods. Population reduction methods include bounties (Reeks 1942; Dodge 1982), poisoning (Faulker and Dodge 1962), trapping (Evans 1987) and biological control (Powell and Brander 1977; Dodge 1982; Conniff 1986). The potential rate of population increase for porcupines is low, as they have just one offspring per year (Roze 1989), and as a result population reduction

methods have a high probability of successfully reducing porcupine numbers. However, such programs have been found to be costly, impact non-target species and have been difficult to monitor to ensure porcupines were being removed from the appropriate location (Reeks 1942; Roze 1989, Sullivan and Cheng 1989).

The three methods which fall into the category of damage reduction are: the use of mechanical barriers, repellents and forest management. Mechanical barriers are effective at preventing porcupines from climbing trees (Dodge 1982; Griesemer et al. 1994), thereby reducing damage. However, material costs and labour make mechanical barriers impractical over a large scale (Dodge 1982).

Repellents, such as predator odors and plant antifeedants, have been shown to reduce feeding damage caused by snowshoe hares and meadow voles (Sullivan and Crump 1984; Sullivan et al. 1992; Zimmerling and Zimmerling 1996). Currently there are no repellents recommended for use against porcupine feeding damage; however, Witmer and Pipas (1998) report promising results from preliminary pen trials using predator based odours.

The use of forest management techniques such as thinning or pruning to reduce porcupine damage has been suggested by several authors (Sullivan and Cheng 1989; Krebs 1994), but has received little attention from researchers. Pre-commercial thinning (removal of trees prior to the stems being large enough to be commercially harvested) is a common practice throughout much of British Columbia. This technique can result in a substantial reduction in the density of trees within a stand. If tree densities can be reduced low enough, the habitat within the stand should become poorer quality for porcupines. Porcupine numbers in the thinned stands should decline owing to a direct exodus of porcupines from the poor quality habitat, or from increased mortality rates of porcupines that remain in these stands. It is the use of pre-commercial thinning to reduce porcupine feeding damage which I explore in this study.

I have followed a number of radio-tagged porcupines, residing in second-growth coniferous forests of northwestern British Columbia, for four winters. In the first two winters of the study the second-growth forest was left unmanaged. During that time I collected data on den use and forage tree selection.

In Chapter 1 of this thesis I examine whether porcupines select their winter den site location based on within-stand variation in tree species composition and size class distribution. The association between particular species and size classes of trees and den site may aid forest managers in predicting where, within a second-growth stand, porcupine feeding damage is likely to be most severe. In addition to den site location, I also examine forage tree selection by porcupines and present data on species and size class preferences.

In Chapter 2 I present the data on den type selection. I examine the thermal cover provided by several different types of den structures used by porcupines during the winter. I also present data in this chapter relating to the lower critical temperature of porcupines in the study area and examine how dens reduce the energetic cost for a porcupine of maintaining body temperature.

After tracking the radio-tagged porcupines for two winters, the study area was divided and pre-commercial thinning to 1200 stems/ha and 400 stems/ha occurred over a portion of the study area. I continued to monitor the radio-tagged porcupines for two consecutive winters after these treatments. I anticipated that the thinning treatments would have a negative impact on porcupine movements, mortality rates and foraging behaviour, such that thinning to low densities (400 stems/ha) could be used as an effective means of controlling porcupine feeding damage within second-growth stands.

In Chapter 3 I present data collected from the post-treatment years and I test four hypotheses relating to the impact of the thinning treatments on the foraging behaviour of porcupines:

H₁: Owing to an increased perceived risk of predation, porcupines will shift their foraging range to avoid the thinned treatment areas.

H_{A1}: Alternatively, porcupines will not shift their foraging ranges out of the thinned areas and will suffer higher rates of mortality owing to predation compared to porcupines in control areas.

H₂: Porcupines that continue to use den sites within thinned treatment areas will forage in a greater radius around den sites and move to new dens more frequently than porcupines using dens in the control areas.

H_{A2}: Alternatively, porcupines will not increase their foraging range around the den site and will not change den location in a shorter time frame because den switching is not based on the rate of foraging that can be achieved.

In Chapter 4 I examine the potential benefits to forest management of using low density pre-commercial thinning treatments (400 stems/ha) to increase porcupine winter energetic expenditures. I compare the influence of the low density thinning to the more standard 1200 stem/ha pre-commercial thinning and control areas (2000 stems/ha), and tested six hypotheses:

H₁: The lower density of trees in thinned areas will reduce the thermal cover afforded by tree canopy. As a result, the thinned treatment areas will be, on average, colder than the control areas.

H_{A1}: Alternatively the thinned treatment areas will maintain the same temperature, on average, as the control areas.

H₂: Porcupines in the thinned stands will travel in the open (away from conifer branch cover) more often, and move through deep snow more often than porcupines in control areas.

H_{A2}: Alternatively, porcupines in treatment areas will restrict their travel routes to areas under the remaining conifers and will travel in the open in the same frequency as porcupines in the control areas.

H₃: Increased energetic cost of travel between trees in the thinned stands increases the amount of vascular tissue removed per feeding event (before leaving the tree) by porcupines feeding in thinned areas.

H_{A3}: Alternatively, porcupines that forage in thinned stands do not remove a larger amount of vascular tissue per feeding event and thus suffer a higher rate of mass loss than porcupines foraging in the control areas.

In Chapter 5 I present data on the short-term benefits of pre-commercial thinning on conifer tree growth rates. I examine the impact of porcupine winter feeding on tree growth rates and I present a conceptual model. The model has been developed based on data collected from this study and other studies from the general area. It is presented as an aid to forest managers in deciding which second-growth stands should be pre-commercially thinned when porcupine feeding damage is a possibility.

I conclude with management recommendations and suggestions into further research into the problem of managing mammalian pest damage in commercial forest plantations.

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CHAPTER 1: RESOURCE SELECTION BY PORCUPINES: WINTER DEN SITE LOCATION AND FORAGE TREE CHOICES.

INTRODUCTION

The porcupine (*Erethizon dorsatum*) is found in a variety of habitats across most of Canada, United States and northwestern Mexico (Dodge 1982). During the spring and summer months, porcupines feed extensively on ground vegetation such as forbs and grasses (Taylor 1935; Dodge 1982; Hendricks and Allard 1988; Griesemer et al. 1998). Over winter, when summer forage has died back or is covered by snow, porcupines feed on the cambium, phloem and foliage of a variety of woody shrubs, and deciduous and coniferous trees (Curtis and Wilson 1953; Van Deusen and Myers 1962; Dodge 1967; Dodge and Canutt 1969; Harder 1980; Tenneson and Oring 1985; Speer and Dilworth 1978; Griesemer et al. 1994; Griesemer et al. 1998).

Although porcupine winter feeding occurs on a variety of tree species, across a large geographic area (Daniel and Barnes 1958; Van Deusen and Myers 1962; Storm and Halvorson 1967; Gill and Cordes 1972; Eglitis and Hennon 1986; Sullivan et al. 1986), similarities in feeding patterns do exist. Roze (1984) reported that the majority of porcupines in the Catskill Mountains of New York State foraged on trees within 30 m of their den site. Speer and Dilworth (1978) reported a similar result in New Brunswick, with most winter feeding being associated with winter den sites. Griesemer et al. (1994) also reported that the majority of winter porcupine feeding occurred close to (<40 m) winter den sites. These results indicate an apparent association between den location and foraging; however, it is unclear as to whether den sites are chosen because of the presence of preferred forage species.

Roze (1984) reported that porcupines feed upon the tree species which is most abundant around their den site and Sullivan et al. (1986) reported that porcupines preferred the most

abundant tree species in the study area, and selected for specific diameter classes of that species. Gill and Cordes (1972) also reported that porcupines feed on the most abundant tree species in close proximity to their den site. None of these previous studies have examined whether porcupines use localized tree species abundance in selecting den sites, or if den sites are randomly located and forage tree selection shifts with respect to available trees near the den site.

The objective of this study was to determine if porcupines select den sites based on within-stand variations in tree species composition or size-class distribution. In addition, I wished to determine whether porcupines choose forage trees around the den site randomly (i.e. show no selection of forage tree), thereby relying on den site location to provide appropriate forage tree availability, or whether porcupines select specific forage trees around the den site, thereby using a single tree scale to make foraging choices.

STUDY AREA

This study took place near Terrace, British Columbia, Canada ($54^{\circ} 35'$, $128^{\circ} 42'$) in the Shames Valley (approximately 30 km west of Terrace). The study site was composed of three second-growth stands, (20 - 25 years old) located in the Coastal Western Hemlock, wet submaritime (CWH_{ws}) biogeoclimatic subzone (Banner et al. 1993). The second-growth forest consisted primarily of western hemlock, amabilis fir (*Abies amabilis*), and sitka spruce (*Picea sitchensis*) with a minor component of western red cedar (*Thuja plicata*).

The study stands were located on a west facing slope with gradient up to 40% present. The lower boundary of the study stands were at approximately 200 m elevation and the upper boundary were at approximately 450 m elevation.

METHODS

In the spring of 1996, 5.64-m radius (100-m^2) tree assessment plots were established within the study area. Plots were systematically placed across the study area at a density of 2 per hectare for a total of 160 plots. The centre of each plot was marked with a stake and flagging. Within each plot all trees with a diameter at breast height ($\text{dbh} = 1.3 \text{ m}$) $\geq 5 \text{ cm}$ were permanently marked. The species and dbh of each tagged tree were recorded to give a species composition and diameter size class distribution for the study area.

In the fall, using systematic searches of the study area, 12 porcupines (7 males, 5 females) were located and captured. Once located, the porcupine was netted, using a large dip-net, if the animal was out of its den. If the animal was in its den, a Tomahawk, single door live-trap (40 x 40 x 100 cm) was placed at the den entrance and left overnight. Once captured, the animal was drugged using a 10:1, ketamine (10mg/kg): xylazine (1mg/kg) combination. To reduce the time to recovery of smaller animals 1 kg was subtracted from body weight when determining dosage. This procedure ensured that smaller animals, that could be processed more quickly and were more susceptible to exposure to cold temperatures, recovered more quickly than larger animals that required more processing time and were less susceptible to exposure to cold temperatures.

Each captured animal was fitted with a radio-collar (Lotek, model SMRC-3RB, with nylon collars; weight = 45 - 50 g), tagged with a numbered ear tag, weighed, and sexed. Throughout the winter months each collared animal was located three times per week (using handheld telemetry), to identify the animal's den location. From its den location snowtracking was used to trace the feeding route of the animal from the previous night. During the snowtracking, the dbh and species of all forage trees encountered were recorded. A forage tree was defined as any tree from which the porcupine removed cambial tissue. Trees that were climbed but not fed

upon were not considered forage trees. Upon encounter, each forage tree was marked, using a spot of orange tree paint, to ensure it was not recorded more than once.

The average number of forage trees used per day by a porcupine was calculated by adding all the forage trees used over a defined time period (> 30 days) and dividing by the number of days in the time period. Any tree that was fed upon on more than a single day was only included once. As a result, this calculation represents only the number of new forage trees.

Porcupine home range size was calculated using minimum convex polygons (Animal movement extension to arcview; Hooge and Eichenlaub 1997) of foraging trees around each den site. Although porcupines may have travelled a considerable distance (> 500 m) between den sites, this distance was not included as part of home range. Instead the range defined in this study may be better termed "foraging range" as it was calculated based solely on foraging locations. Where more than one den site was used, the area around each den site was added together to give a foraging range estimate.

In the spring of 1997 and 1998, four tree assessment plots were established at each den site identified during the winter. The assessment plots were placed, 10 m from the den site in the cardinal directions. Within each plot, dbh and species of every tree ≥ 5 cm dbh were recorded. These data were used to estimate a size-class distribution and species composition of trees close to the den site. In several cases, individual porcupines spent time at multiple den sites. In these cases tree assessment plots were established at each den site and the data were combined.

STATISTICAL ANALYSIS

Data from the assessment plots and from porcupine foraging were split into 15 resource categories based on tree species and dbh. The resource categories were based on dbh size classes of 5.0 - 9.9, 10.0 - 14.9, 15.0 - 19.9, 20.0 - 24.9 and > 24.9 cm, for each of three species (western hemlock, sitka spruce, amabilis fir). Western red cedar was not included in the analysis, as it made up < 5% of the trees in the study area.

Selection analysis was performed using the Chi-squared goodness-of-fit test used by Neu et al. (1974), with the associated Bonferroni z-test to determine specific resource category differences. This method has been assessed by Alldredge and Ratti (1986), Manly et al. (1993) and McClean et al. (1998) and found to provide good consistency across several scales of analysis and acceptable Type I and Type II errors when applied to resource selection analysis, such as that required for this study.

RESULTS

Porcupines used an average of 3.75 den sites per individual (range 1 - 5) throughout the winter months of this study. The porcupines had a mean foraging range of 1.53 ha (range 0.14 ha to 5.80 ha) over which foraging on conifer trees occurred. Within this foraging range, porcupines used a mean of 0.54 (s.d. = 0.40 trees) new forage trees per day. The number of new forage trees used/day varied considerably among porcupines, with a range from 0.18 trees/day to 1.33 trees/day (Figure 1.1). Field observation revealed a potential relationship between porcupine size and number of new forage trees used per day. Mid-winter weight measurements were available for ten of the porcupines and subsequent regression analysis of new forage trees per day on mid-winter weight of these ten individuals revealed a strong positive relationship ($r^2 = 0.92$) when a polynomial regression line was used ($y = 0.0032x^3 - 0.0234x^2 + 0.0048x + 0.3612$) (Figure 1.1).

As a "new forage tree" constituted everything from a small, 1 cm² patch up to the complete removal of all vascular tissue from a tree, it was of interest to determine if there was a relationship between porcupine mid-winter weight and the amount of vascular tissue removed per forage tree. Regression analysis of the mean vascular tissue removed per forage tree on porcupine mid-winter weight revealed no significant relationship ($F = 2.36$, d.f. 1, 10; $p = 0.16$). The mean vascular tissue removed per tree by an individual porcupine ranged from 533.13 cm² to 15623 cm².

A comparison of the proportion of trees in each resource category around winter den sites and in the entire study area (Table 1.1) produced a significant difference ($X^2 = 343.0$, d.f. = 14), indicating that porcupines show some resource category selection or avoidance. Bonferroni z-statistic revealed that porcupines avoided den sites with smaller hemlock trees (5.0 - 9.9 and 10.0 - 14.9 cm dbh) and showed a trend towards selecting sites with high proportions of sitka spruce (Table 1.1). A statistical selection was found for sitka spruce in the 15.0 - 19.9 cm dbh resource category (Table 1.1).

A comparison of the proportion of forage trees in each category and trees around the den sites (Table 1.2) also produced a significant difference ($X^2 = 337.2$, d.f. = 14). Porcupines avoided amabilis fir in all categories (Table 1.2) and the smallest diameter category (5.0 - 9.9 cm dbh) of sitka spruce. There was also a trend towards avoidance of western hemlock in the smallest category (Table 1.2). Western hemlock larger than 9.9 cm dbh were selected by porcupines as forage trees (Table 1.2). Selection was statistically significant for the 10.0 - 14.9 cm dbh, 15.0 - 19.9 cm dbh and 20.0 - 24.9 cm dbh resource categories. Porcupines displayed a trend towards selection of the largest resource category (> 24.9 cm dbh) as well; however, the selection was not statistically significant.

DISCUSSION

An unexpected observation from this study was the strong relationship between porcupine size and the number of new forage trees used/day. Although this relationship indicates that larger animals tend to feed on more new trees (compared to smaller animals), there was no relationship between porcupine size and the amount of vascular tissue removed per forage tree. In general there was considerable variation in the amount of vascular tissue removed per tree, even within individual porcupines.

Despite the lack of a relationship between the amount of vascular tissue removed and the size of the porcupine, the results do indicate that larger porcupines cause a greater proportion of

observed feeding damage (trees with bark removed) in second-growth stands, relative to the damage caused by smaller porcupines. Thus, the percentage of trees damaged within a stand may be related as much to the size of porcupines, as to the number of porcupines in the stand. This finding is important for forest management, as it indicates that gaining an estimate of the number of porcupines within a particular stand will provide little information on the expected level of porcupine feeding damage, without some idea of the size (related to age and sex) of the individuals within the stand.

Porcupines in my study used different criteria for choosing den site location than they did to select forage trees. With respect to den site location, porcupines select sitka spruce as a key habitat characteristic. I do not know if the higher proportion of sitka spruce around den sites is the ultimate characteristic porcupines are selecting for when choosing a den site, or if sitka spruce is merely correlated with an unknown variable. Spruce trees may intercept snow better than other species, or may provide greater protection from predators when used as a roost tree, or it may be an indication of other site characteristics such as higher soil moisture (Lavender et al. 1990; Pojar and MacKinnon 1994). Mattson (1980), in a review of plant nitrogen content, suggested that increased soil moisture results in increased nitrogen levels within plants. If this is the case for western hemlock trees, then an area with a higher density of sitka spruce within a stand may be an indication to porcupines of a location where forage trees will have higher nitrogen content.

Speer and Dilworth (1978) noted that porcupine den sites were located on more moist soils, and speculated that this may be owing to the higher probability of blowdown occurring on these soil types, which creates more den sites. On my study site, blowdown was not an issue as the valley is not subject to high winds, and dens were not located in blowdown (Chapter 2).

The selection for sitka spruce around den sites would be easily explained if porcupines were also selecting sitka spruce when foraging; however, this is not the case (Table 1.2). Roze

(1984) suggests that porcupines choose their foraging areas based on the relative density of their primary food choice. My results do not support this, as sitka spruce are selected when choosing a den site and western hemlock, in the larger diameter categories, are selected when foraging around the den site.

