WINTER FEEDING ECOLOGY OF THE NORTH AMERICAN PORCUPINE (*Erethizon dorsatum*) IN AN ISOLATED POPULATION OF EASTERN HEMLOCK (*Tsuga canadensis*) IN NORTHEASTERN MINNESOTA

A THESIS

SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF THE UNIVERSITY OF MINNESOTA

BY

KRISTIN NANCY SCHMIDT

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

MASTER OF SCIENCE

MARCH 1990

ACKNOWLEDGMENTS

I thank Diane Schulte for her regular assistance in field data collection. I also thank the members of my graduate committee,, Dr. John Pastor and Dr. David J. Schimpf for their willingness to give advice and assistance, and my major advisor, Dr. Donald P. Christian for providing his expertise, assistance, and steady encouragement throughout this project.

The field research for this study was supported, in part, by a grant from the Minnesota Department of Natural Resources Non-game Wildlife Program.

ABSTRACT

The North American porcupine, Erethizon dorsatum, is a generalist herbivore that, during winter, feeds on coniferous foliage and the inner bark of conifers and hardwood trees. Winter feeding by porcupines may sometimes cause the decline or mortality of trees due to girdling of the bole and limbs or defoliation of the crown. In the north-central and northeastern portion of its range, the porcupine often selects the bark or foliage of eastern hemlock, Tsuga canadensis, as a winter food item.

Hemlock Ravine Scientific and Natural Area (HRSNA) in northeastern Minnesota contains an unusual, isolated population of eastern hemlock; it is the largest population in this state and the only one showing substantial regeneration. Porcupines also use this area, and are protected within it; thus concern developed for the well-being of the hemlock population in HRSNA. This study was conducted during the winter and spring of 1988 to determine whether the hemlock population attracts large numbers of porcupines to this area, and if the porcupines at HRSNA seek out and preferentially use the hemlocks with greater frequency than predicted on the basis of the relative abundance of hemlock in the stand.

Results indicated that the number of porcupines using HRSNA does not differ from porcupine densities found elsewhere in the north-central and northeastern portions

of the range. Porcupines significantly selected the hemlock trees for all types of feeding (trunk-bark, limb-bark, and foliage feeding), but during the study season did not cause serious damage to this hemlock population. Thus, porcupine use of hemlock does not appear as intensive in HRSNA as in other areas where eastern hemlock is more numerous. Instead, the porcupines in HRSNA made heavy use of white cedar (<u>Thuja occidentalis</u>), white pine (<u>Pinus strobus</u>), and sugar maple (<u>Acer saccharum</u>), the latter two species to such an extent that survival was unlikely for certain of the trees fed upon.

TABLE OF CONTENTS

PAGE

LIST OF TABLES.................................... i

LIST OF FIGURES.................................... iii

INTRODUCTION.................................... 1

STUDY AREA AND METHODS.................................... 8

Study Area.................................... 9

Feeding Transects.................................... 9

Assessment of Adjacent Habitat.................................... 13

Vegetation Transects.................................... 14

Data Analysis.................................... 15

RESULTS.................................... 18

Trunk-bark and Total Feeding.................................... 18
Sugar maple.................................... 18
White pine.................................... 23
Eastern hemlock.................................... 23
Northern white cedar.................................... 24
Other species.................................... 24

Limb-bark Feeding.................................... 25
Sugar maple.................................... 25
White pine.................................... 25
Eastern hemlock.................................... 27
Other species.................................... 27

Foliage Feeding.................................... 27

Selectivity for Tree Size.................................... 28

Seasonal Feeding Patterns.................................... 34

Den Sites and Roost Trees.................................... 37
Assessment of Adjacent Habitat.................................... 40
Other Observations.................................... 40

DISCUSSION.................................... 42

CONCLUSION.................................... 54

LITERATURE CITED.................................... 58

TABLE OF CONTENTS

PAGE

APPENDIX I.. 63

APPENDIX II....................................... 64

LIST OF TABLES

TABLE PAGE

1 Dominant tree species used as winter food by porcupines in various locations in the north-central and northeastern U. S. and New Brunswick.. 3

2 Availability of tree species and use as feed trees by porcupines in HRSNA, February-May 1988.. 19

3 Electivity indices for total feeding, trunk-bark, limb-bark, and twig feeding by porcupines at HRSNA during winter and spring 1988........... 20

4 Preference ratios for total feeding, trunk-bark, limb bark, and twig feeding by porcupines at HRSNA during winter and spring 1988............. 21

5 Proportion ($\underline{\bar{x}} \pm$ s.d.) trunk bark removed for the four trunk-bark feed tree species at HRSNA 22

6 Number of trees in which porcupines fed on limb-bark, the mean ($\underline{\bar{x}} \pm$ s.d.) number of branches per tree showing light, moderate, and heavy feeding, and the total number of branches fed upon per tree.. 26

7 Height (m) and dbh (cm) of tree species occurring in the vegetation transects at HRSNA not used recently by porcupines, compared to the

LIST OF TABLES

TABLE PAGE

same species used elsewhere as feed trees......... 30

8 Height (m) and dbh (cm) of all hemlock trees in HRSNA.. 31

9 Comparison of size ($\underline{x} \pm$ s.d.) of all feed trees, trunk-bark feed trees, and limb-bark feed trees to size of trees in the vegetation transects...... 33

10 Porcupine locations in HRSNA on each sampling date... 38

LIST OF FIGURES

FIGURE PAGE

1 Hemlock Ravine Scientific and Natural Area and vicinity.. 10

2 Cumulative proportion of trunk bark removed from major feed-tree species during winter and spring 1988.. 35

3 Cumulative proportion of limb-bark feeding on major feed tree species during winter and spring 1988.. 36

INTRODUCTION

The North American porcupine, *Erethizon dorsatum*, is a large rodent found throughout much of the continent (Hall 1981). In the northern and eastern portions of its range it inhabits boreal forest communities. This species is well known for its habit of feeding in winter primarily on the inner bark of boles, limbs, and branches, and on foliage of trees. Winter feeding by porcupines has been well-documented in many studies by foresters because of the apparent damage to valuable timber; scarring, girdling, and pruning of branches may permanently damage or kill trees (Gabrielson 1928; Curtis 1944; Curtis and Kozicky 1944; Rudolph 1949; Shapiro 1949; Stoeckeler 1950; Curtis and Wilson 1953; Faulkner and Dodge 1962; Krefting et al. 1962; Van Deusen and Myers 1962; Brander and Stearns 1963; Storm and Halvorson 1967). Studies of winter feeding by porcupines also have been conducted to assess damage to plant, communities with non-commercial value. These communities are important for other reasons such as aesthetics or intrinsic ecological value. For example, Gill and Cordes (1972) reported that since the turn of the century large numbers of porcupines have been threatening the existence of non-merchantable stands of limber pine (*Pinus flexilis*) occurring as low-elevation Krummholz in southern Alberta. Tenneson and Oring (1985) investigated whether porcupine feeding threatened the few remaining old-growth white pines (*P. strobus*) in Itasca State Park in northwestern Minnesota, and Spencer (1964) observed serious destruction by porcupines feeding in stands of pinyon pine (P. edulis) and ponderosa pine (P. ponderosa) in Mesa Verde National Park in southwest Colorado. The present study was conducted to assess damage by porcupines to the eastern hemlock (Tsuga canadensis), a rare tree species in northeastern Minnesota.

The impact of porcupines on forests in winter is in part a result of diet selectivity, This selectivity may be rather consistent within an area, but can vary widely among areas. In winter, porcupines have been recorded feeding on many tree species throughout the northern and eastern parts of the range (Table 1). Porcupines also feed on trees, both within and among species, that vary in height and diameter throughout different parts of the animal's range (Curtis,1941; Rudolph 1949; Shapiro 1949; Krefting et al. 1962; Harder 1980).

Eastern hemlock, Tsuga canadensis (L.) Carr., is a highly selected winter food of porcupines over much of the area where the two species co-occur (Curtis 1944; Curtis and Kozicky 1944; Shapiro 1949; Krefting et al. 1962; Brander and Steams 1963; Brander 1973; Roze 1984; but see Spear and Dilworth [1978] for conflicting information). The main portion of the range of eastern hemlock (hereafter, "hemlock") in the United States is from

Table 1. The dominant hardwood species* and conifer species** used as winter food by porcupines as reported in studies in various locations in the north-central and northeastern United States and New Brunswick. Food items are listed in approximate order of use as reported in the studies.