Forage species selection is common among mammalian herbivores (Radwan 1972; Freeland and Janzen 1974; Belovsky 1981). Both the nutrient value of a forage species and the concentration of secondary compounds (antifeedants) influence forage choice, and one or both of these factors have been related to forage selection in a wide range of mammals, including: moose (Belovsky 1981), snowshoe hares (Bryant 1981; Sinclair et al. 1982), white-tailed deer (*Odocoileus virginianus*) (Swihart and Picone 1998), black-tailed deer (*Odocoileus hemionus columbianus*) (Radwan 1972), black bears (*Ursus americanus*) (Kimball et al. 1998), Orkney voles (*Microtus arvalis orcadensis*) (Hartley et al. 1995), pocket gophers (*Geomys bursarius*) (Epple et al. 1996), tassel-eared squirrel (*Sciurus aberti*) (Farentinos et al. 1981) and porcupines (Gill and Cordes 1972). Selection of particular individual plants within a species, or a specific part of a plant is also influenced by nutrient and secondary compounds (Freeland and Janzen 1974; Bryant 1981).

Van Deusen and Myers (1962) noted that porcupines select large diameter, dominant and codominant trees for forage in the forests of New Brunswick. Sullivan et al. (1986) also reported that porcupines damaged more large diameter hemlock trees in coastal British Columbia. I found that porcupines use tree diameter when making foraging choices. Western hemlock and sitka spruce in the smallest dbh category (5.0 - 9.9 cm) were avoided during foraging as were all size classes of amabilis fir. Larger diameter western hemlock were selected as forage trees.

I do not know why porcupines select for the larger, more vigorous hemlock trees; however, work by Nolte et al. (1998) reported that Douglas fir (*Pseudotsuga menziesii*) grown in thinned

stands had an increased concentration of sugars and a decrease in terpenes compared to unthinned trees. In addition, it is known that more vigorous trees have a thicker cambial layer compared to suppressed trees (Jozsa and Middleton 1994). As a result, the larger trees selected by porcupines are expected to have a larger amount of vascular tissue per unit area and (if the hemlock is similar to Douglas fir) the vascular tissue has a higher concentration of nutrients.

My results indicate that porcupines feed selectively when they leave their den site to forage. Speer and Dilworth (1978), Tenneson and Oring (1985), and Sullivan et al. (1986) all reported species selection preferences by porcupines; however, these three studies compared feeding trees to the study site as a whole, and not to trees available directly adjacent to the den site. The small winter foraging range of the porcupines in this study (1.53 ha) indicates that comparing forage choices to entire forest stands may be misleading, because porcupines cover only a small portion of the area. My results suggest that porcupines use within-stand variation in tree species composition to select den sites, and forage selectively from around the den site.

SUMMARY

This study was undertaken to examine the importance of tree species composition and tree size class distribution in determining the selection of winter den sites and forage trees by porcupines. I used data collected from 12 radio-tagged porcupines over two winters to examine den site location and forage tree selection.

I found that porcupines in the study area fed on a mean of 0.54 new forage trees per day. Regression analysis showed heavier porcupines used more new forage trees/day and therefore cause a larger proportion of the observed, newly damaged conifer trees in second-growth stands, than smaller porcupines. This result indicates that to predict potential future porcupine feeding damage within a stand it is important to gain information on both the number of porcupines in the stand and the size of the porcupines.

My results showed that porcupines selected winter den sites based on within-stand variation in the density of sitka spruce trees. The reason for sitka spruce being selected around den sites is not known, as porcupines did not select spruce as forage trees. It is possible that spruce trees are used by porcupines to identify locations of higher soil moisture, which is related to higher nutrient content in forage.

When foraging around the den sites, porcupines avoided amabilis fir in all size classes and selected western hemlock in the larger size classes. This selection may be related to an increase in the amount of vascular tissue available in the larger trees, and an increase in the concentration of nutrients within the vascular tissue. Based on the results of my study, it is clear that porcupines use within-stand variation in species composition to select den sites, and feed non-randomly on specific species and size classes of trees around the den site.

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Table 1.1: Composition of trees around porcupine winter den sites and in surrounding second-growth forest (95% confidence intervals, based on Bonferroni z-statistic, in brackets).

DBH of Trees (cm)	Western Hemlock		Sitka Spruce		Amabilis Fir	
	Second- growth stand (P_{i_0})	Den site trees (P_i)	Second- growth stand (P_{i_0})	Den site trees (P_i)	Second- growth stand (P_{i_0})	Den site trees (P_i)
5.0-9.9	0.445	0.362 ($0.327 \leq P_1 \leq 0.401$)*	0.008	0.145 ($0.118 \leq P_6 \leq 0.127$)	0.061	0.070 ($0.051 \leq P_{11} \leq 0.089$)
10.0-14.9	0.188	0.145 ($0.118 \leq P_2 \leq 0.172$)*	0.041	0.053 ($0.036 \leq P_7 \leq 0.070$) ⁺⁺	0.045	0.056 ($0.038 \leq P_{12} \leq 0.074$)
15.0-19.9	0.052	0.049 ($0.032 \leq P_3 \leq 0.066$)	0.005	0.026 ($0.014 \leq P_8 \leq 0.038$)**	0.033	0.029 ($0.016 \leq P_{13} \leq 0.042$)
20.0-24.9	0.015	0.013 ($0.004 \leq P_4 \leq 0.022$)	0.003	0.010 ($0.002 \leq P_9 \leq 0.018$) ⁺⁺	0.020	0.022 ($0.011 \leq P_{14} \leq 0.033$)
>24.9	0.003	0.005 ($0.000 \leq P_5 \leq 0.010$)	0.001	0.008 ($0.001 \leq P_{10} \leq 0.015$) ⁺⁺	0.007	0.006 ($0.000 \leq P_{15} \leq 0.012$)

Note: P_i represents theoretical composition of trees around den sites and is compared to corresponding P_{i_0} (expected) to determine if the hypothesis of no selection/avoidance of the resource is rejected.

* Resource categories making up a statistically lower proportion of trees around den sites than expected when compared to composition of trees within the second-growth stand (i.e. avoidance of resource by porcupines).

** Resource categories making up a statistically higher proportion of trees around den sites than expected when compared to composition of trees within the second-growth stand (i.e. selection of resource by porcupines).

⁺⁺ Resource categories showing a trend toward selection by porcupines, but not statistically significant.

Table 1.2: Composition of porcupine forage trees and trees around porcupine winter den sites (95% confidence intervals, based on Bonferroni z-statistic, in brackets).

DBH of Trees (cm)	Western Hemlock		Sitka Spruce		Amabilis Fir	
	Den site trees (P_{i_0})	Forage trees (P_i)	Den site trees (P_{i_0})	Forage trees (P_i)	Den site trees (P_{i_0})	Forage trees (P_i)
5.0-9.9	0.364	0.319 (0.268 $\leq$ $P_1 \leq$ 0.370)+	0.145	0.082 (0.052 $\leq$ $P_6 \leq$ 0.112)*	0.082	0.013 (0.001 $\leq$ $P_{11} \leq$ 0.025)*
10.0-14.9	0.145	0.278 (0.277 $\leq$ $P_2 \leq$ 0.279)**	0.053	0.052 (0.027 $\leq$ $P_7 \leq$ 0.077)	0.052	0.007 (0.000 $\leq$ $P_{12} \leq$ 0.016)*
15.0-19.9	0.049	0.115 (0.080 $\leq$ $P_3 \leq$ 0.150)**	0.026	0.039 (0.018 $\leq$ $P_8 \leq$ 0.077)	0.029	0.006 (0.000 $\leq$ $P_{13} \leq$ 0.015)*
20.0-24.9	0.013	0.040 (0.018 $\leq$ $P_4 \leq$ 0.062)**	0.010	0.009 (0.000 $\leq$ $P_9 \leq$ 0.018)	0.009	0.006 (0.000 $\leq$ $P_{14} \leq$ 0.015)*
>24.9	0.005	0.020 (0.005 $\leq$ $P_5 \leq$ 0.035)++	0.008	0.004 (0.000 $\leq$ $P_{10} \leq$ 0.011)	0.006	0.001 (0.000 $\leq$ $P_{15} \leq$ 0.004)*

Note: P_i represents theoretical composition of forage trees and is compared to corresponding P_{i_0} (expected) to determine if the hypothesis of no selection/avoidance of the resource is rejected.

* Resource categories making up a statistically lower proportion of forage trees than expected when compared to composition of trees around den sites (i.e. avoidance of resource by porcupines).

** Resource categories making up a statistically higher proportion of forage trees than expected when compared to composition of trees around den sites (i.e. selection of resource by porcupines).

+ Resource categories showing a trend toward avoidance by porcupines, but not statistically significant.

++ Resource categories showing a trend toward selection by porcupines, but not statistically significant.

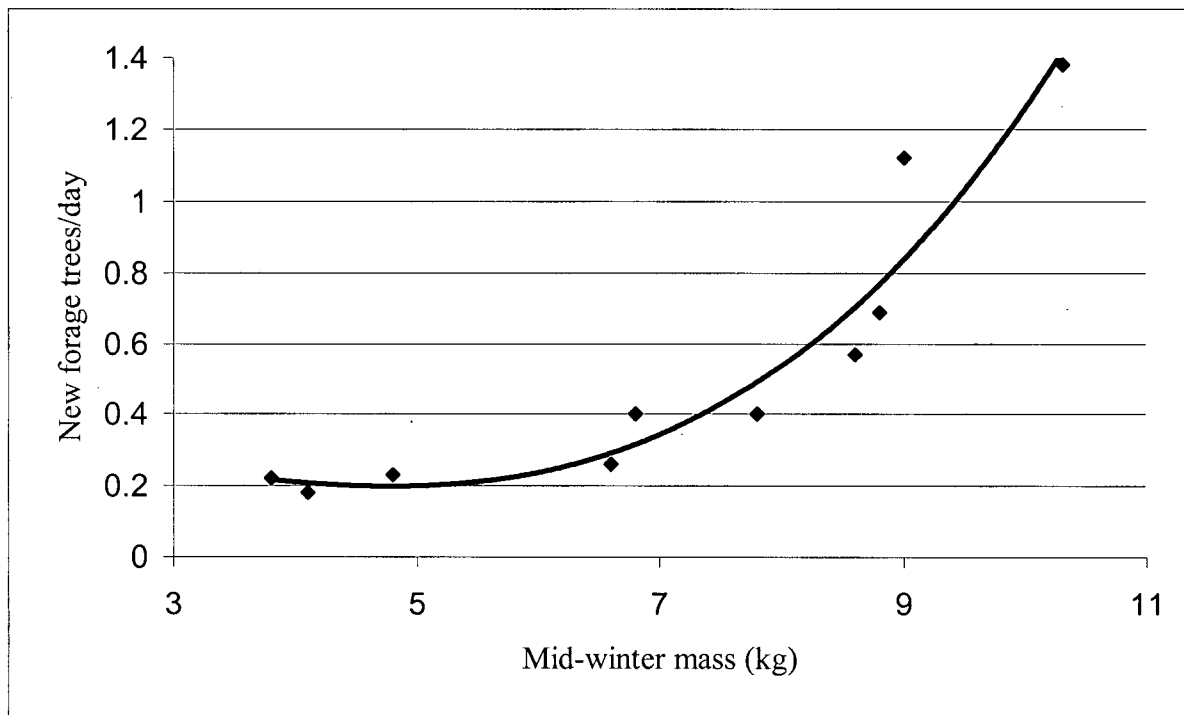


Figure 1.1: Number of new forage trees used by porcupines per day in relation to mid-winter mass (regression line $y = 0.0032x^3 - 0.0234x^2 + 0.0048x + 0.3612$; $r^2 = 0.92$).

CHAPTER 2: WINTER DEN USE BY PORCUPINES

INTRODUCTION

Cold temperatures can have dramatic impacts on mammals, including increasing individual mass loss and mortality rates (Moore and Kennedy 1985; Saether and Graven 1988; Sweitzer and Berger 1993). Despite the extreme cold weather conditions which may be encountered throughout the northern portions of the porcupine's (*Erethizon dorsatum*) range, the porcupine appears to be poorly adapted for survival in colder climates. Its dorsal pelage is sparse in comparison to other northern furbearers, and the soles of its feet are hairless and large (Folk 1966). Under winter conditions the lower critical temperature (ambient temperature at which the porcupine must increase its basal metabolic rate above resting rate to maintain body temperature) for porcupines is estimated to be between -12°C (Irving et al. 1955) and -4°C (Clarke 1969), which is high compared to other mammals living in northern climates (Scholander et al. 1950a, 1950b; Irving et al. 1955).

Given that porcupines have a high, lower critical temperature, cold ambient temperatures must constitute a major energy cost for them. To survive in cold temperature conditions the porcupine has evolved a number of physiological and behavioural adaptations (Clarke and Brander 1973; Roze 1987). One of the behavioural adaptations is the use of a winter den.

Sweitzer and Berger (1993) and Roze (1989) found that porcupines alter their foraging patterns in response to cold weather and spend more time in dens. Radiometric measurements (Clarke and Brander 1973) indicate that cover above the back of a porcupine, such as a conifer branch, reduces radiative heat loss, and presumably a winter den (not measured in the Clarke and Brander study) provides even greater thermal protection than a conifer branch.

The objective of this study was to determine the relative thermal protection provided to a porcupine by different den structures and to examine whether porcupines choose den types with

respect to the thermal protection provided. Den switching and den sharing by porcupines was also examined to compare winter denning behaviour of this study population with those from other areas.

STUDY AREA

Please see Chapter 1 for a full description of the study area.

METHODS

During the winter of 1996 and 1997, 33 porcupines were located, captured and fitted with radio transmitters as per the methods described in Chapter 1. Throughout the winter months from 1996 to 2000 each collared animal was located 3 times per week, using handheld telemetry. When an animal was found in a den the location was recorded using a Trimble ProXL GPS unit with differential correction (accurate to ± 1 m), and a temperature measurement from inside and outside the den was made. The temperature was measured using a Barigo digital indoor/outdoor thermometer (accurate to $\pm 1^{\circ}\text{C}$) with a 3 m probe cable. The probe was taped to heavy gauge electrical wiring to give stiffness and to allow manipulation into the porcupine den. When the porcupine could be seen within the den, the probe was placed beside (but not touching) the animal. When the animal could not be seen the probe was inserted to a maximum of 2 m. In all cases the probe was positioned so as not to be resting on the den floor. The probe was left for 10 minutes to gain a stable temperature reading. Once the den temperature had been recorded the probe was then removed and placed at snow level, in a forest opening, closest to the den site, to record ambient temperature.

Although a single porcupine may have used the same den over several weeks during the winter or during two or more winters, only a single temperature measurement was taken from each den site over the course of this study. In addition to the den use by collared porcupines, den use by uncollared porcupines was also noted (the type of den used) when discovered

fortuitously. Temperatures were not recorded at these den sites unless it was confirmed (through visual observation) that the porcupine was occupying the den at the time.

Porcupines within the Shames Valley study area used four distinct den types: 1) log dens, which were defined as dens within fallen, hollow logs or dens located under a fallen tree (usually having been created by trees that had been cut down during commercial harvesting, but left on-site). 2) Stump dens, which were defined as dens located beneath the stump of a previously harvested tree. In all cases these dens were located in the rootwad of the stump, not in any kind of hole within the stump itself. 3) Rock dens, which were dens located within the crevices of rock outcroppings. These dens were usually very deep and often had multiple, potential entrances. 4) Pre-excavated dens, which were rare in the study area, consisted exclusively of dens excavated by coyotes (*Canis latrans*) into soft soils on gully slopes.

STATISTICAL ANALYSIS

I compared the thermal protection provided by each den type using a single factor analysis of variance of the temperature differentials for each den type. Where required a Tukey test was used to determine which means were different (Zar 1974). Temperature differentials were calculated by subtracting the ambient temperature from the den temperature to give a positive number. When den temperatures were lower than ambient temperatures the differential was negative.

RESULTS

A total of 46 dens were measured to determine the temperature differential between den and ambient temperatures. Unfortunately, owing to the low number of pre-excavated dens used, no measurements for this den type were obtained. Rock and stump dens provided almost identical thermal protection, with mean temperature differentials of +5.4°C and +5.2°C, respectively (Figure 2.1). Log dens provided the poorest insulation for porcupines, as the best temperature differential recorded for a log den was +4°C and the mean was +1.3 °C (Figure 2.1). This

compares with the best temperature differential for a rock den of +9°C and a stump den of +10°C. Analysis of variance, with the associated Tukey test, showed log dens provide significantly less thermal protection than both rock and stump dens (ANOVA $p = 4 \times 10^{-4}$; d.f. = 2, 43; $F = 9.42$).

In the single case where a log den was measured while ambient temperature was below -12°C, the den temperature was also below -12°C (-16°C ambient, -15.3°C den). In nine cases where den temperatures were recorded in stump and rock dens while ambient temperatures ranged from -12°C to -20°C, the den temperatures remained above -12°C.

Of 24 observations of porcupines out of their dens during the day, only one occurred when the ambient temperature was below -4°C (temperature was -5°C). This observation involved a porcupine moving down a tree and travelling to a stump den, which it entered. All other observations of active animals involved porcupines feeding or resting in trees when temperatures were between -2°C and +6°C.

If -4°C is the lower critical temperature for porcupines, then log den temperatures were at or below the lower critical temperature in all eight cases where ambient temperature was below -4°C. Rock den temperatures were at or below -4°C in four out of twelve cases where ambient temperature was below -4°C, and stump den temperatures were at or below -4°C when ambient temperatures were below -4°C in four out of fifteen instances. In the cases where stump and rock den temperatures were below -4°C, the ambient temperature was -12°C or colder and the level of thermal protection provided by the den was high (+6.7°C to +10.0°C temperature differential).

The use of pre-excavated and log dens was similar from year-to-year, with pre-excavated dens being used in only one year (1996/97) and log dens being used infrequently in all years (Table 2.1). In three of the four years the majority of dens used were stump and rock dens, the two den types with the best temperature differentials. The biggest single change in den use,

from year-to-year was in the use of stump dens in 1997/98. During this winter, the use of stump dens dropped to the lowest usage of the study (13.8%), while the use of rock dens increased to the highest usage (69.0%) (Table 2.1). The winter of 1997/98, based on average weekly temperatures, was the warmest winter of the four- year study (Table 2.2). January was the only month in which 1997/98 did not have the warmest maximum and minimum average temperatures, compared to the three other study years.