Region	Hardwood species	Conifer species
Northwestern Minnesota (Spencer 1964; Tenneson and Oring 1985)	Bigtooth aspen Northern red oak American elm American basswood	White pine American larch Balsam fir White spruce Black spruce
Northern Michigan (Brander and Stearns 1963; Brander 1973)	Sugar maple American elm American basswood Red maple	Eastern hemlock
Northeastern New York (Shapiro 1949)	Sugar maple Striped maple Yellow birch	Eastern hemlock Red spruce Balsam fir
Southeastern New York (Roze 1984)	Beech Sugar maple	Eastern hemlock
Maine (Curtis and Kozicky 1944)	Sugar maple	Eastern hemlock Northern white cedar Red spruce American larch
New Brunswick (Speer and Dilworth 1978)	Gray birch Paper birch	Spruce White pine Balsam fir

---

*:
Bigtooth aspen = *Populus grandidentata*
Northern red oak = *Quercus rubra*
American elm = *Ulmus americana*
American basswood = *Tilia americana*
Sugar maple = *Acer saccharum*
Red maple = *A. rubra*
Striped maple = *A. spicatum*
Yellow birch = *Betula lutea*
Beech = *Fagus grandifolia*
Gray birch = *B. populifolia*
Paper birch = *B. papyrifera*

**:
White pine = *Pinus stobus*
American larch = *Larix laricina*
Balsam fir = *Abies balsamea*
White spruce = *Picea glauca*
Black spruce = *P. mariana*
Eastern hemlock = *Tsuga canadensis*
Red spruce = *P. rubra*
No. white cedar = *Thuja occidentalis*

northern Wisconsin, around the Great Lakes, east to Maine, south through New England, and south along the Appalachians to northern Georgia and Alabama (Petrides 1972). The western limit of the range is northeastern and east-central Minnesota, where the species is confined to a few outlier populations. These outliers are thought by some to be remnants of a once larger range (citations in Calcote 1986), but pollen diagrams indicate that hemlock never was more abundant in Minnesota than it is today (Calcote 1986). At present, 15 historically recorded hemlock populations in Minnesota are listed by the Department of Natural Resources Natural Heritage Program; at least eight of these outliers survived into the-1950s, and are from 60-130 km disjunct from the main range of the species in Wisconsin. The species has been designated "of special concern" in Minnesota (Smith 1988); the number of mature trees may be as low as 34. Fourteen post-seedling trees (11,canopy trees and 3 intermediate saplings) plus about 100 seedlings are located in Hemlock Ravine Scientific and Natural Area (HRSNA), adjacent to the northern border of Jay Cooke State Park in Carlton County, Minnesota. The Hemlock Ravine population is the only one in the state with significant regeneration, and represents the greatest concentration of hemlocks in Minnesota (Calcote 1986). A stand of 5,000 trees of all size classes was recorded in Land Survey notes for 1873 as occurring on the north side of the St. Louis River near Paupores in St. Louis County, Minnesota. In 191.8 a logger's slash fire jumped the swampland surrounding the stand and burned it to the ground. No hemlocks have been found on the site during recent surveys of the area (Calcote 1986).

Much of our knowledge about porcupine winter food habits is from the perspective of the forester. Concern gradually developed about the porcupine's impact in hemlock forests. For example, Stoeckeler (1950) reported that during a survey of porcupine damage in a northern hardwood-hemlock forest in northeastern Wisconsin, between 9Vand 500 of all trees in the stand were damaged by porcupines. Krefting et al. (1962) reported that in the Lake States, bark feeding by porcupines in forests resulted in "lower quality timber"; hemlock had the highest food preference when tree species were weighted according to relative abundance. Curtis and Kozicky (1944) found that in New England hemlock foliage was preferred above all other species sampled. Brander and Steams (1963) reported that in forests of northern Michigan, porcupine activity was concentrated in the vicinity of hemlock. The present study was instigated in part due to observations of porcupines in hemlocks on three separate occasions at HRSNA (Calcote 1986) .

Because of these and similar observations, porcupines and other animals that produce economic loss or that destroy human property often are viewed narrowly as "pests" or nuisances. As a result, porcupines have been "controlled" by a variety of means including baiting dens with poison (Gabrielson 1928 Faulkner and Dodge 1962), paying bounties for killed animals (Reeks 1942; Faulkner and Dodge 1962), and delegating foresters to shoot porcupines during timber cruises (Krefting et al. 1962). However, porcupines continue to maintain high population densities in some areas despite large numbers of the animals being killed every year (Curtis 1941). and despite the relatively low reproductive rate (one young produced per year with sexual maturity at 2.5 years: Hazard 1982; Nowak and Paradiso 1983). A better approach to this type of "native" nuisance (as opposed to introduced, or true pest, species) may be to view the animal in terms of its role in shaping the ecology of an area. For example, it might be important to test whether the animal's method of feeding and food preferences alter or affect the structure of the plant community in which it is found. Also important are the long-term implications for a plant community when herbivores such as porcupines increase in number, and the implications for potential predators and competitors with which they share the habitat.

A few of those who have explored the life history of the porcupine have cautioned against hasty control measures in the absence of information on the biology of the species

(Curtis and Kozicky 1944; Spencer 1964). Curtis and Kozicky (1944) claimed that the damage wrought by porcupines in a stand of timber is "infinitesimal" compared with the volume of timber damaged by fire, insects, or fungi. Clearly, effective management of this species should be based on more understanding of its habits rather khan merely destroying individuals to no sensible end. Yet the issue remains that in some areas there may be too many porcupines resulting in long-term negative effects on plant communities. Humans have eliminated potential predators of porcupines over many parts of the range of this species, thus indirectly contributing to the observed porcupine population increases (Spencer 1946; Cook and Hamilton 1957;. Gill and Cordes 1972). Therefore, it is warranted that we develop sensible schemes for managing porcupines in problem areas.

Because porcupines feed so intensively and extensively on hemlocks in the eastern portion of the range of this tree species, and because hemlock is a rare species in Minnesota and is becoming scarce in portions of the range in western Upper Michigan (Hix and Barnes 1984; Frelich and Lorimer 1985), it is necessary to determine whether porcupine feeding has an important effect on the hemlocks at HRSNA. This study was designed to assess the impact of winter feeding by porcupines on eastern hemlock in HRSNA during one field season. In particular, I attempted to determine 1) whether the hemlock population at HRSNA attracts large numbers of porcupines to the area, 2) whether porcupines seek out and preferentially use these hemlocks with greater frequency than their relative abundance in the stand would predict, 3) the number of porcupines in the area and their food habits in this area, 4) how porcupine use of a small population of hemlocks, like that at HRSNA, compares with studies in areas of more numerous hemlocks, 5) if porcupines are damaging the hemlocks at HRSNA, some possible management strategies that would not involve direct elimination of porcupines.

STUDY AREA AND METHODS

Study Area. This study took place in Hemlock Ravine Scientific and Natural Area (HRSNA) in winter and spring of 1988. Hemlock Ravine is located adjacent to the northern border of Jay Cooke State Park in Carlton County, Minnesota, 30 km southwest of Duluth (N 46°40', W 92° 21', USGS 19$3). The total area of this site is approximately 20 hay the boundary lines create a triangle on a map: The area is delineated by County Road 151 to the west, an open field to the north, and an old railroad grade (now the Willard Munger State Trail) that extends northeast to southwest. A steep, artificial embankment occurs at the southwest end of the railroad grade where it is intersected by the ravine. The perennial stream valley contained within HRSNA extends from northwest to southeast, and is part of a steep-sided gorge that connects with the St. Louis River valley (Fig. 1). The flora of HRSNA was grouped into five vegetation types by the Minnesota Department of Natural Resources Natural Heritage Program (1984). These include Northern Hardwoods-Conifer Forest (upland), Northern Hardwoods-Conifer Forest (ravine slope), Black Ash Wetland, Paper Birch-Maple-Oak, and Trembling Aspen-Maple-Birch. Ten of the 11 canopy-size hemlocks plus the three saplings are located on north-facing ravine slopes, thus fall into the Northern Hardwoods-Conifer Forest (ravine slope) vegetation type. The other canopy hemlock is located on the upland top slope on the west side of the ravine in the Hardwoods-Conifer Forest (upland) vegetation type.