The number of dens used by a single porcupine in one winter was constant over three winters of the study. In 1996/97, 1998/99 and 1999/00 individual porcupines used an average of 3.44 dens/porcupine, 3.33 dens/porcupine and 3.25 dens/porcupine, respectively. The average number of dens used by a porcupine dropped in 1997/98 to 2.12.

Throughout the four winters of this study individual porcupines did not always use the same den sites from year-to-year. In some cases new dens were used every winter and in a small number of instances the same den was used by different porcupines in two different years. Only one instance of two porcupines using the same den at the same time was noted. This den sharing occurred in the winter of 1998/99 and involved an adult female and a juvenile female. It was unknown if the two animals were related, but they shared the same den for 22 days without any indication of disputes occurring within the den (no sounds when den was observed by researchers).

Average minimum monthly temperatures (Table 2.2) varied considerably from month-to-month and from year-to-year over the four winters of the project. Fourteen of the 20 months of this study had average minimum temperatures of -4°C or lower and 6 of the 20 months had average minimum temperatures of -12°C or lower.

DISCUSSION

Porcupines in this study used four distinct den types (log, stump, rock or previously excavated dens); however, previously excavated dens were only used to a minor degree during

a single winter. Unlike the results reported by Roze (1987) and Griesemer et al. (1994), all animals in this study used dens extensively throughout the winter and although roosting in trees during the day was noted, none spent more than a day in the shelter of conifer trees rather than in a den.

The relative use of the three common den types mirrored closely the temperature differentials found between them. Rock and stump dens had the largest temperature differentials and were used equally often through most of the study. An exception to this was the winter of 1997/98, when rock dens were used more than in any other year and stump dens were used less often. This winter was also the warmest winter of the study. The warmer average temperature resulted in more mid-winter snowmelt than in other study years, and this may have influenced den choice by porcupines. Stump dens tend to be low-lying and are susceptible to water seepage. As a result, increased snowmelt may have resulted in water in the den and thus lower use by porcupines.

Log dens had the poorest temperature differential and were used least often among the three common den types. Even in years of increased snowfall, when the large snowpack would be expected to provide increased thermal cover to a log, porcupines did not increase the use of this den type. In all years, when ambient temperatures dropped below -4°C , log dens did not provide adequate thermal protection to porcupines.

Roze (1989) found similar results in den use by porcupines in the Catskill Mountains of New York State. Rock crevices were the most used denning structure (70% of dens) and hollow logs were least often used ($< 10\%$ of dens). A key difference between the porcupines in the Catskill Mountains and the porcupines in the Shames Valley is the use of stump dens and standing, hollow trees. In the study area chosen by Roze (1989), porcupines used standing trees with hollow openings for dens 20% of the time, and never used stump dens, as seen in my study. The difference in den use is related to forest structure. My study site is a second-growth

forest, 20–25 years of age, and, as a result, there are no trees within the study area that are old enough to have developed hollow openings in the stem. The high use of stump dens is related to previous logging activities. The removal of the large coastal old-growth trees resulted in large stumps being left behind. As the root structure of these stumps begins to decay a natural opening is created beneath the stump in the root wad. Although Roze's study area was an abandoned farm, he mentions no evidence of recent (in the last 30 years) logging on the site. As a result, stumps would only be created through natural mortality of trees.

Speer and Dilworth (1978) also reported that the majority of den sites in their New Brunswick study site were located in the roots of trees. These dens, however, were not under stumps, but located in the roots of wind-thrown trees. Only one of 69 dens was located in a standing, hollow tree.

Based on behavioural observations of porcupines during my study, I assumed that the lower critical temperature for porcupines in the study area is closer to -4°C as reported by Clarke (1969), rather than the -12°C reported by Irving et al. (1955). In my study area, under most winter temperature conditions, porcupines are able to rely solely on the thermal cover provided by a rock or stump den to reduce the energy requirements for maintaining body temperature, as den temperatures are maintained above -4°C . When ambient temperatures drop below -12°C , it appears porcupines are forced to increase their metabolic rate to maintain body temperature within rock and stump dens, however, on average, temperatures within the study area were above -12°C .

Porcupines in my study were usually solitary in their den occupancy, but there was one instance where two porcupines used the same den at the same time. The sharing of dens by porcupines has been reported by Roze (1987), who found 12% of dens to be occupied by two porcupines (usually a male-female pair). Dodge (1967) also described den sharing by porcupines in western Massachusetts. In contrast, Dodge and Barnes (1975), Brander (1973)

and Shapiro (1949) found that porcupines rarely shared dens in their studies. The occurrence of winter den sharing appears to be directly correlated with the abundance of den sites in a particular area. All three studies where porcupines were found to rarely share dens were described as having an abundance of den sites, whereas Roze (1987) describes both his study site and that of Dodge (1967) as having limited den sites. The results from my study also support this argument as the Shames Valley has a large number of potential den sites (as indicated by numerous unoccupied, but previously used dens).

Despite the large number of available dens, porcupines in the Shames Valley used only a few dens per individual during a single winter (3.25 - 3.44 dens/porcupine during 1996/97, 1998/99, and 1999/00). In the warm winter of 1997/98 the average number of dens used per porcupine dropped to 2.12. Increased snowmelt in this year may have reduced the number of dens available to porcupines, owing to water seeping into den sites. Alternatively, the warmer temperatures may have also increased the energetic cost of travel for porcupines by creating a soft snowpack, thereby restricting porcupine movements. Roze (1989) reported a similar impact, with high snowfall events reducing porcupine winter movements and numbers of dens used.

SUMMARY

In this chapter, I investigated den type selection by porcupines, in relation to the thermal cover provided by the den type, over a period of four winters. Porcupines used log dens, stump dens and rock dens in proportion to the thermal cover provided by each den type. Based on behavioural observations I assumed that the lower critical temperature for porcupines in my study area is -4°C . Both stump and rock dens provided adequate thermal protection under most ambient conditions, to allow porcupines to maintain their body temperature, without increasing basal metabolic rate. In most cases rock and stump dens maintain den temperatures above -4°C until ambient temperatures reach -12°C or lower. In contrast log dens provided poor thermal

protection, even in years of high snowfall. When ambient temperatures dropped below -4°C , den temperatures within log dens were also recorded below -4°C .

The use of rock dens has been reported in other studies; however, the use of stump dens appears to be related to unique stand structure of my study area. Previous logging activities have created a large number of potential stump dens for porcupines. As a result, in addition to rock dens, which are available to porcupines in other study areas (Roze 1989), porcupines in the Shames Valley also have the opportunity to use stump dens, which provide similar levels of thermal protection as rock dens.

Despite the large number of potential dens available to porcupines within the Shames Valley, den use is generally limited to about 3 dens per porcupine per winter. The limited use of dens by an individual porcupine during winter may be related to the energetic cost of finding a new den or it may be related to specific selection criteria used by porcupines (Chapter 1). These criteria may make many dens unsuitable owing to the species or size of trees in the immediate vicinity of the den.

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Table 2.1: Winter den type selection by porcupines in the Shames Valley (1996 - 2000).

Winter	n	Den Type			
		Log	Stump	Rock	Dirt
1996/97	47	17.0%	38.3%	38.3%	6.4%
1997/98	29	17.2%	13.8%	69.0%	0.0%
1998/99	24	12.5%	50.0%	37.5%	0.0%
1999/00	23	17.4%	52.2%	30.4%	0.0%
TOTAL	123	16.3%	37.4%	43.9%	2.4%

Table 2.2: Maximum and minimum temperatures (°C) for the Shames Valley study site (1996 - 2000), based on weekly averages (± 1 s.d.).

	1996/97		1997/98		1998/99		1999/00	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
November	-2.5 (4.9)	-11.0 (8.5)	11.5 (2.1)	1.0 (5.7)	10.0 (1.0)	-4.0 (0.0)	2.0 (4.2)	-3.0 (3.8)
December	-3.8 (10.0)	-14.8 (10.2)	4.7 (4.7)	-2.3 (2.5)	0.5 (1.3)	-7.2 (5.6)	-3.3 (6.8)	-6.5 (5.2)
January	1.3 (2.2)	-12.5 (9.3)	-0.6 (5.4)	-13.2 (9.0)	0.0 (0.7)	-8.3 (3.9)	-9.8 (0.4)	-16.5 (2.1)
February	5.5 (2.5)	-4.8 (3.8)	8.3 (2.2)	-3.3 (2.1)	0.0 (0.0)	-12.5 (6.4)	-1.0 (1.3)	-14.0 (4.0)
March	11.0 (2.4)	-4.4 (3.7)	11.0 (5.5)	-3.0 (1.8)	8.0 (4.8)	-3.0 (3.7)	1.8 (2.3)	-8.8 (6.5)

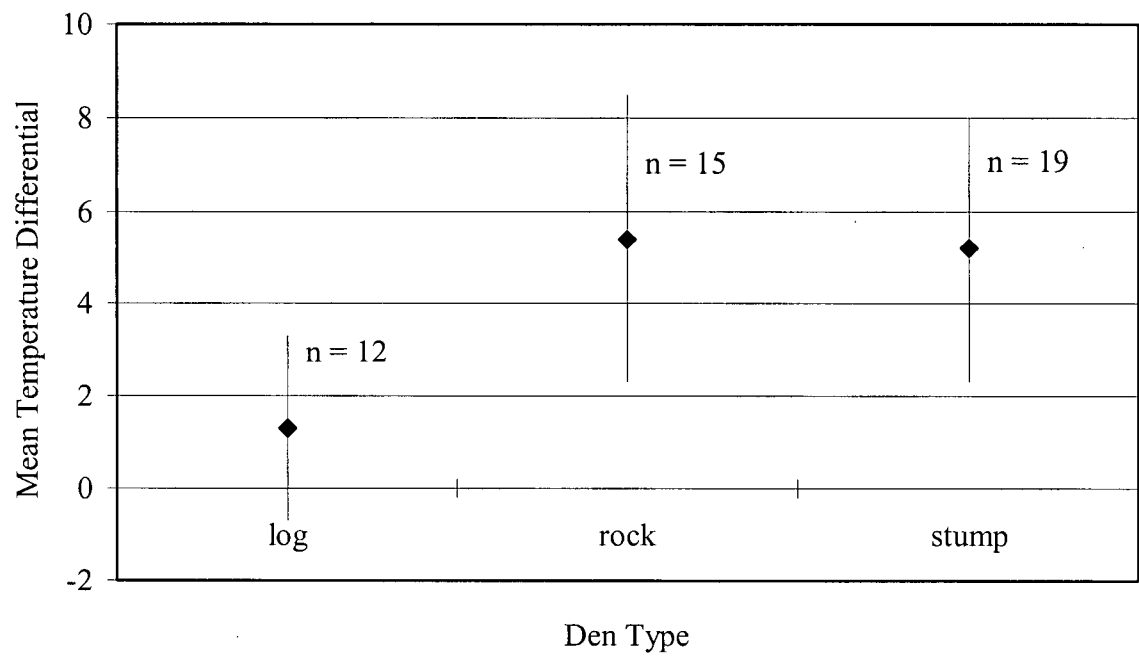


Figure 2.1: Mean temperature differential (den temperature – ambient temperature in $^{\circ}\text{C}$) (± 1 s.d.) of winter den types used by porcupines in the Shames Valley.

CHAPTER 3: IMPACT OF PRE-COMMERCIAL THINNING ON PORCUPINE WINTER FORAGING BEHAVIOUR AND PREDATION RATES.

INTRODUCTION

The porcupine (*Erethizon dorsatum*) is a serious threat to timber production in northwest British Columbia. Sullivan and Cheng (1989), MacHutchon (1990) and Krebs (1994) have all identified the potential for the porcupine to create "not satisfactorily restocked" (NSR) stands and thus reduce allowable annual cut (AAC) in some areas of British Columbia. Unfortunately, current trends in intensive forest management practices appear to be increasing the potential for extensive porcupine damage in many second-growth stands within northwestern British Columbia. With the continued decrease of the available forested landbase, there is increasing pressure for forest managers to produce a larger volume of timber per stem, in a shorter rotation. As a result of this pressure, an increasing number of second-growth stands in British Columbia are being targeted for pre-commercial thinning treatments. This silvicultural practice eliminates less healthy and suppressed trees, thereby reducing competition between the remaining stems, and increasing growth rates (Assmann 1970; Kozlowski 1971; Carter et al. 1986; Jozsa and Middleton 1994). Thinning practices are continuing despite evidence from Harder (1979), Eglitis and Hennon (1986), Sullivan et al. (1986) and Sullivan and Cheng (1989) that porcupines prefer to feed on vigorously growing trees. This feeding preference means that the current emphasis on thinning second-growth stands may enhance porcupine feeding opportunities by providing a large number of areas with vigorously growing trees, which may ultimately exacerbate the porcupine damage problem by increasing porcupine survival and reproductive rates.

The winter diet of porcupines (cambium, phloem and foliage of a variety of woody shrubs, deciduous and coniferous trees) is of poor quality (0.5% -8% crude protein or nitrogen,

Stricklan 1986; Roze 1989), compared to the minimum protein requirements found for other small mammals of 15% (Wallach and Hoff 1982) and 11% (Sinclair et al. 1982). One consequence of this low quality diet is that starvation is a major cause of mortality in porcupine populations (Roze 1989; Hale and Fuller 1996). The poor quality food means that porcupines are nutritionally stressed for most of the winter and are not maintaining body mass, but merely attempting to slow the rate of mass loss through their foraging choices (Oveson 1983; Roze 1985; Sweitzer and Berger 1992, 1993). The fact that porcupines are nutritionally stressed in winter means that each foraging choice of when, where and what to eat, becomes important. The selection exhibited by porcupines for specific species and diameter classes of trees (Chapter 1) suggests that alteration of habitat may influence the foraging choices made by individual porcupines, and may be useful in managing porcupine feeding damage within particular second-growth stands. In this chapter I examine the influence of habitat alteration, in the form of pre-commercial forest thinning, on porcupine foraging behaviour during winter. I examine the potential beneficial use of pre-commercial thinning to 400 stems/ha versus a more common 1200 stems/ha and control areas of 2000 stems/ha and I test four hypotheses relating to these treatments:

H₁: Owing to an increased perceived risk of predation, porcupines will shift their foraging range to avoid the thinned treatment areas.

Several studies indicate that porcupines alter their behaviour to avoid foraging in open areas (Keller 1935; Earle and Kramm 1982; Sweitzer and Berger 1992; Krebs 1994). Predators such as cougar (*Felis concolor*), fisher (*Martes pennanti*), wolverine (*Gulo gulo*), and coyote (*Canis latrans*) appear to be more effective at killing porcupines in open areas (Robinette et al. 1959; Powell and Brander 1977; Powell 1982; Stricklan 1986; Sweitzer and Berger 1992; Krebs 1994). Although the density of predators within my study area is unknown, Sih (1992) indicates that prey species often make foraging decisions based on perceived risk and often stay

within refuge habitat long after predators have been removed from the system (either experimentally or naturally). As a result, porcupines should avoid open habitats when possible.

H_{A1}: Alternatively, porcupines will not shift their foraging ranges out of the thinned areas and will suffer higher rates of mortality owing to predation compared to porcupines in control areas.

If porcupines are not able to adequately sample their environment to determine the potential threat of predation (Lima and Dill 1990), then they will not perceive an increased predation risk. As a result, porcupines that continue to forage within the thinned stands will suffer higher rates of mortality, owing to the increased effectiveness of predators in more open habitats (Robinette et al. 1959; Powell and Brander 1977; Powell 1982; Stricklan 1986; Sweitzer and Berger 1992; Krebs 1994).

H₂: Porcupines that continue to use den sites within thinned treatment areas will forage in a greater radius around den sites and move to new dens more frequently than porcupines using dens in the control areas.

Griesemer et al. (1994) experimentally prevented porcupines from using feed-trees close to den sites, and found that these animals increased the radius around the den from which they foraged. The same work showed that porcupines shifted den locations more often throughout the winter whenever feed tree selection was limited. The marginal-value theorem (Charnov 1976; Stephens and Krebs 1986) predicts that a rate-maximizing forager will choose the residence time for each patch type so that the marginal rate of gain at the time of leaving equals the long-term average rate of energy intake in the habitat. If the forage area around the den site is assumed to be the patch from which the porcupine must decide when to leave, then porcupines feeding in the thinned areas will stay at one den site for a shorter period of time

compared to control animals. The smaller number of forage trees available in the thinned areas will be used more quickly, thereby reducing the marginal rate of gain within the patch to that of the long-term average in the area, in a shorter period of time. This prediction assumes the cost of moving to a new den is equal between the control area and the thinned areas, and that the energetic value of forage trees is similar between thinned and control areas.

H_{A2}: Alternatively, porcupines will not increase their foraging range around the den site and will not change den location in a shorter time frame because den switching is not based on the rate of foraging that can be achieved.

The number of stems left around the den after thinning may still be adequate to meet the minimum foraging demands of the porcupines. As a result porcupines will stay at a particular den location beyond the time that would be predicted under the marginal-value theorem because the den site provides good protection from predators, or because the extra energy cost of finding a new den site is higher than the gains from finding a den site with more available forage trees.

STUDY AREA

Please see Chapter 1 for a full description of the study area.

METHODS

In the spring of 1996 tree assessment plots were established within three second-growth stands (38 ha, 48 ha and 58 ha in size). The assessment plots were circular, 5.64-m radius (100-m²) plots, systematically placed across the study stands at a density of 2 per hectare (total of 160 plots). The centre of each plot was marked with a stake and flagging. Within each assessment plot, all trees with a diameter at breast height (dbh = 1.3 m) $\geq$ 5 cm were permanently marked.

In the fall of 1996 12 porcupines were located, captured and fitted with radio transmitters as per the methods described in Chapter 1. An additional 21 animals were captured and fitted with radio transmitters during the winter of 1996 and 1997. Of the 33 animals radio-collared only 18 maintained all of their activity within the study area and could be used for analyses in this study.