Feeding Transacts. Preliminary surveys of the area in mid-January suggested that porcupine activity was concentrated in the ravine and on the upland on the east side of the ravine. I concentrated my effort by sampling in these areas and not in the upland aspen grove in the southwest corner of HRSNA or in the spruce-fir forest growing on the railroad embankment; these two areas were clearly visible from the transacts and were viewed for porcupine activity only casually. Porcupine feeding activity on the various tree species in HRSNA was documented throughout the winter by making observations

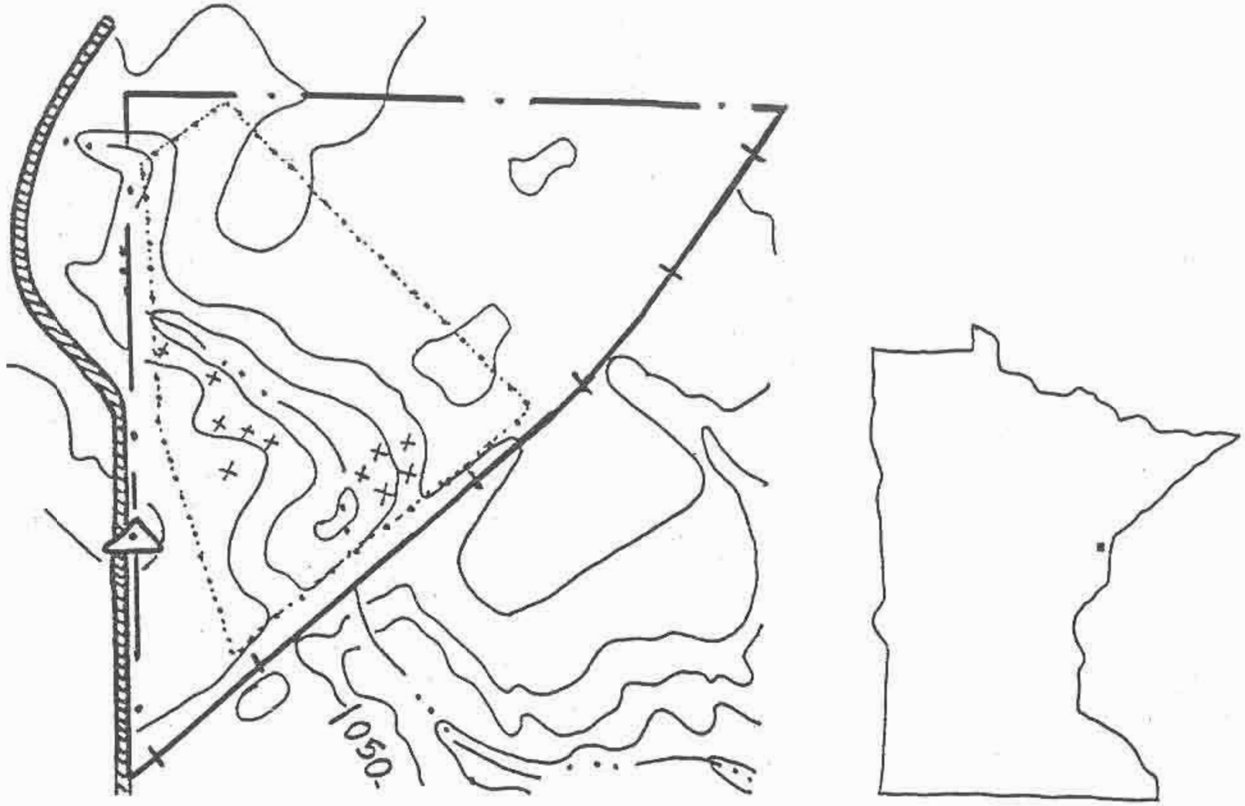


Figure 1. Hemlock Ravine Scientific and Natural Area and vicinity. HRSNA boundaries,——·——·—; approximate area of transects, ···················; approximate locations of canopy hemlock trees, x.