Throughout the winter months from 1996 to 2000 each collared porcupine was located 3 times per week, (using handheld telemetry), to identify the animal's den location. From its den location snowtracking was done to trace the feeding route of the animal from the previous night. During the snowtracking, the dbh and species of all forage trees encountered were recorded. A forage tree was defined as any tree from which the porcupine had removed cambial tissue. Trees that were climbed but not fed upon were not considered forage trees. Upon encounter, each forage tree was marked to ensure it was not recorded more than once.

In the spring of 1998 each of the three study stands (Stand 1, 2 and 3) was split into three equal size, rectangular sections (Unit A, B and C), running from the lower boundary of the study stands (approximately 200 m elevation) to the upper boundary of the study stands (approximately 450 m elevation). Each section was randomly assigned a treatment. One section of each study stand was left as a control (Unit A) at approximately 2000 trees/ha; one section was pre-commercially thinned to a density of 1200 stems/ha (Unit B); and one section was pre-commercially thinned to a density of 400 stems/ha (Unit C). For two winters after the pre-commercial thinning treatments the porcupine monitoring continued, and in the spring of each year the damage assessment plots were re-visited and data were collected as described above.

As part of the weekly porcupine monitoring, predator tracks were noted to determine if predation pressure in different stand densities influenced porcupine use of an area. Within each treatment area (post-treatment) one transect was walked three times a week. While walking this

transect the researcher recorded all tracks of potential porcupine predators that crossed the transect line. The number of tracks counted per unit transect distance was used to index the relative predation pressure within each treatment unit.

STATISTICAL ANALYSIS

For comparison of feeding damage rates within the stands between pre- and post-treatment years, the pre-treatment damage assessment plots were split based on their location with respect to the boundaries of the treatments in the post-treatment years (i.e. plots that were in the 400 stems/ha treatment area after thinning were grouped together for the pre-treatment analysis).

When examining the distance from den sites to forage trees for each porcupine, data from different den sites of the same porcupine were combined to provide a single average maximum distance. Analysis of variance with Tukey test (Zar 1974), was used to compare maximum distance travelled from den sites to forage trees between porcupines in the control areas and the two treatment areas. To examine the influence of outliers the same analysis was done on the closest 95% of forage trees to the den site.

To examine shifts in a porcupine's foraging range as a result of the thinning treatment I plotted the GPS location of each forage tree used by an individual porcupine during the winter of 1997/98 (winter before treatments). I estimated the minimum convex polygon foraging range of each porcupine by including the closest 95% of all forage trees around the den site and using the animal movement extension to arcview (Hooge and Eichenlaub 1997). In some cases multiple den sites were used by a single porcupine. In these cases a polygon was drawn around each den site based on the closest 95% of forage trees. This procedure produced a pre-treatment foraging range map for each porcupine. The same procedure was then carried out for each porcupine based on forage trees used during the winter of 1998/99 (first winter after thinning treatment), to produce a post-treatment foraging range map. The similarity between the pre-treatment and post-treatment foraging ranges was then calculated based on the

percentage of area overlap between pre- and post-treatment (i.e. if the post-treatment foraging range overlapped 3 ha of the 4 ha pre-treatment foraging range then there was a 75% overlap). A comparison of the amount of foraging range shift between porcupines in the two treatment areas and control was done using analysis of variance on the arcsine transformed, percentage of overlap data. A power curve was developed to examine the likelihood of this test detecting a difference between the control and treatment porcupines.

RESULTS

Foraging range shifts

Two out of six porcupines left the 400 stems/ha area after treatment. Two out of 10 porcupines left the control area and one out of seven left the 1200 stems/ha area, during the same time frame. Porcupines within the control area had a mean of 53.8% (s.d. = 30.2%; n = 10) foraging range overlap between post-treatment and pre-treatment years. In the treatment areas foraging range overlap was 50% (s.d. = 26.7%; n = 7) and 40.7% (s.d. = 32.1%; n = 6) for porcupines in the 1200 stems/ha and 400 stems/ha areas respectively. No significant difference in the degree of overlap of post-treatment and pre-treatment foraging ranges was found (ANOVA $p = 0.69$; d.f. = 2, 20; $F = 0.37$); however, power analysis revealed that given the low sample size in each group, and the high degree of variation between individuals, overlap within the 400 stems/ha area would have to be approximately 65% less than the overlap in the control before a statistical difference could be established at $p = 0.05$.

While porcupines tended to change some of their den site locations from year-to-year, the number of winter dens located in areas of thinning treatments was similar before and after the treatments. In addition, the mean number of dens used by porcupines throughout the winter was similar between the control and two treatment areas (control - 2.75, 1200 stems/ha - 3.0, 400 stems/ha - 2.5).

Predation

In the four winters of this study only three predation events on porcupines were noted, all by wolverines. Two of the three occurred in the pre-treatment winters, prior to the track transects being established. The third case occurred in the control area the first winter after thinning. In all three cases the predation occurred in openings within the stand (no trees for a 3 m radius), and involved adult porcupines. There was no other evidence of any interaction between a porcupine and any predator during 13,692 radio-collared porcupine days.

In the two post-treatment winters, only one set of wolverine tracks was encountered on the transects. In this case the wolverine traversed the entire study area, crossing all three treatment units within all three study stands. The only other tracks of a potential predator that were observed were those of martens (*Martes americana*). Although martens were incidentally captured in porcupine traps I observed no incidence where marten had disturbed a porcupine in a trap, nor did I find evidence that marten disturbed porcupines in dens or foraging trees.

Porcupine foraging

All three study stands had low levels of porcupine damage across all areas in the pre-treatment years (Table 3.1). The one anomaly was in stand 2, Unit B where mean percentage of trees damaged per plot was 7.96% compared to 0.56% and 0.09% in Units A and C respectively (Table 3.1). In the post-treatment years damage rates increased in all three 400 stems/ha treatment areas compared to pre-treatment damage. The percentage of trees damaged in the 400 stems/ha treatment areas of each stand varied considerably (0.50 % - 16.87 %), with Stand 2 having the highest damage percentage post-treatment (16.87%) (Table 3.1).

The proportions of hemlock trees fed upon by porcupines in each dbh category varied considerably between the control and two treatment areas (Figure 3.1). In the control area the highest proportion (0.37) of forage trees was in the 5.0 – 9.9 dbh category, with the proportion

declining as size class increases. For the 1200 stems/ha there is a similar trend as in the control, with the smallest size class having the highest proportion (0.35) and the largest size class having the smallest proportion (0.04). In the 400 stems/ha area the 15.0 – 19.9 dbh size class made up the largest proportion (0.33) of the forage trees, while the smallest size class had the lowest proportion (0.08).

The maximum distance travelled from a den site to a forage tree (Table 3.2) was significantly greater for porcupines with den sites in the 400 stems/ha treatment area ($n = 4$ porcupines; 3 male, 1 female) compared to the control ($n = 8$ porcupines; 4 male, 4 female) and the 1200 stems/ha treatment area ($n = 6$ porcupines; 4 male, 2 female) (ANOVA $p = 0.019$; d.f. = 2, 15; $F = 5.50$; with Tukey test). Comparing the distance from den site to the closest 95% of forage trees revealed no significant difference between the two treatments and the control (ANOVA $p = 0.059$; d.f. = 2, 15; $F = 3.46$); however, there is a trend towards the porcupines in the 400 stems/ha area travelling farther to forage trees (Table 3.2).

Using the GPS locations of the forage trees, I calculated the distance to nearest neighbour (next forage tree) for each forage tree, of each porcupine. The average distance between forage trees was then compared between control and treatments. The mean distance between forage trees for control porcupines (4.1 m) was not statistically different from 1200 stems/ha (5.7 m) or 400 stems/ha (4.6 m) porcupines (ANOVA $p = 0.38$; d.f. = 2, 13; $F = 1.06$). This distance indicates that if trees were randomly distributed in these stands then a porcupine would on average walk passed one tree between each forage tree in the control and 1200 stems/ha stands, and would stop at every tree to forage in the 400 stems/ha stands.

DISCUSSION

The risk of predation is most simply defined as the probability of being killed during a specified time period. The three basic components for defining the level of predation risk are the rate of encounter between predator and prey, the probability of escape given an encounter,

and the time spent vulnerable to an encounter (Lima and Dill 1990). One of the purposes of this study was to determine if a thinning treatment could be used as a method to reduce porcupine numbers within a stand, by influencing at least one of these components of predation risk, or creating the perception for porcupines that one of these components has been influenced, and thus elicit a similar response.

Thinning of lodgepole pine stands has been shown to reduce red squirrel (*Tamiasciurus hudsonicus*) (Sullivan and Moses 1986) and snowshoe hare (*Lepus americanus*) (Sullivan and Sullivan 1988) populations. I hypothesized that the thinning treatments in this study would reduce porcupine numbers, either through a direct exodus of porcupines from the treatment areas owing to a perceived increase in predation risk (H_1) or through a direct increase in predation rates (H_{A1}). Sweitzer and Berger (1992) and Krebs (1994) found that the majority of predation events on porcupines occurred in open habitat and Sweitzer and Berger (1992) and Powell and Brander (1977) reported that porcupines alter their foraging patterns in response to predation risk.

My results indicate no support for hypothesis 1, as despite the open habitat created by the thinning treatments, porcupines did not show any statistically significant change in foraging range locations to avoid treatment areas. This lack of response may be directly related to low sample size, as power analysis indicated a low probability of detecting foraging range changes; however, the majority of porcupines in the 1200 stems/ha area and 400 stems/ha areas prior to treatments (when stem density was at 2000 stems/ha) remained in the same location after the thinning treatments.

Although intuitively a reduction in tree cover within a stand should be perceived by a porcupine as an increase in predation risk, this may not be the case. The rate of encounter between a porcupine and a predator is based on the density of predators in the stand, and the rate of detection between predator and prey. Based on the predator track transects from the

study area there was no increase in predator use of the thinned stands compared to control areas. The ability of a porcupine to detect its predator or for a predator to detect the porcupine is also likely to be unchanged. Porcupines are most exposed to predation at night when they leave their dens. As a result, it would be expected that the porcupine and its predators are using sound and scent to detect one another, not sight. If this is the case, the removal of stems from a stand is not likely to influence rates of detection between predator and porcupine.

The probability of escape once an encounter occurs between a porcupine and its predator is another aspect a porcupine must assess. Again, given the predator presence in my study area, this component of predation risk may be unchanged in the thinned stands compared with control stands. Numerous tracks of marten were observed; however, there was no evidence of marten interacting with porcupines at any time and work by Slough et al. (1989), Douglas et al. (1983) and Lensink et al. (1955) all indicate that marten concentrate on microtine rodents as a prey source. Wolverines were the only predator noted in the study area and, given that wolverines can climb trees, the only location for a porcupine to escape from a wolverine is likely to be a den. As the thinning treatment did not alter density of dens the probability of escaping a wolverine encounter should be unchanged.

The last component of predation risk which a porcupine would have to assess is the time spent vulnerable to encounter. This component would be impacted by thinning if the porcupine were to travel farther between forage trees (assuming risk of encounter is higher on the ground versus in a tree); however, my results indicate that porcupines travel the same distance between forage trees in the thinned stands and the control. The one additional component which may add to the time vulnerable to encounter is the distance travelled from the den site to the first forage tree in a foraging bout and distance travelled from the last forage tree to the den site after a foraging bout. My results indicate that the maximum distance from den site to forage trees

did increase in the 400 stems/ha stands, but this increased travel did not cause porcupines to leave the thinned treatment areas.

Hypothesis A1 indicated that porcupines remaining in the thinned areas would suffer higher rates of mortality owing to predation, compared to porcupines in the control areas. This hypothesis was not supported from my data. Over four winters of radio-tracking only three predation events on porcupines were recorded, none of which occurred in a treatment area. In addition, during two winters of predator transects only one set of predator tracks (a wolverine) was recorded. Low mortality rates owing to predation were also reported by Griesemer et al. (1994) and Hale and Fuller (1996).

The third hypothesis I examined was that porcupines in the thinned treatment areas would forage in a greater radius around their den sites and would change den sites more often compared to porcupines in control stands. Griesemer et al. (1994) experimentally prevented porcupines from using forage trees close to den sites, and found that porcupines responded by increasing the radius around the den from which they foraged and moved to new dens sooner. My results showed a similar response with porcupines in the 400 stems/ha treatments travelling farther from den sites to forage trees than porcupines in the control and 1200 stems/ha area. However, I found no difference in distance travelled from den to forage trees between porcupines in the 1200 stems/ha area and those in the control areas. When the distance between forage trees was compared to the density of stems in each stand I found that on average, porcupines in the 1200 stem/ha areas and control areas pass by the same number of trees during foraging, which may be related to the similarity in distance travelled to forage trees.

Based on the assumption that porcupines are rate maximizing foragers (Charnov 1976; Stephens and Krebs 1986), I predicted that porcupines in the treatment areas would shift den locations more often throughout the winter compared to control porcupines; however, this was not the case. Although I did not monitor the number of days each den was in use, porcupines in

the control and treatment areas used, on average, a similar number of dens throughout the winter. This indicates that the lower number of trees around dens in the treatment areas did not translate directly into increased den switching.

Despite the lack of den switching occurring in a shorter number of days, based on the models developed by Charnov (1976) and Cowie (1977), porcupines may still be rate maximizing foragers if in response to travelling farther to reach a forage tree more vascular tissue is removed per tree. This possibility is examined in more detail in Chapter 4.

I found only partial support for hypothesis A2. While porcupines in the treatment areas did not change den sites in a shorter period of time compared to control; porcupines in the 400 stems/ha areas did increase their foraging range.

Porcupines fed upon smaller trees in the control and 1200 stems/ha area compared with the 400 stems/ha area. Feeding on larger trees in the 400 stems/ha area is a direct result of thinning having removed a large proportion of the smaller diameter trees. The resulting shift in the size-class distribution of stems available to the porcupines results in a higher proportion of large diameter stems being used as forage trees. In Chapter 1 of this thesis, I showed that porcupines in untreated stands select hemlock trees over 9.9 cm dbh and avoid smaller diameter trees.

Overall, I found no discernable difference in the foraging patterns of porcupines in the control versus the 1200 stems/ha treatments. As 1200 stems/ha is a common thinning density in the Prince Rupert Forest Region, this result provides evidence that current thinning practices in British Columbia are likely to exacerbate the porcupine damage problem. Through a thinning treatment, the percentage of trees damaged by porcupines immediately increases; owing to a reduction in the total number of trees/ha, but the number of trees being damaged remains the same. In addition, thinning treatments generally remove the suppressed stems which porcupines tend to avoid in control stands (see Chapter 1). As a result, although thinning

reduces the number of trees/ha, it does not reduce the number of forage trees/ha, from the point of view of the porcupine.

Based on my results, pre-commercial thinning to 1200 stems/ha or even to the low value of 400 stems/ha is not likely to reduce porcupine feeding damage in second-growth stands. Although some shifts in foraging behaviour were seen by the porcupines in the 400 stems/ha areas, the changes were not such that a reduction in porcupine feeding damage could be expected. Despite the lack of reduction in porcupine numbers in the first two years post-treatment, increased energetic requirements of porcupines in thinned stands may reduce numbers in some years (Chapter 4). Also, where predators are more abundant and porcupines perceive greater predation risk, porcupines may show more avoidance of thinned stands. In general, however, it may be prudent for forest managers to pre-commercially thin stands to higher densities (1200 stems/ha and above). In untreated stands porcupines will include small diameter trees as some proportion of their diet (Chapter 1), thereby providing a natural thinning mechanism. Pre-commercial thinning to higher densities and maintaining some component of smaller diameter trees within the stand may provide some level of buffer for the dominant trees. Further research into the benefits of increased growth rates from pre-commercial thinning versus the potential losses caused by porcupines (Chapter 5) is required to better determine optimal thinning densities from a silvicultural point of view.

SUMMARY

In this chapter I examined the impact of pre-commercial thinning to 400 stems/ha and 1200 stems/ha on porcupine foraging behaviour. I found that predators were at low densities within the study site and porcupines did not perceive an increased risk of predation owing to the habitat alteration caused by the thinning treatments.

No differences in foraging behaviour were observed between control porcupines and porcupines in the 1200 stems/ha treatment area. There were differences observed between the

control porcupines and those that continued to forage within the 400 stems/ha treatments. As predicted by hypothesis 2, porcupines in the 400 stems/ha area increased the radius of foraging area around their dens. Despite the increase in foraging radius, there was no difference in the number of dens used throughout the winter between porcupines in the 400 stems/ha area and the control. As well, there was no difference in the distance between forage trees in either of the treatments or control.

This study has found no benefit of commercial thinning in reducing porcupine feeding damage in second-growth stands. Instead there is evidence that thinning will increase the rate of feeding damage.

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Table 3.1: Mean percentage ($\pm$ 1 s.d.) of trees damaged by porcupines within each tree assessment plot.

UNIT	PRE-TREATMENT			POST-TREATMENT		
	A	B	C	A-control 2000sph	B-1200 sph	C-400 sph
Stand 1	0.25 (0.36)	0	0	3.1 (8.7)	0	0.50 (1.90)
Stand 2	0.56 (0.58)	7.96 (1.93)	0.09 (0.55)	0.20 (0.89)	1.85 (6.11)	16.87 (5.65)
Stand 3	1.50 (1.80)	0	0	0.69 (2.08)	1.54 (5.43)	1.65 (5.43)

Note: A, B, C refer to one third of each study stand and are the same areas in both pre-treatment and post-treatment years. Each area was untreated (2000 stems/ha) in pre-treatment years.

Table 3.2: Maximum distance (± 1 s.d.) from den site to forage trees (n = number of porcupines) during winters of 1998/99 and 1999/00.

	Control (2000 stems/ha) n = 8	1200 stems/ha n = 6	400 stems/ha n = 4
Mean Maximum Distance to Forage Trees (m)	40.5 (25.1)	57.1 (21.3)	100.1 (12.4) ^a
Mean Distance to 95% of Forage Trees (m)	36.8 (25.2)	49.6 (25.7)	88.2 (7.2)

^a Significantly farther than control and 1200 stems/ha (ANOVA $p = 0.019$, $df = 2, 15$ $F = 5.498$).

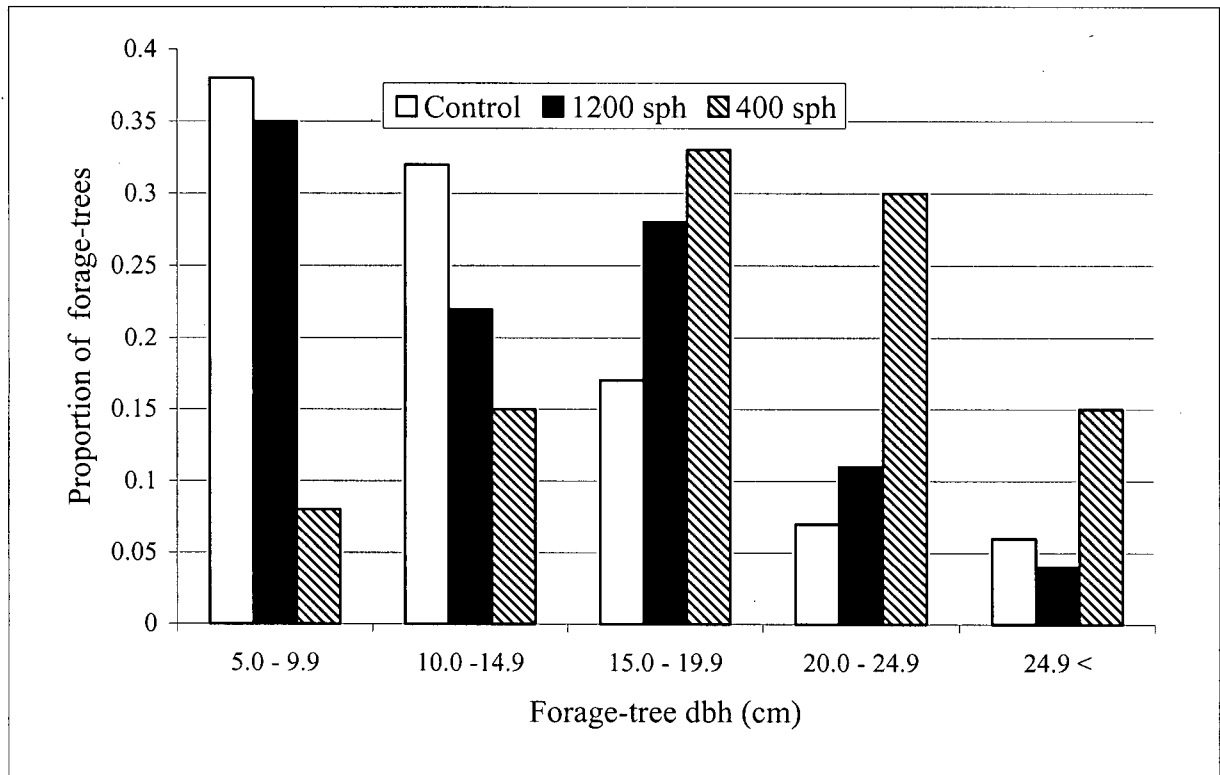


Figure 3.1: Size class distribution of hemlock forage trees chosen by porcupines in the control, 1200 stems/ha and 400 stems/ha treatment areas (Shames Valley).

CHAPTER 4: IMPACT OF PRE-COMMERCIAL THINNING ON PORCUPINE WINTER ENERGY EXPENDITURES.

INTRODUCTION

Two important energetic costs for mammals that remain active during the winter are the cost of maintaining body temperature, and the cost of travel during foraging. The cost of maintaining body temperature is directly related to the differential between body surface temperature and ambient temperature (Irving et al. 1955; Clarke and Brander 1973; Bradley and Deavers 1980). As ambient temperature decreases mammals must expend more metabolic energy to maintain body temperature.

The cost of travel during foraging can account for a large amount of winter energy expenditure for mammals (Bunnell and Harestad 1989). This cost is most influenced by the distance travelled during foraging, but can also be increased as a result of snow depth (Pruitt 1959; Jenkins and Wright 1987; Halfpenny and Ozanne 1989).

For porcupines (*Erethizon dorsatum*), with a lower critical temperature close to -4°C (Clarke 1969; Chapter 2), and short legs making movement through deep snow difficult (Roze 1989), a decrease in average ambient temperature within a stand of trees, or an increase in average snow cover on the forest floor has the potential to have a significant impact on winter energy expenditure. Although pre-commercial thinning treatments have not been shown to cause an immediate reduction in porcupine numbers within thinned stands (Chapter 3), the use of pre-commercial thinning treatments to low densities (400 stems/ha) has the potential to negatively impact winter energy budgets of porcupines. The reduction in forest canopy as a result of pre-commercial thinning should result in lower ambient temperatures within a stand, as heat energy will more easily radiate to the sky rather than being trapped and re-radiated back to the ground by conifer branches (Clarke and Brander 1973). A reduction in forest canopy will also result in

a reduction in snow interception by the canopy and therefore a higher average snowfall reaching the forest floor. Both of these changes resulting from pre-commercial thinning should translate into an increase in winter energy expenditure for porcupines using the area. An increase in winter energy expenditure has the potential to cause a long-term reduction in porcupine populations owing to an increased rate of starvation (Roze 1989; Hale and Fuller 1996) and a decrease in reproductive output (Bunnell and Harestad 1989).

In this chapter I examine the potential benefits to forest management of using low density pre-commercial thinning treatments (400 stems/ha) to increase porcupine winter energetic expenditures. I compare the influence of the low density thinning to a more standard 1200 stem/ha pre-commercial thinning treatment and control areas (2000 stems/ha) and tested six hypotheses:

H₁: The lower density of trees in thinned areas, will reduce the thermal cover afforded by tree canopy. As a result, the thinned treatment areas will be, on average, colder than the control areas.

Clarke and Brander (1973) showed that overhead cover in the form of hemlock branches (*Tsuga canadensis*) significantly increased thermal cover for porcupines, relative to an open field. The increased thermal cover was explained as being a combination of re-radiation of energy stored in the tree during the day being released at night, and the reflection of long-wave radiation from the snow surface back from the hemlock branches down to the snow surface. A reduction in stem density in the treatment areas will also result in increased convective heat loss from wind.

H_{A1}: Alternatively the thinned treatment areas will maintain the same temperature, on average, as the control areas.

There is a threshold of canopy removal that is required before there is a measurable impact on the level of thermal cover provided within a second-growth conifer stand. Thinned areas will maintain enough of the original tree canopy that there will be no measurable impact on average stand temperatures at ground level (where porcupines travel) or at tree top level (where porcupines feed).

H₂: Porcupines in the thinned stands will travel in the open (away from conifer branch cover) more often, and move through deep snow more often than porcupines in control areas.

Speer and Dilworth (1978) and Roze (1989) report that porcupines tend to travel on the firm snow under conifer branches whenever possible. With a reduction in the density of conifers in the treatment stands porcupines will be restricted in their ability to travel in this manner.

H_{A2}: Alternatively, porcupines in treatment areas will restrict their travel routes to areas under the remaining conifers and will travel in the open in the same frequency as porcupines in the control areas.

Rather than travel in the open more often and move through deep snow, porcupines in the treatment areas will reduce the area they cover during foraging events and will be limited to travel routes that are under conifer branch cover.

H₃: Increased energetic cost of travel between trees in the thinned stands increases the amount of vascular tissue removed per feeding event (before leaving the tree) by porcupines feeding in thinned areas.

In relation to this hypothesis, the optimal foraging models developed by Charnov (1976) and Cowie (1977) indicate that, if a porcupine is foraging optimally, it should increase the amount of time spent foraging on a single tree (and therefore increase the amount of vascular tissue removed) in relation to the energetic cost of travel to reach the tree. Energy spent travelling to a patch (or forage-tree in the case of this hypothesis) can be thought of as an energetic investment on the part of the foraging animal. In order to make up for the increased energetic investment an animal must spend more time in a patch feeding.

H_{A3}: Alternatively, porcupines that forage in thinned stands do not remove a larger amount of vascular tissue per feeding event and suffer a higher rate of mass loss than porcupines foraging in the control areas.

Based on the work of Charnov (1976) and Cowie (1977), I predict that porcupines expending more energy to reach a tree should remove more vascular tissue from the tree; however, the total amount of vascular tissue consumed may be constrained by gut capacity. Numerous authors have indicated that gut capacity or time to satiation can play an important role in determining the optimal foraging strategy of an animal (Pulliam 1975; Belovsky 1978; Pyke 1984; Stephens and Krebs 1986). Given that porcupines are nutritionally stressed throughout most of the winter (Roze 1989; Sweitzer and Berger 1993) it is expected that upon reaching a forage-tree, porcupines in control areas should feed until satiated. In this case, porcupines in thinned areas, although they have to expend more energy to reach a forage tree, will not be capable of ingesting more vascular tissue, as these animals will be constrained by gut capacity.

The hypotheses tested in this chapter are based on a number of basic assumptions. Based on the work of Clarke (1969) and the results of Chapter 2 of this thesis, I assume that the lower critical temperature of porcupines in this study area is -4°C . In addition, I assume the energetic cost of winter travel is directly related to the snow sinking depth of the animal and the energetic benefit of foraging is directly related to the amount of vascular tissue removed. These assumptions allow for an index of energetic costs and benefits to be examined to compare energy expenditures between animals in different treatment areas.

STUDY AREA

Please see Chapter 1 for a full description of the study area.

METHODS

In the fall of 1996 12 porcupines were located, captured and fitted with radio transmitters as per the methods described in Chapter 1. An additional 21 animals were captured and fitted with radio transmitters during the winter of 1996 and 1997. Owing to some animals shifting their activity outside of the study area at various times during the study, not all animals could be used for all analyses that were undertaken. Throughout the winter months each collared animal was located 3 times per week, using handheld telemetry, to identify the animal's den locations and to track its movements.

In January and March each animal was re-captured to determine its weight and footpad measurements for calculating foot loading. All four feet were measured on all animals. To standardize between animals, measurements were made across the widest part of the footpad, and from the heel of the footpad to the insertion of the toes into the footpad. As a result, the surface area calculations for this study assumes a rectangular foot surface, and includes only the area of the footpad and not any additional surface area that is provided by the toes. I assumed that the proportion of surface area provided by the toes would be similar for all footpad sizes and, as a result, this bias would be equal across all animals.

In the spring of 1998 each of the three study stands was pre-commercially thinned, as described in Chapter 3. For two winters after the pre-commercial thinning treatments the porcupine monitoring continued. In the winter of 1998/99 and 1999/00 (winters after treatment), measurements were made of the proportion of travel by porcupines in the different treatment areas under cover versus in the open. Cover was defined as any object that intercepted snowfall (e.g. tree branch or fallen log). Upon encountering a fresh porcupine track, a random 25 m section of the trail was selected. Within that 25 m section, the proportions of the trail under cover and in the open were estimated.

In addition to the proportion of travel under cover, estimates were made of the energetic cost of travel to porcupines. At three locations under cover along the trail and three locations in the open along the trail a 300 g weight, with a circular bottom with a 3.75 cm radius, was dropped from 10 cm above the snow surface. The sinking depth of the weight was recorded as an index of the cost of travel for porcupines in different treatment areas.

To estimate the average temperature at snow level, where porcupines travel, and at tree canopy level, where porcupines feed, three monitoring sites were established within each treatment and control area of each study stand. Each monitoring station had one max/min thermometer (Taylor indoor/outdoor maximum/minimum mercury thermometer) at snow level attached to the north side of a tree, and a second max/min thermometer located 5 m above snow level attached to the north side of the same tree. These locations were visited once per week throughout the winters of 1998/99 and 1999/00, and the weekly max/min temperatures were recorded.

STATISTICAL ANALYSIS

Analysis of variance and t-tests were used to compare between means. Where percentage data were collected, data were transformed using arcsine transformation. Where significant results

were recorded using analysis of variance a Tukey test was used to determine which means were different.

RESULTS

Temperature

Weekly maximum and minimum temperature readings from the three study blocks were similar across treatments. Analysis of variance showed no difference between the blocks, with respect to temperatures within each treatment area ($p = 0.71$; d.f. = 2, 24; $F = 0.35$), and, as a result, the blocks were combined for further analysis between treatment areas.

The mean minimum temperatures recorded at snow level (where porcupines are travelling) were similar between the control and two treatment areas (Table 4.1) and analysis of variance found no significant difference ($p = 0.80$; d.f. = 2, 84; $F = 0.22$). Within the control area, minimum temperatures at snow level ranged from -3.5°C to -18.8°C .

The maximum temperatures recorded at snow level showed a similar trend as the minimums, with no significant difference between the treatments and control (ANOVA $p = 0.84$; d.f. = 2, 84; $F = 0.18$; Table 4.1). Maximum temperatures at snow level ranged from a mean of -0.5°C in the control to $+0.1^{\circ}\text{C}$ in the 400 stems/ha area. The temperature variation between weekly minimum and maximum temperatures was 10.8°C for control, 11.7°C for 1200 stems/ha and 11.3°C for 400 stems/ha.

At 5 m above snow level (where porcupines feed) maximum and minimum temperatures were also similar between the treatments and control (Table 4.1). Analysis of variance found no significant difference in the minimum temperatures recorded (control = -12.4°C , 1200 stems/ha = -11.6°C , 400 stems/ha = -12.0°C ; $p = 0.84$; d.f. = 2, 84; $F = 0.17$). As well, with maximum mean weekly temperatures (control = $+1.9^{\circ}\text{C}$, 1200 stems/ha = $+2.7^{\circ}\text{C}$, 400 stems/ha = $+2.7^{\circ}\text{C}$) no significant difference was found ($p = 0.78$, d.f. = 2, 84; $F = 0.24$). At 5 m above the snow surface the temperature variation between weekly minimum and maximums

was slightly greater than at snow level, with the control having a mean difference of 14.2 °C, 1200 stems/ha having a mean difference of 14.2 °C and 400 stems/ha having a mean difference of 14.7 °C.

Porcupine movements

Mean foot loading did not differ between sexes, but juveniles (mean of 64.1 g/cm²) had significantly lower foot loading than both adult males (mean of 102.0 g/cm²) and adult females (mean of 89.4 g/cm²) (Table 4.1; ANOVA $p = 2.77 \times 10^{-7}$; d.f. = 2, 30; $F = 26.04$ with Tukey test).

The index of sinking depths in the open was 8.7 cm (s.d. = 6.4; $n = 36$ trails), which is significantly deeper than the mean of 2.7 cm (s.d. = 2.9; $n = 36$) under cover (t-test, one-tailed, $p = 2.18 \times 10^{-6}$; d.f. = 49; $t = 5.16$). This indicates that travelling in open areas results in an approximate 3 fold increase in sinking depth, relative to travel under cover.

There was considerable variation in the snow sinking depth index throughout the winter months. In open areas sinking depth varied from 33 cm to 0.6 cm. In contrast, the variation under cover was only 13.33 cm to 0 cm. Sinking depths under cover were recorded as less than 1 cm on 12 of 36 occasions, whereas in the open, sinking depth was less than 1 cm on only one occasion.

The mean proportion of travel by porcupines under cover in the control area was 0.41 (s.d. 0.25, $n = 16$ trails), which was significantly greater than animals in the 1200 stems/ha (mean = 0.19; s.d. 0.21; $n = 14$ trails), and for animals in the 400 stems/ha (mean = 0.19; s.d. 0.08, $n = 14$ trails). The two treatment areas did not differ (ANOVA on Arcsine transformed data $p = 0.02$; d.f. = 2, 41; $F = 4.39$; with Tukey test).

Foraging

Porcupines foraging within the 400 stems/ha treatment area removed approximately five times the amount of vascular tissue per forage tree (mean = 6985 cm²) compared to 1434 cm²

and 1289 cm² by porcupines in the 1200 stems/ha and control respectively. Although porcupines in both treatment areas removed more tissue per tree than porcupines in the control, only the 400 stems/ha treatment was significantly different (ANOVA $p = 0.64 \times 10^{-5}$; d.f. = 2, 15; $F = 34.40$; with Tukey test; Table 4.2).

The percentage of girdled forage trees (vascular tissue removed from the entire circumference of the stem) differed little between the two treatments or control (47.5% - 64.2%) (ANOVA $p = 0.20$; d.f. = 2, 15; $F = 1.78$; Table 4.2).

Mass Loss

Mid-winter mass (January mass) of porcupines captured in this study range from 2.1 kg to 12.3 kg. Adult males averaged 9.0 kg and were significantly heavier than adult females (mean 6.4 kg) and juveniles (mean = 3.4 kg) (ANOVA $p = 9.5 \times 10^{-11}$; d.f. = 2, 30; $F = 54.87$; with Tukey test)(Table 4.3). The heavier adult males had the largest average total foot surface area, and the lighter juveniles had the smallest total foot surface area (Table 4.3). Mid-winter mass was closely correlated with total foot surface area ($r = 0.91$; Figure 4.1), indicating that porcupine mass is closely related to skeletal size (assuming foot size is related to skeletal size).

Mass loss by porcupines was calculated based on mid-winter mass, measured in January, and late winter mass, measured in March. This period included the coldest months of the winter (Chapter 2). ANOVA on arcsine transformed data revealed no significant difference in the percentage of mass loss between porcupines in the three areas ($p = 0.88$; d.f. = 2, 16; $F = 0.128$), these being 10.5%, 13.3% and 12.5% respectively in the control, 1200 stems/ha and 400 stems/ha areas. A correlation analysis between mid-winter mass (January) and percent mass loss (between January and March) revealed a positive, but weak relationship ($r = 0.43$; Figure 4.2).

Over the four winters of radio-tracking four animals in this study appear to have died from starvation. All four died in March or April and showed no obvious signs of any disease,

although autopsies were not performed. Three of the animals were juveniles with post-death weights of 2.1 kg, 2.3 kg and 2.6 kg. The fourth porcupine was an adult female that weighed 7.6 kg in February and had declined to 6.0 kg by April 9 (time of death). The adult female was the only animal to die of starvation after the thinning treatments occurred, and her foraging range was in the control area.