while walking a series of flagged transacts. Transacts were spaced so the entire area could be surveyed, that is, a transact was placed within view of adjacent transacts so that any part of a tree used by a porcupine would be visible from at least one of the transacts. Eight transacts, four on either side of the ravine, were marked with flagging. On each side of the ravine, one transact was placed across the level top slope well away from the ravine edge, two transacts were placed on the midslope, and one transact was placed on the bottom slope along the creek. The total length of the eight transacts was approximately 1,$00 m. Topography and, to a lesser extent, such obstacles as windthrown trees determined transact placement.

Transacts directly intercepted seven of the 14 mature (post-seedling) hemlocks. One of those intercepted was growing on the western top-slope. Another was on the west side about midslope at the junction of the main ravine with a side-ravines the remaining five hemlocks were clustered together on the east side of the ravine, just north of the railroad grade, between the bottom and midslope (Fig. 1). Two canopy hemlocks and three saplings grow in the highly dissected, steep-sided annual stream channel on the west side of the ravine. Many hemlock seedlings were scattered throughout this area. Transacts located in this side ravine were abandoned when it became apparent that walking on this slope could cause erosion detrimental to hemlock regeneration. These five hemlocks were spot-checked regularly for signs of porcupine feeding activity. Two canopy hemlocks were located north of this annual stream channel on the western slope of the main ravine (Fig. 1). This area also is very steep, and these trees also were spot-checked at regular intervals. Perhaps this terrain was too steep for porcupines, as there was no evidence,(e.g., trails, other tree species fed upon, old feeding scars) of activity in this section of the ravine during the study period.

Data were collected weekly from 31 January 1988 to 1 May 1988. The objectives were to walk the transacts every week (each transact every other week) to 1) quantify feeding activity by observing and flagging feed trees, draw scars of bark removal, and note the presence on the ground of gnawed twigs and branches, and 2) to search for den sites and porcupines.

Feed-tree scars were drawn beginning on 13 February on a standardized diagram of a tree bole on gridded paper. The bole of the tree was "unrolled" and flattened in the manner of a world map; whenever possible 180°-opposite sides of the tree bole were sketched. Scar height was drawn to the nearest 0.5 decimeter and viewing aspect was determined with a compass to ensure uniformity in sketching from week to week and among observers. Location on the tree bole of primary and secondary limbs fed upon also was recorded on the diagram (Appendices I and II). Limb feeding was designated slight (<10% bark removal), moderate (10-50% bark removal), and heavy (>50% bark removal). Twig or foliage feeding on conifers was noted as slight, moderate, or heavy on a subjective scale depending on the amount of accumulation beneath the feed tree (Speer and Dilworth 1978). Deer frequently feed on twigs dropped by ,porcupines (Shapiro 1949). Trees also were considered feed trees if porcupine claw marks were present on the bole and tracks indicated deer had been milling about under the tree, but these trees were not used in tallies of intensity of twig feeding.

Porcupine trails crossing a transect were followed, either to a den site or to a feed or roost tree. Distances (m) from occupied dens to roost trees were measured. I attempted to mark porcupines with spray paint and succeeded in marking one individual with orange on the right rear flank.

For every feed tree, diameter at breast height (dbh) and height were measured (to the nearest centimeter and meter, respectively) and the presence or absence of scars from previous years was noted. Minimum and maximum air temperatures for the week before sampling were obtained with a Taylor maximum-minimum thermometer.

<u>Assessment of Adjacent Habitat</u>. On 22 April 1988 the

ravine adjacent to HRSNA was surveyed to assess use of feed trees there relative to HRSNA. An observer not familiar with location of feed trees at HRSNA walked for 100 minutes both in HRSNA and the adjacent ravine. Several paired transects were walked in each area at a standardized rate and the number of feed trees from the current year was recorded for each transect. Numbers of porcupines also were noted in this area.