DISCUSSION

In this chapter I have examined the influence of pre-commercial thinning to 400 stems/ha and 1200 stems/ha on winter energy expenditures of porcupines. The impetus for this study was to determine if low density thinning (400 stems/ha) had the potential to reduce porcupine populations over the long-term by increasing energetic costs of porcupines that continued to use thinned stands during winter.

The energy expenditure required to deal with cold temperatures can have a dramatic impact on mammals, including increased rate of mass loss and a higher probability of mortality (Moore and Kennedy 1985; Saether and Graven 1988; Sweitzer and Berger 1993). I predicted that the reduction in tree density in the thinned treatments would reduce average temperatures, owing to increased radiative heat loss from the ground, and increased convective heat loss from wind (H_1). This hypothesis was rejected, as no significant difference was measured in the temperature regimes of thinned areas compared to control areas. Instead hypothesis A1 is supported, as the amount of forest canopy remaining within the thinned stands is still enough to provide the same level of thermal cover afforded porcupines in control areas. As a result, porcupines have no increased energetic cost for maintaining body temperature in thinned stands compared to control stands.

The question remains as to why a porcupine would forage during the night rather than during the day. Porcupines spend most winter days in their dens and emerge at night to feed in

the canopy of trees (Clarke and Brander 1973; Roze 1989), when temperatures are generally coldest. In my study the mean minimum temperature at snow level for the control area was -11.3°C as compared to the mean maximum of -0.5°C (Table 4.1). The minimum temperature (which generally occurs at night) is well below the assumed lower critical temperature for porcupines in this area of -4°C (Clarke 1969; Chapter 2).

As the most common porcupine predators such as cougar (*Felis concolor*), fisher (*Martes pennanti*), wolverine (*Gulo gulo*), and coyote (*Canis latrans*) (Robinette et al. 1959; Powell and Brander 1977; Powell 1982; Stricklan 1986; Roze 1989; Sweitzer and Berger 1992; Krebs 1994) are not considered to be diurnal, there does not appear to be any obvious predator avoidance benefit to foraging at night. This is particularly true in the Shames Valley study area where predator indices indicate low densities of predators (Chapter 3).

In hypothesis 2, I predicted that the pre-commercial thinning treatments would cause porcupines in the treatment areas to travel in open areas more often, and that this would be much more energetically costly owing to movement through increased snow depths. I found that this was in fact the case. Porcupines in both thinned treatments travelled in the open more often than porcupines in control areas. Based on the snow sinking index, travelling in the open was substantially more energetically costly compared to under cover. Assuming that snow sinking depth is proportional to cost of travel, porcupines in the thinned areas must have exerted more energy during travel compared to porcupines in the control area.

There was no support found for hypothesis A2. On the contrary, despite the significantly deeper snow sinking depths found in the open, and the potential energetic saving resulting from travelling under cover, porcupines in the control area travelled in open areas the majority of the time. Although control animals travelled under cover significantly more than animals in the two treatment areas, there was no significant difference found in the proportion of travel under cover by porcupines in the 1200 stems/ha and 400 stems/ha. Clearly there are more stems/ha in

one of the treatment areas, and porcupines in this treatment, should, in theory, have three times more area under tree cover, although they do not appear to have taken advantage of this increased cover.

It is possible that travel in the open is not as energetically costly for porcupines compared to travel under cover as I had assumed. Travelling in open areas may not increase energy use substantially, compared to travelling under cover, if an animal has low foot loading. Species such as snowshoe hares (*Lepus americanus*) and lynx (*Lynx canadensis*) are highly adapted for northern winter conditions and have foot loading values of approximately 12 g/cm² and 33 g/cm² respectively (Halfpenny and Ozanne, 1989). The porcupine on the other hand has high foot loading and does not appear well adapted to travelling on snow. Halfpenny and Ozanne (1989) present a figure showing a linear relationship between mammal weight (kg) and foot load (g/cm²). The best fit line indicates that a mammal with a weight of 9 kg (average weight of adult male porcupines in this study) should have a foot load of approximately 48 g/cm². Adult male porcupines captured within this study area had a mean foot load of 101 g/cm². This foot load was calculated only on footpad size and did not include surface area of toes in the calculation. As a result, the 101 g/cm² is likely higher than the actual foot load; however, the addition of toe surface area would have to double the total foot surface area in order for the porcupine foot load to fit the line presented by Halfpenny and Ozanne (1989). Even with toe surface area included, it would appear that porcupines have a poorer than average foot load as compared to other mammals, which should in turn mean that travel in open areas presents more of an energetic expense for them.

One factor that I did not consider in calculating foot load for porcupines was the influence of the tail. When porcupines travel their tail often drags; however, it is not known how much weight is supported by the tail. A porcupine's tail is muscular, and is used to support the body during climbing (Roze 1989). If the tail were also used to support body weight during travel

across snow, the foot load for porcupines would be dramatically reduced, making travel in open areas that much less energetically costly.

I hypothesized that the increased energetic cost of travel for porcupines in the thinned stands would result in an increase in the amount of vascular tissue removed per forage tree (H_3). This hypothesis was supported as porcupines in the treatment areas did remove more vascular tissue per forage tree, as predicted by the optimal foraging models (Charnov 1976; Cowie 1977). As a result, although porcupines in the thinned areas were expending more energy to reach forage trees, they were compensating by gaining more energy from each tree.

Hypothesis A3 predicted that porcupines in thinned areas would be limited by gut capacity in the amount of vascular tissue that could be consumed per tree. As a result, porcupines in the treatment areas would lose mass at a higher rate compared to porcupines in the control area. I found no evidence to support this hypothesis. Porcupines in the treatment areas did remove more vascular tissue per tree as discussed above, and despite the increased tendency to travel in open conditions, in both treatment sites relative to controls, there were no significant differences in porcupine mass loss observed across treatments. In other studies mass loss by porcupines over winter (October to March) ranged from 17% in the northeast New York (Roze 1985) to 31% in Nevada (Sweitzer and Berger 1993). Sweitzer and Berger (1993) suggest that most mass loss occurs from October to January, and found negligible mass loss in porcupines from February to April. In my study, mass loss from January to March ranged from 10.5% to 13.3%.

Porcupines feed on a poor quality diet in winter (0.5% - 8% crude protein or nitrogen; Stricklan 1986; Roze 1989), and can suffer considerable weight loss throughout the winter months. As with previous studies (Roze 1989; Hale and Fuller 1996), starvation was a major cause of winter mortality in my study. In four winters of porcupine monitoring three porcupines were killed by predators (Chapter 3); however, four animals died from what was

believed to be starvation. Three of the four animals were juveniles, and all suspected starvations occurred in March or April, near the end of the winter, after porcupines had been feeding on conifer cambial tissue for four to five months. Mass loss in porcupines throughout the winter is related to the use of fat deposits to compensate for a poor quality diet (Roze 1989; Stricklan 1986). Oveson (1983) measured fat reserves in the rump of porcupines and found them to be depleted by late winter, the time at which most starvations occur.

Despite the potential impacts of the pre-commercial thinning on porcupine energetics, the thinning treatments had no measurable impact on porcupine starvation. An adult female was the only animal to die of starvation post-treatment, and her foraging range was located within the control area. Given the similarity in mass loss between porcupines in the treatment and control areas it is unlikely that the thinning treatments will have any long-term impacts on porcupine survival or reproductive rates.

SUMMARY

In this chapter I examined the impact of pre-commercial thinning to 400 stems/ha and 1200 stems/ha on porcupine winter energetics. I found that even in stands thinned to 400 stems/ha there was no measurable difference in maximum and minimum temperatures compared to control areas (2000 stems/ha). As predicted by hypothesis A1 thinning treatments still maintain enough forest canopy to provide equivalent thermal cover to porcupines compare to control areas.

Porcupines in the treatment areas were found to travel in open areas more often and through deep snow more often compared to control areas, which supported hypothesis 2. However, porcupines compensated for the increased energetic cost of travel in thinned areas by removing more vascular tissue per forage tree, which supported hypothesis 3.

Owing to the increased vascular tissue removed per forage tree by porcupines in the treatment areas compared to porcupines in the control areas, there was no difference in the rate of mass loss between the three groups of porcupines.

I found no evidence that pre-commercial thinning to low densities can negatively impact porcupine energy expenditures to the extent required to reduce porcupine numbers within second-growth stands. I conclude that if pre-commercial thinning is to occur in areas where porcupine feeding damage is a concern, thinning should be conducted at a higher density (≥ 1200 stems/ha). Higher stem densities should reduce the size of feeding scars on trees, thereby increasing the probability of stem survival. As well, thinning to higher densities will allow for a larger number of stems to be damaged before a stand becomes non-commercially viable.

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Table 4.1: Temperatures (± 1 s.d.) at snow level and 5 m above snow level for the control and two treatment areas, based on weekly maximum and minimum readings throughout the post-treatment winters.

		Min. temp. at snow level			Max. temp. at snow level			Min. temp. 5 m above snow level			Max. temp. 5 m above snow level		
		Control	1200 stems/ha	400 stems/ha	Control	1200 stems/ha	400 stems/ha	Control	1200 stems/ha	400 stems/ha	Control	1200 stems/ha	400 stems/ha
Mean		-11.3	-12.0	-11.2	-0.5	-0.3	+0.1	-12.4	-11.6	-12.0	+1.9	+2.7	+2.7
(°C)		(5.0)	(5.1)	(5.2)	(4.1)	(4.8)	(3.9)	(5.3)	(5.0)	(5.3)	(4.6)	(5.0)	(5.8)
Range		-3.5	-3.0	-1.5	+3.5	+15.5	+8.0	-2.5	-3.5	0.0	+11.0	+12.5	+13.5
(°C)		-18.8	-18.5	-20.0	-9.5	-6.5	-8.0	-23.0	-19.5	-19.5	-6.5	-6.0	-8.0

Table 4.2: Vascular tissue removal and tree girdling rates (± 1 s.d.).

	Control (2000 stems/ha) n = 4 male, 4 female	1200 stems/ha n = 4 male, 2 female	400 stems/ha n = 3 male, 1 female
Mean of Vascular Tissue Removed/Forage tree (cm ²)	1289 (859)	1435 (706)	6985 (1566) ^a
Percentage of Girdled Forage trees ^b	64.2 (18.1)	52.9 (21.8)	47.5 (4.8)

^a Significantly greater than control and 1200 stems/ha (ANOVA $p = 0.64 \times 10^{-5}$; d.f. = 2, 15; $F = 34.40$; with Tukey test).

^b No significant difference between groups (ANOVA $p = 0.20$; d.f. = 2, 15; $F = 1.78$).

Table 4.3: Mid-winter mass (± 1 s.d.) and total foot surface area for porcupines in the Shames Valley study area.

	Adult Males (n = 18)	Adult Females (n = 5)	Juveniles (n = 10)
*Mean mid-winter mass (kg)	9.0 (1.6)	6.4 (1.4)	3.4 (0.8)
Range of mid-winter mass (kg)	6.0 – 12.3	4.8 – 8.4	2.1 – 4.3
Mean total foot surface area (cm ²)	89.2 (13.0)	70.8 (6.0)	52.7 (6.6)
Range of total foot surface area (cm ²)	63.5 – 109.2	64.9 – 80.8	41.5 – 61.9
**Mean foot loading (g/cm ²)	102 (15)	89 (14)	64 (10)
Range of foot loading (g/cm ²)	69 – 125	68 – 104	51 – 78

*Mid-winter mass was significantly different between all three groups (ANOVA $p = 9.5 \times 10^{-11}$, $F = 54.87$, $DF = 2, 30$; with Tukey test).

**There was no significant difference between adult males and adult females in foot loading; however, juveniles had significantly lower foot loading than both adult groups (ANOVA $p = 2.77 \times 10^{-7}$, $F = 26.04$, $DF = 2, 30$; with Tukey test).

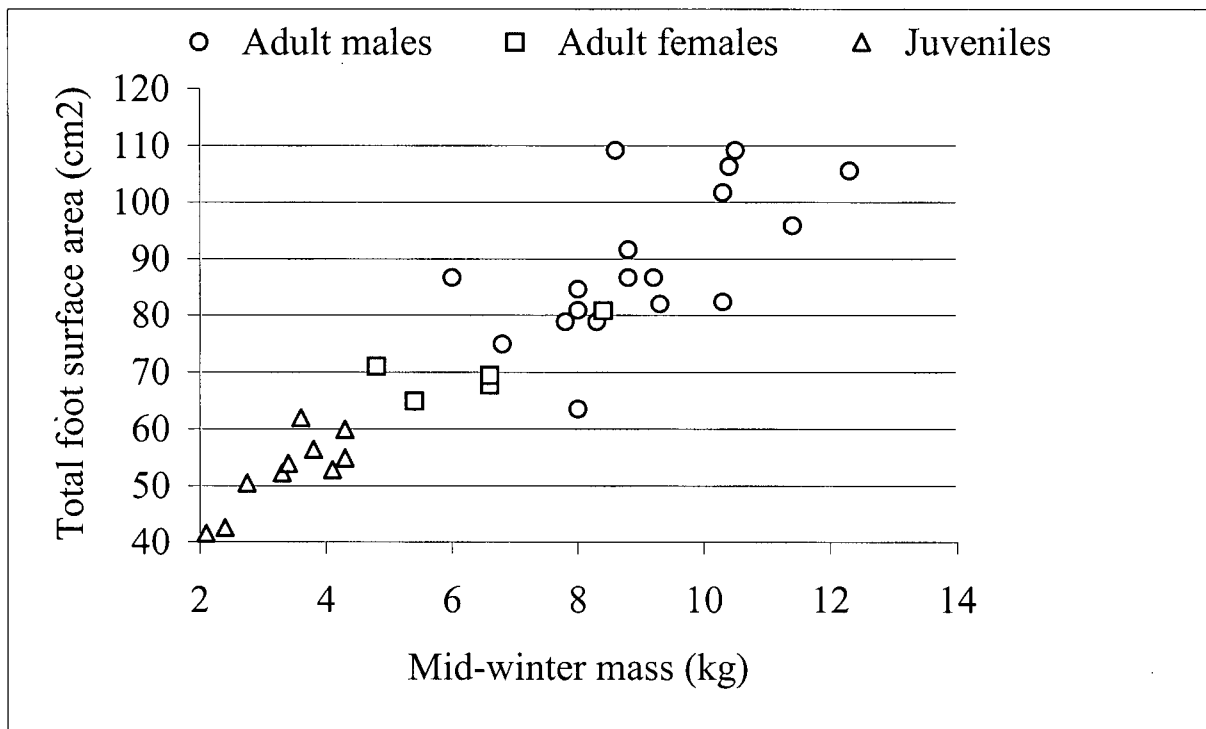


Figure 4.1: Relationship between mid-winter mass (kg) and total foot surface area (cm²) for porcupines in the Shames Valley study area (1996 – 2000) ($r = 0.91$).

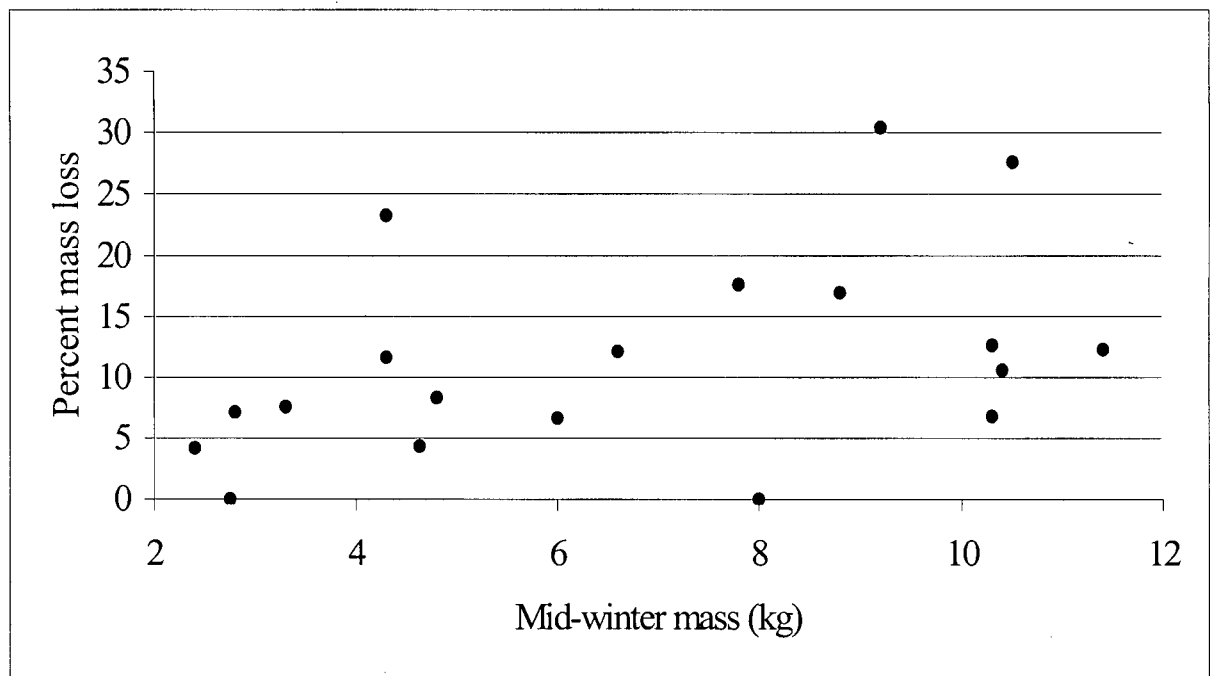


Figure 4.2: Relationship between mid-winter mass and the percent body mass lost between January and March for porcupines in the Shames Valley study area (1996 – 2000) ($r = 0.43$).

CHAPTER 5: PRE-COMMERCIAL THINNING AND THE MANAGEMENT IMPLICATIONS OF PORCUPINE FEEDING DAMAGE

INTRODUCTION

The North American porcupine (*Erethizon dorsatum*) ranges from the tree line in the Arctic, south to northwestern Mexico (Dodge 1982) and from the northeast coast of the United States and eastern Canada (Speer and Dilworth 1978; Hale and Fuller 1996) to the western rain forests of British Columbia and Alaska (Eglitis and Hennon 1986; Sullivan and Cheng 1989). Across this large range, the porcupine's winter forage includes a wide variety of conifer tree species, including: lodgepole pine, (*Pinus contorta*; Daniel and Barnes 1958); scots pine (*Pinus sylvestris*; Rudolf 1949); ponderosa pine, (*Pinus ponderosa*; Storm and Halvorson 1967); limber pine, (*Pinus flexilis*; Gill and Cordes 1972); white pine (*Pinus strobus*; Speer and Dilworth 1978); pinion pine (*Pinus edulis*; Spencer 1964); sitka spruce (*Picea sitchensis*; Eglitis and Hennon 1986); red spruce (*Picea rubens*; Speer and Dilworth 1978); western hemlock (*Tsuga heterophylla*; Eglitis and Hennon 1986); eastern hemlock (*Tsuga canadensis*; Griesemer et al. 1994); amabilis fir (*Abies amabilis*; Krebs 1994); balsam fir (*Abies balsamea*; Speer and Dilworth 1978); and Douglas fir (*Pseudotsuga menziesii*; Harder 1979). In most of these cases, with respect to the forest industry, porcupine feeding is considered to be a serious threat to conifer growth and survival.

In northwestern British Columbia porcupine winter feeding on the vascular tissue (cambium and phloem) of western hemlock, sitka spruce, and to a lesser extent amabilis fir has also been identified as a threat to timber production in localized areas (Sullivan and Cheng 1989; MacHutchon 1990; Krebs 1994). Winter feeding by porcupines causes the removal of the outer bark and the exposure of the inner sapwood (Lawrence et al. 1961; Roze 1989), and can result in a reduction in radial growth or mortality of the stem, directly due to the loss of

vascular tissue, or indirectly through insect or disease penetration into the sapwood (Curtis 1941; Storm and Halvorson 1967; Sullivan et al. 1986; MacHutchon 1990; Krebs 1994).

In conjunction with the recognized threat that porcupines pose to timber production, is an increase in the number of second-growth stands in British Columbia. These stands are reaching the age/size at which decisions on potential silviculture thinning treatments must be made. Thinning treatments are employed under the assumption that the merchantable yield of a stand can be maximized through timely reductions in stand density that cause the remaining trees to rapidly increase their diameter growth (Assmann 1970; Kozlowski 1971; Carter et al. 1986; Smith 1986; Jozsa and Middleton 1994). The shift in a stand from a large number of small diameter trees to a smaller number of large diameter trees does not necessarily increase total production; however, it is meant to increase the merchantable yield (volume actually harvested) of the site.

Based on the potential economic benefits of thinning, forest managers employ this silviculture practice wherever feasible; however, the theoretical benefits of thinning can be affected by damaging agents such as the porcupine. Porcupine feeding damage does not occur randomly across the landscape, but is often concentrated in small patches of high intensity and generally focuses on the dominant and codominant trees within the stand (Speer and Dilworth 1978; Roze 1984; Griesemer et al. 1994; Chapter 1 and Chapter 3 of this thesis). Porcupines attack healthy trees, rather than the weaker, suppressed trees that many diseases or insects attack. As a result, although thinning makes sense on a landscape level, where damaging agents and positive response of trees are averaged out; at a stand level where porcupine damage is known to be a possibility, and where the response of trees (in terms of growth rate) may not be exceptional (Smith 1986), thinning may not be beneficial in terms of merchantable yield.

To account for the potential losses owing to porcupine feeding damage in second-growth stands, the British Columbia Ministry of Forests uses the criterion that any tree that has 1/3 or

more of the stem circumference damaged by porcupines should be considered non-merchantable (Anonymous 2000). To date, however, there is little information indicating what level of porcupine feeding damage constitutes a serious threat to timber production. As a result, forest managers are left with few guidelines as to when the potential losses to porcupine damage may outweigh the potential benefits of thinning.

In this chapter I explore information on the short-term impacts of porcupine feeding damage on conifer growth rates, and potential stand yield (measured in terms of basal area increment) and compare these results to changes in tree growth rates (measured in terms of diameter) resulting from various levels of pre-commercial thinning. I use these data to develop a conceptual model to aid forest managers in determining at what point porcupine feeding damage will result in non-commercially viable stands at rotation age (80 years).

STUDY AREA

Please see Chapter 1 for a full description of the study area.

METHODS

In fall 1998, tree assessment plots were established within two study stands (Stand 1 and Stand 2). The assessment plots were circular, 5.64-m radius (100-m²) plots, systematically placed across the study area at a density of 2 per hectare. The centre of each plot was marked with a stake and flagging. Within each assessment plot all trees with a diameter at breast height (dbh = 1.3 m) of 5 cm or greater were permanently tagged with a coloured, plastic disc. The species and dbh of each tagged tree were recorded, along with the presence of any porcupine feeding damage from the winter of 1997/98. Damage was recorded as occurring in the bottom, middle or top third of the bole. As well, the total area of vascular tissue removed was estimated by measuring the length and width of each feeding patch. The percentage of stem circumference damaged was also measured at the point of damage.

Each of the study stands was then divided into three equal sections and two of the sections were pre-commercially thinned: one to a density of 400 trees/ha (low density thinning) and one to a density of 1200 trees/ha (high density thinning). The control section retained approximately 2000 trees/ha.

In fall 2000, after tree growth had ceased for the year, all tree assessment plots were re-visited and the dbh of all trees was re-measured to determine growth rates over two full growing seasons. As well, the mean basal area increment/tree was recorded by calculating basal area at breast height in the fall of 2000 and subtracting the basal area at breast height in the fall of 1998, for each tree assessed. To determine the short-term impact of the thinning treatments on merchantable yield at the stand level the total basal area increment per assessment plot (basal area increment of all trees in the plot added together) was averaged for each treatment and control area and multiplied by 100 to give a mean basal area increase/ha (each plot in $100 \text{ m}^2 \times 100 = 10000 \text{ m}^2$). To determine the impact of thinning on tree growth and basal area all trees damaged by porcupines were removed from the analysis. Since the vast majority of trees damaged by porcupines were western hemlock, all analyses dealing with damaged trees used only western hemlock.

STATISTICAL ANALYSIS

Damaged trees were analyzed based on the treatment they were located in (control, 1200 stems/ha or 400 stems/ha) and grouped into diameter size classes (5.0-9.9 cm, 10.0-14.9 cm, 15.0-19.9 cm, 20.0-24.9 cm and >24.9 cm dbh). Where sample size of damaged trees was sufficient (≥ 10) they were compared to a similar grouping of undamaged western hemlock, using general linear model ANOVA (GLM). All percentage data were arcsine-transformed. Where ANOVA produced a significant result the Tukey test was used to perform a multiple comparison (Zar 1974).

RESULTS

Thinning

The shift in species composition after thinning varied between the two study stands. In Stand 1, the 1200 stems/ha treatment area was very similar to the control area. The biggest change was a four-fold decline in the percentage of sitka spruce and a slight increase in the percentage of western hemlock and amabilis fir (Table 5.1). In the 400 stems/ha treatment area the change in species composition was much larger; western hemlock declining by approximately 20% and amabilis fir increasing by a similar amount (Table 5.1). In contrast, the two treatment areas in Stand 2 had very similar species compositions, both having approximately 40% western hemlock and 60% amabilis fir, compared to the control with 64% western hemlock and 36% amabilis fir (Table 5.1).

The thinning treatments also altered the size class distribution of stems in the stands. The smallest diameter size class was most abundant in the control areas of both stands, with 46% and 40% of stems being in the 5.0-9.9 cm dbh class in Stands 1 and 2 respectively (Table 5.2). In the treatment areas the size class distribution shifted to larger sizes. In both stands and across both treatments the shifts were similar, with the 15.0-19.9 cm dbh size class making up the largest single percentage of stems per class, and the 20.0-24.9 cm dbh and 24.9 cm < dbh classes making up two to three times more of the stems in the treatments as compared to the control (Table 5.2).

After two full growing seasons there was a trend for the trees in the thinned areas to have higher growth rates (based on percent increase in dbh) (Table 5.3); however, no statistical differences were found between the two treatment areas and the control in either of the study stands (ANOVA on arcsine transformed, % dbh increase/tree: Stand 1 $p = 0.28$; $df = 2, 80$; $F = 1.31$ and Stand 2 $p = 0.22$; $df = 2, 57$; $F = 1.54$).

A comparison of the mean basal area increment added/tree over the two growing seasons revealed a significant difference of 1.5 – 2 times, between the control and both treatment areas in Stand 1 (ANOVA $p = 0.0004$; $df = 2, 80$; $F = 8.52$) (Table 5.3). The same trend was observed in Stand 2, with the mean basal area increase/tree in the 1200 stems/ha and 400 stems/ha being 27.0 cm^2 and 28.5 cm^2 respectively, compared to 15.4 cm^2 in the control area (Table 5.3). In Stand 2, however, the differences between the treatments and control were not significant (ANOVA $p = 0.077$; $df = 2, 80$; $F = 8.52$).

To determine the short-term impact of thinning on merchantable yield at the stand level, the mean basal area increase/ha was compared between the treatments and control area for each stand. The result was the same in both Stand 1 and 2 with the increase for 400 stems/ha treatment area being significantly less compared to the 1200 stems/ha and control areas (ANOVA – Stand 1 $p = 0.0004$; $df = 2, 80$; $F = 8.61$; Stand 2 $p = 0.002$; $df = 2, 57$; $F = 6.95$).

Damaged Trees

Throughout this study 78.1% of all trees damaged by porcupines were western hemlock, 15.5% were amabilis fir, and 6.4% were sitka spruce. Of the 1466 western hemlock that were identified as damaged by porcupines, only 206 (14%) had signs of previous year feeding damage, indicating the majority were newly damaged trees. Damage by porcupines was concentrated on the top third of most stems (38%), however, 32% were damaged from the middle third and up, and 30% were fed upon from the bottom third of the stem and upwards.

Of the 882 western hemlock trees for which the percentage of stem circumference damaged by porcupines was recorded, 73% had 1/3 or more of the stem circumference vascular tissue removed at some point along the stem. The majority of the damaged trees (58%) had vascular tissue removed around the entire circumference of the stem (girdled). No trend in growth rates (percent increase in dbh) in relation to the percentage of the stem circumference damaged by

porcupine feeding was evident (Table 5.4; correlation coefficient = 0.06; t-test, 1-tailed, $p > 0.50$, $df = 150$, $t = 0.736$).

When comparing growth rates (percent increase in dbh) in relation to total area of vascular tissue removed from the tree, there was a trend for trees with more vascular tissue removed to have smaller diameter growth rates at breast height (Table 5.5). Correlation analysis using all damaged trees revealed a correlation coefficient of 0.28, which was significantly different from zero (t-test, 1-tailed, $p < 0.001$, $df = 150$, $t = 3.57$).

Owing to small sample sizes of damaged stems, not all diameter size classes of trees could be examined for the impact of porcupine feeding on growth rates. Within the control areas (2000 stems/ha), western hemlock trees in 5.0-9.9 cm, 10.0-14.9 and 15.0-19.9 cm dbh classes that were damaged by porcupines, had diameter growth rates similar to undamaged trees of the same diameter classes (GLM ANOVA $p = 0.16$; d.f. = 2, 312; $F = 1.88$) (Table 5.6). In the 1200 stems/ha area damaged trees were in the 10.0-14.9 cm and 20.0-24.9 cm dbh classes; whereas in the 400 stems/ha area sufficient trees were available in the 15.0-19.9 cm and 20.0-24.9 cm dbh classes to allow for analysis. In both the 1200 stems/ha and 400 stems/ha treatment areas porcupine feeding damage significantly reduced diameter growth rates compared to those of undamaged trees (GLM ANOVA $p = 0.02$; d.f. = 1, 82; $F = 5.79$ and $p = 0.001$; d.f. = 1, 72; $F = 13.46$ respectively) (Table 5.6).

DISCUSSION

Thinning

The thinning treatments appear to be creating the desired response, for diameter growth rate, with a trend towards higher growth rates in the thinned areas in both stands. The lack of statistical difference between the controls and treatments is likely owing to the short time period over which the data were collected (two growing seasons). Analysis of growth rates from similar stands in the area have produced mixed results over the short-term. Zimmerling

(1999a) reported that western hemlock trees in thinned stands (800 and 1250 stems/ha) within the Little Cedar Valley, showed no statistical difference in diameter growth rates, over the first three growing seasons. It was not until the end of the fifth growing season that a significant difference in diameter growth rates was observed. However, even at that time, only trees in the 800 stems/ha area were significantly different from control areas (trees in the 1250 stems/ha showed no significant difference). In contrast, a similar study in the Kwinhak Creek Valley reported that western hemlock trees in thinned stands (600 stems/ha and 1200 stems/ha) did have a significantly higher diameter growth rate within the first three growing seasons after thinning (Zimmerling 1999b). The variation in the diameter growth response, even over the short term, is an indication of the potential influence of site conditions on the expected benefits of thinning treatments. Smith (1986) points out that thinning on poor sites may not produce sufficient growth response to increase merchantable yield.

Short-term impacts of porcupine damage

The majority of trees damaged by porcupines in this study were western hemlock (78%). Chapter 1 showed that porcupines tended to select western hemlock trees in the larger diameter classes (larger than 9.9 cm dbh) when foraging. Similar selection was noted by Krebs (1994), MacHutchon (1990), and Sullivan et al. (1986), all of whom worked in western hemlock/amabilis fir/sitka spruce forests in northwestern B.C., and found that porcupines selected dominant and codominant western hemlock as a preferred forage species.

Krebs (1994) found that between 14% and 27% of porcupine damaged trees had been damaged in previous years. Results from my study fall in this range, with 14% of damaged trees having previous years' feeding damage. When considering circumference of damage, 58% of damaged western hemlock trees in my study were girdled, and a total of 73% of damaged stems in my study would not meet the British Columbia Ministry of Forests criteria

for merchantable yield, as 1/3 or more of the stem circumference was damaged (Anonymous 2000).

Within the thinned areas, porcupine damaged trees had significantly reduced diameter growth rates when compared to undamaged stems in the same treatment. The reduced growth rate was seen in both the 1200 stems/ha area and the 400 stems/ha area, but was not evident in the control stands. The lack of a difference between damaged and undamaged stems in the control area may be related to porcupines including smaller diameter stems within their diet when feeding in control stands (Chapter 1). Damage to a tree that is already growing slowly may not produce a significant reduction in radial growth.

Both Storm and Halvorson (1967) and Krebs (1994) reported significant reductions in tree diameter growth rates after porcupine feeding damage. Krebs (1994) reported a significant negative relationship between the circumference of stem damaged and growth rates. However, Storm and Halvorson (1967) and my study, found no such relationship. Sullivan and Sullivan (1986), studying snowshoe hare (*Lepus americanus*) damage to lodgepole pine and Cerezke (1974) assessing weevil (*Hylobius warreni* Wood) damage to lodgepole pine, both reported significant reductions in radial growth of stems as a result of vascular tissue feeding damage. In the case of Cerezke (1974) a decline in radial growth was not noted until 60% or more of the stem circumference was damaged. Beyond this level, an increase in the percentage of stem circumference decreased radial growth (similar to the relationship noted by Krebs (1994)).

Storm and Halvorson (1967) examined ponderosa pine for eight years after porcupine feeding damage. They showed the largest reduction in annual diameter growth occurred in the first two years after damage. The difference between damaged and undamaged stems steadily decreased over time, until by year eight, there was no significant difference in annual growth increment between damaged and undamaged stems. After ten years, the accumulated loss in

radial growth for damaged trees versus undamaged amounted to a mean of 8%. Whether or not western hemlock will show the same level of resilience as lodgepole pine remains to be seen.

Long-term Implications

It is well documented that porcupines demonstrate tree species selection when foraging (Speer and Dilworth 1978; Roze 1984; Tenneson and Oring 1985; Hendricks and Allard 1988). In the North Coast and Kalum Forest Districts of the Prince Rupert Forest Region, porcupines select western hemlock in mixed stands of western hemlock, amabilis fir and sitka spruce (Chapter 1 of this thesis; Krebs 1994; MacHutchon 1990; Sullivan and Cheng 1989; Sullivan et al. 1986). In such stands, between 78% (this study) and 89% (Sullivan and Cheng 1989) of trees damaged by porcupines are western hemlock. Although thinning can be used to reduce the percentage of western hemlock in the stand, thinning leads to an increase in the percentage of stems in the diameter class preferred by porcupines (stems > 9.9 cm dbh) (Table 5.2; and see Chapter 1). The stand composition after thinning is a direct result of the selection criteria used by the thinning crews. In most places within the Prince Rupert Forest Region amabilis fir is selected as a crop tree, over western hemlock, based on results from Krebs (1994), MacHutchon (1990), and Sullivan et al. (1986) indicating that porcupines prefer western hemlock trees.

A number of scenarios can be examined to determine the potential long-term impacts of porcupine feeding damage. If it is assumed that a porcupine will damage 0.18 to 1.33 new trees/day during the winter months (Chapter 1), and that winters last 121 days (December 1 – March 31), then in a single winter a porcupine will damage between 28 and 161 trees. Using the percentage of western hemlock damaged in this study (78%) it can then be assumed that between 22 and 126 of the damaged trees would be western hemlock, with the remainder divided between amabilis fir and sitka spruce.

The winter range estimations for porcupines vary considerably from location to location and from winter to winter depending on weather conditions (Roze 1989). Winter home range

estimates range from 0.2 ha in northwestern Minnesota (Tenneson and Oring 1985) to 83.5 ha in western Washington (Dodge and Barnes 1975). Krebs (1994) found winter home ranges for porcupines in northwestern British Columbia to average 8.6 ha; however, in my study winter foraging range size varied from 0.14 ha to 5.80 ha, with a mean of 1.5 ha (Chapter 1). The likely reason for this smaller foraging range estimate versus that of Krebs (1994) is that while Krebs used locations of radio tagged animals, regardless of the animals' activity, to determine home range size, I used only foraging locations. As a result, my estimates provide a better indication of the area over which the feeding damage will be disbursed (1.5 ha for the purposes of this discussion).

Based on the results from my study and others from the area, I have developed a predictive model to aid forest managers in making decisions about thinning in the Prince Rupert Forest Region of northwestern British Columbia. Using conservative numbers, assuming that 28 trees are damaged/winter (78% western hemlock) by a single porcupine, over a 1.5 ha area, and 27% of trees have been previously damaged (Krebs 1994), effectively 16 western hemlock trees will be newly damaged/year. These same parameters result in 2 amabilis fir and 2 sitka spruce stems having new damage in each year, within the 1.5 ha foraging range. Approximately one quarter of the damaged stems would have less than 1/3 of the stem circumference damaged and would therefore still be considered merchantable under the British Columbia Ministry of Forest guidelines (Anonymous 2000). As a result, every winter of feeding from a single porcupine would produce 12 western hemlock, 2 amabilis fir and 2 sitka spruce that are non-merchantable. In northwestern British Columbia 350 – 400 stems/ha is generally considered the minimum for a commercially harvestable stand (Sullivan and Cheng 1989; Krebs 1994). Based on the conservative parameters presented, a stand thinned to 400 stems/ha would have fewer than 350 merchantable stems after 5 years of porcupine feeding (Table 5.7).

In the case of stands thinned to 1200 stems/ha it would not be until after 60 years of cumulative porcupine feeding damage that the stand would begin to approach the 400 stems/ha critical value (Table 5.7). By this time; however, the stand should be at rotation age (if it is assumed that damage begins around age 20 and harvest can occur at age 80). For untreated stands (around 2000 stems/ha), after 60 years of cumulative damage the stand would be approaching 1800 stems/ha. This level of stocking is well above the 350 – 400 stems/ha threshold for commercial harvesting and provides a large buffer for other potential damaging agents to have an impact.

Using more liberal estimates and assuming that 161 trees are damaged/winter (78% western hemlock) by a single porcupine, over a 1.5 ha area and 14% are previously damaged (this study) 108 western hemlock trees will be newly damaged/year. These same parameters result in 15 amabilis fir and 15 sitka spruce stems having new damage in each year, within the 1.5 ha foraging range. Under this scenario not even the unmanaged stand that begins at 2000 stems/ha will be considered commercially viable at rotation, as within 30 years 2081 stems/ha are non-merchantable (Table 5.8).

Models developed by Sullivan and Cheng (1989) reached similar conclusions. With annual porcupine damage levels greater than 1%, stands that begin at 900 stems/ha do not reach rotation age before stem density is below minimum harvestable levels. Krebs (1994), reached the same conclusion for thinned stands in his study.

Two important assumptions of my model are that 1) porcupine feeding damage occurs at the same rates over long periods of time, and 2) porcupine damage is spread evenly throughout the stand. Evidence from Spencer (1964) and Payette (1987) indicates that porcupine populations may fluctuate, with 10-20 years of high numbers followed by a similar number of years of reduced numbers. If the results of Spencer (1964) and Payette (1987) apply to all areas of the

porcupine's range, porcupine feeding damage may only be sustained at any given rate, for a maximum of 20 years.

Whether or not porcupines are spread throughout a stand is likely to be stand specific. There is wide variation in the size of winter home ranges reported in the literature (Dodge and Barnes 1975; Tenneson and Oring 1985; Roze 1987; Krebs 1994) and it is likely that this variation also leads to wide variation in the density of porcupines in any given stand of trees.

The main question that forest managers must answer when deciding to pre-commercially thin a stand is; will increased growth rates resulting from thinning allow the stand to reach a merchantable size before cumulative porcupine feeding damage reduces the number of merchantable trees below commercially viable levels. Based on the model I have developed, forest managers should closely examine the likely level of porcupine feeding damage expected to occur in a particular managed stand, before investing in pre-commercial thinning. If porcupine damage levels are 1% or less, thinning to densities as low as 1000 stems/ha should result in a commercially viable stand if rotation age is 80 years; however, if damage levels are above 1%, thinning should be avoided. If the rotation age of a stand can be reduced then the level of porcupine feeding damage that can be incurred is increased.

SUMMARY

In this chapter I examined the changes in species composition and diameter growth rates after pre-commercial thinning. Because thinning is done to favour amabilis fir in northwestern British Columbia, tree species composition shifts; however, the thinning also increases the percentage of western hemlock trees in a diameter class preferred for feeding by porcupines. Thus, the percentage of porcupine feeding in thinned stands will be much higher than in control areas.

Although my study was carried out for only two growing seasons, there was evidence that thinning increased growth rates. It is unclear, however, if the increased growth rate will be

enough to offset the losses resulting from porcupine feeding. In the short-term, over 50% of trees damaged by porcupines were girdled, resulting in stem mortality above the damage location. In addition, in thinned stands, damaged trees had significantly smaller diameter growth rates than undamaged trees. This same result was not observed in the control stands.

Long-term porcupine feeding damage, assuming damage levels remain constant, is likely to result in non-merchantable stands if the stand is thinned to levels below 1000 stems/ha and a conservative level of porcupine feeding is assumed over a 60 year period. Using the maximum estimates for porcupine feeding damage, even untreated stands (2000 stems/ha) are predicted to have merchantable stem densities below harvestable levels by the age of rotation (80 years). If porcupine feeding damage within a stand is greater than 1% of stems, then forest managers should avoid pre-commercial thinning.

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Table 5.1: Species composition after pre-commercial thinning (percentage of stems).

	Tree Species	Control (2000 stems/ha)	Thinning to 1200 stems/ha	Thinning to 400 stems/ha
Stand 1	Western hemlock	60.1	66.8	44.2
	Amabilis fir	21.2	28.8	47.8
	Sitka spruce	18.7	4.0	8.0
	Western red cedar	0.0	0.4	0.0
Stand 2	Western hemlock	63.6	38.6	42.0
	Amabilis fir	35.9	60.9	58.0
	Sitka spruce	0.5	0.5	0.0
	Western red cedar	0.0	0.0	0.0

Table 5.2: Size class distribution, based on diameter at breast height (1.3 m), after pre-commercial thinning (percentage of stems).

Treatment		5.0 – 9.9 cm	10.0 – 14.9 cm	15.0 – 19.9 cm	20.0 – 24.9 cm	24.9 cm <
Stand 1	Control (2000 stems/ha)	45.9	31.1	14.4	5.6	3.0
	Thinning to 1200 stems/ha	18.6	24.3	25.3	19.9	11.9
	Thinning to 400 stem/ha	9.4	23.8	30.9	23.7	12.2
Stand 2	Control (2000 stems/ha)	40.2	35.7	16.1	6.0	2.0
	Thinning to 1200 stems/ha	20.1	21.8	30.3	18.8	9.0
	Thinning to 400 stem/ha	20.7	22.3	33.1	19.8	4.1

Table 5.3: A comparison of growth rates after two growing seasons for different levels of pre-commercial thinning (western hemlock-ambilis fir forests in the Kalum Forest District of northwestern British Columbia) (standard deviation in brackets).

	Control (2000 stems/ha)				Thinning to 1200 stems/ha				Thinning to 400 stems/ha			
	Mean % DBH Increase/Tree	Mean Basal Area Increase/Tree	Mean Basal Area Increase/Ha		Mean % DBH Increase/Tree	Mean Basal Area Increase/Tree	Mean Basal Area Increase/Ha		Mean % DBH Increase/Tree	Mean Basal Area Increase/Tree	Mean Basal Area Increase/Ha	
Stand 1	9.7 (2.9)	29.7 cm ² (15.9)	39630 cm ² (217)		10.1 (3.6)	52.2 cm ² (33.4)	41900 cm ² (226)		10.9 (3.6)	55.0 cm ² (23.2)	22830 cm ² (141)	
Stand 2	5.4 (2.8)	15.4 cm ² (12.6)	25280 cm ² (125)		5.8 (1.8)	27.0 cm ² (10.1)	22390 cm ² (93)		7.1 (3.7)	28.5 cm ² (19.0)	13680 cm ² (99)	

Table 5.4: The relationship between percentage of stem circumference damaged by porcupine feeding and percent diameter growth rates (measured over two growing seasons), for western hemlock.

	Percentage of stem circumference vascular tissue removed.				
	1 - 20%	21 - 40%	41 - 60%	61 - 80%	81 - 100%
Mean percent diameter growth rate (s.d.)	11.6 (9.4)	11.6 (4.3)	10.3 (5.3)	12.0 (4.3)	12.0 (4.4)
Number of trees	26	37	33	31	103

Table 5.5: The relationship between amount of vascular tissue removed (surface area) by porcupine feeding and tree diameter growth rates (measured over two growing seasons), for western hemlock.

	Surface area of vascular tissue removed.			
	1 – 1000 cm ²	1001 – 2000 cm ²	2001 – 3000 cm ²	> 3000 cm ²
Mean % diameter growth rate (s.d.)	11.3 (5.0)	10.8 (3.5)	7.2 (4.2)	9.2 (1.5)
Number of trees	111	19	8	5

Table 5.6: Impact of porcupine feeding damage on western hemlock diameter growth rates (measured in percent increase over two growing seasons).

Treatment	Control (2000 stem/ha)		1200 stems/ha		400 stems/ha	
Dbh class (cm)	5.0-9.9	10.0-14.9	15.0-19.9	10.0-14.9	15.0-19.9	20.0-24.9
Damaged trees diameter growth (s.d.)	10.9% (4.9) n = 65	11.8% (4.3) n = 50	10.8% (4.4) n = 12	8.6% (3.0) n = 10	4.2% (1.3) n = 19	4.8% (2.1) n = 14
Undamaged trees diameter growth (s.d.)	9.8% (4.3) n = 100	11.4% (6.1) n = 68	9.2% (3.4) n = 22	11.2% (4.4) n = 38	8.3% (4.8) n = 23	8.3% (4.7) n = 19

Table 5.7: Predicted number of non-merchantable stems/ha based on conservative estimates of porcupine feeding (16 western hemlock, 2 amabilis fir and 2 sitka spruce newly damaged every year within a 1.5 ha foraging range area).

Cumulative years of porcupine feeding damage														
	1	5	10	15	20	25	30	35	40	45	50	55	60	
Western hemlock	11	45	86	127	168	209	251	292	333	374	416	457	498	
Amabilis fir	2	6	11	16	21	26	31	36	41	46	51	56	61	
Sitka spruce	2	6	11	16	21	26	31	36	41	46	51	56	61	
Total non-merchantable trees	15	57	108	159	210	261	313	364	415	466	518	569	620	

Table 5.8: Predicted number of non-merchantable stems/ha based on liberal estimates of porcupine feeding (108 western hemlock, 15 amabilis fir and 15 sitka spruce newly damaged every year within a 1.5 ha foraging range area).

	Cumulative years of porcupine damage						
	1	5	10	15	20	25	30
Western hemlock	63	279	549	819	1089	1359	1629
Amabilis fir	9	39	76	114	151	189	226
Sitka spruce	9	39	76	114	151	189	226
Total non-merchantable trees	81	357	701	1047	1391	1737	2081

CONCLUSION AND MANAGEMENT RECOMMENDATIONS

In this study I have found that porcupines (*Erethizon dorsatum*) use within stand variation in the density of sitka spruce (*Picea sitchensis*) trees to select den site locations. Given that porcupines tend to forage within 50 m of their den site within unmanaged stands (Speer and Dilworth 1978; Roze 1984; Griesemer et al. 1994; Chapter 3), this selection allows forest managers an opportunity to identify where, within a second-growth stand, porcupine feeding damage is likely to be most severe. Two management options should be considered when an area containing a potential porcupine den has been identified. The first is to leave a 50 m radius around the den site unmanaged. This approach is likely only practical where a smaller number of dens are located within a second-growth stand.

A second management option, which takes advantage of the avoidance of amabilis fir (*Abies amabilis*) by porcupines (Chapter 1), is to selectively thin the area around the den site to remove western hemlock (*Tsuga heterophylla*) and leave only amabilis fir. This management option may also be successful in reducing porcupine feeding damage if applied to an entire second-growth stand. In fact, many thinning treatments do selectively remove western hemlock and leave amabilis fir, but in most cases amabilis fir only accounts for 30% - 40% of the trees within a stand (Kevin Derow, personal communication). As a result, removing the majority of western hemlock within 50 m of a porcupine den site may be the only practical way of using the forage selection of porcupines to the advantage of the forest manager. Although intuitively the removal of the preferred forage species should result in porcupines finding the habitat less suitable, there has been some evidence to suggest that porcupines will switch their forage selection when the preferred tree species is unavailable (Sullivan and Cheng 1989). Although I found that, in general, porcupines avoided amabilis fir in my study area, I still documented some cases where amabilis fir trees were used as forage (Chapter 1).

The use of a winter den is an important adaptation, which porcupines employ to ensure their survival during winter months (Roze 1989). Porcupines used both rock outcroppings and stumps extensively for winter dens. Both of these den structures were found to provide adequate thermal protection, under most ambient conditions, to ensure that porcupines did not have to increase their resting metabolic rate to maintain body temperature. From a management perspective there is little that can be done to reduce the availability of rock outcroppings for den sites. However, the stumps, which were being used by porcupines, were left from the initial logging of the old-growth forests, and the density and location of these potential denning structures can be manipulated. If, after logging, large stumps were to be removed from the site through burning or mechanical means, the availability of suitable denning structures could be dramatically reduced in many second-growth stands. The practicality of stump removal will vary depending on individual cut block characteristics, but it should be possible in some situations.

Although predators are more effective at killing porcupines in open areas (Robinette et al. 1959; Powell and Brander 1977; Powell 1982; Stricklan 1986; Sweitzer and Berger 1992; Krebs 1994), I found no increase in predation rates in thinned areas versus controls. This result is related to the low abundance of predators within the study area (Chapter 3). In areas where predator abundance is higher, the open habitat may result in higher predation rates, and a corresponding decline in porcupine numbers within the thinned stands. Attempts to increase predator abundance through habitat manipulation, use of attractants (Clapperton et al. 1989; Zimmerling and Sullivan 1994) and reducing trapping or hunting in specific areas, may aid in increasing predation rates in thinned areas.

Despite previous studies indicating that porcupines may be attracted to thinned stands (Van Deusen and Myers 1962; Dodge 1982; Eglitis and Hennon 1986; Sullivan et al. 1986), I have found no evidence to suggest any such attraction (Chapter 3). Instead, as suggested by Krebs

(1994), the number of trees damaged by porcupines in thinned stands does not differ from control stands (Chapter 3). The perceived attraction is an influence of increased rates of damage, owing to lower total tree density, rather than an increase in actual numbers of trees damaged (Krebs 1994; Chapter 3). Thinning treatments generally remove the suppressed stems which porcupines tend to avoid in control stands (Chapter 1). As a result, although thinning reduces the number of trees/ha, it does not reduce the number of forage trees/ha, from the point of view of the porcupine.

Although I found no attraction of porcupines to thinned stands, I also found no evidence that porcupines will avoid thinned stands (Chapter 3). Porcupines did not change their foraging range location or increase the number of dens used per winter as a result of the thinning treatments. I found no discernable difference in the foraging patterns of porcupines in the control versus the 1200 stems/ha treatments. Porcupines in the 400 stems/ha areas did increase their foraging range from the den site, but this increase did not result in a decline in porcupine abundance or damage rates within the stand. As 1200 stems/ha is a common thinning density in the Prince Rupert Forest Region, the results provide evidence that current thinning practices in British Columbia are likely to exacerbate the porcupine damage problem, as rates of damage are likely to increase, while porcupine numbers remain unchanged.

Based on the work of Charnov (1976) and Cowie (1977), I predicted that porcupines expending more energy to reach a tree would remove more vascular tissue from the tree before leaving. I found that porcupines that travelled farther to reach forage trees did indeed compensate for the increased energy expenditure by increasing the amount of vascular tissue removed per tree. As a result, damaged stems within the 400 stems/ha had a larger amount of vascular tissue removed compared to trees in the control area.

Thinning also influenced porcupine winter energy expenditures by increasing the amount of travel porcupines had to do in the open, through deep snow. Travelling under tree cover did

provide for significantly lower snow sinking depths. Despite the apparent increased cost of travel for porcupines in the thinned areas, there was no corresponding increase in mass loss or starvation rates.

Porcupine feeding damage significantly reduced tree growth rates in the control and both treatment areas. In addition, approximately 3/4 of all trees damaged were considered to be non-merchantable based on the Prince Rupert Forest Region guideline of 1/3 of stem circumference damaged (Anonymous 2000). Thinning treatments resulted in increased tree growth rates; however, it is unclear as to whether the increased merchantable volume obtained will be greater than the rate of volume lost owing to porcupine feeding damage.

Although the results of my study indicate that on an annual basis porcupine feeding damage rates may be low in unmanaged stands (Chapter 3), there are numerous examples of the cumulative impact of porcupines causing serious damage to second-growth conifer forests. Porcupine feeding damage in pre-commercially thinned stands in Alaska have been documented as high as 25% of western hemlock and 51% of sitka spruce trees (Eglitis and Hennon 1986). In addition, Sullivan et al. (1986) reported cumulative porcupine feeding damage to 52% of western hemlock trees in unmanaged second-growth stands of northwestern British Columbia.

The key question that forest managers must examine when deciding to pre-commercially thin a stand is; will increased growth rates allow the trees within the stand to reach merchantable size before cumulative porcupine feeding damage reduces the number of merchantable trees below commercially viable levels. The model I present along with those developed by Sullivan and Cheng (1989) and Krebs (1994) all indicate that annual damage rates above 1% will create non-commercially viable stands before an 80 year rotation age is reached if the stand is thinned to 1000 stems/ha or less. As a result, unless the thinning treatment is

expected to reduce rotation age dramatically, stands that suffer annual porcupine damage rates of greater than 1% should not be pre-commercially thinned.

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