Vegetation Transects. Abundances of tree species in the entire ravine and adjacent top slopes were estimated to determine whether porcupines preferentially selected or avoided certain tree species as potential food items. Sample plots 10 m long by 6 m wide centered on the feeding transects were located at 20-m intervals for the entire length of each of the eight transects (Roze 19$4). In addition to sampling vegetation along the feeding transects, vegetation also was sampled in plots along transects on both sides of the previously abandoned side ravine, and midslope along the northwest side of the main ravine where hemlocks previously were only spot-checked. Every tree in the sample plots >3 cm dbh was measured with a dbh tape. Tree heights were estimated to the nearest 1 m and a clinometer was used periodically to check accuracy of estimates. No "shrubs" (e.g., mountain maple [Aver spicatum], alder [Alnus sp.]) were included in the survey even if >3 cm dbh; there was no indication that porcupines fed on bark or twigs of these plant species in HRSNA.

Data Analysis. Surface area of bark removed on each of the feed trees was calculated based on the area of a cylinder; by computing the area of one square on the gridded paper (based on the dbh and height of the tree) total area of bark removed per tree was calculated. No adjustment was made for taper or for that portion of the tree height that was "crown". When comparing the values for total trunk-bark removed with observations of individual trees it was apparent that some calculations were inaccurate. For example, one sugar maple feed tree was so heavily fed upon that by the end of the field season only small patches of bark remained, yet the computed value appeared to underestimate the amount of bark removed. More accurate values were obtained by dividing' the number of squares of bark removed by the number of squares,accounting for the bole of the tree only, with crown excluded. Generally, these adjustments affected estimates only for trees that had >1.Oo trunk bark removed.

Average height and dbh were calculated for feed tree species and all tree species occurring in the vegetation samples. The proportion of bark removed and mean number of limbs fed upon for each species also was calculated. Cumulative bark removal per sampling period was plotted for each species. Selection by porcupines for certain tree species was determined by electivity indices (Jacobs 1974;

see also Jenkins 1979; 1980) and preference ratios. The electivity values (E_i) were calculated as:

$$E_i = \ln[r_i (1 - p_i) / p_i (1 - r_i)]$$

where r_i = the proportion of species *i* in the diet and p_i = the proportion of the species *i* available. A positive E_i indicates selection for a food item. In this study, r_i was calculated as the number of trees of species *i* used for feeding, divided by the total number of trees fed upon. Separate calculations were made using r_i computed as the number of trees of species *i* fed upon in one or more of the three feeding categories (trunk bark removed, limb bark removed, foliage [twigs] fed upon), divided by the total number of trees fed upon in that category. In this study, r_i was calculated as the number of trees of species *i* occurring in the vegetation transects divided by the total number of trees sampled in the vegetation transects.

Significance of E_i values was tested by computing:

$$X^2 = r_i^2 / [1/x_i + 1/ (m - x_i) + 1/y_i + 1/ (n - y_i)]$$

Where X_i and y_i are the number of trees of species *i* used by porcupines as a food source and the number of trees of species i available, respectively, and m and n are the total number of trees used and available, respectively. The term x_i was calculated separately for all trees of species i fed upon in totality, and for feeding on trunk bark, limb bark, or foliage. X^2 was compared with a Chi-square distribution with one degree of freedom (Fienberg 1977; see also Jenkins 1979).

For comparison, preference ratios also were used as an indication of food selection by porcupines. The preference ratios for each species i were calculated as r_i/p_i where r_i and p_i were computed as for calculation of E_i. A preference ratio greater than 1.0 indicates selection for a food item and a ratio less than 1.0 indicates selection against a food item. Jacobs (1974) showed that the preference ratio may be less appropriate than the electivity index when available food types differ in abundance.

I also tested whether the trees of each species selected as food by porcupines differed significantly in size from the average for each species in HRSNA.

RESULTS

Trunk-bark and Total Feeding

Sugar maple.-- Sugar maple occurred in the diet in proportions slightly greater than in the area (Table 2). For all types of feeding combined (total feeding), electivity values ($\underline{E}_i$) indicated that porcupines did not significantly select sugar maple as a food source (Table 3). However, the $\underline{E}_i$ for trunk-bark feeding indicated strong selection ($\underline{X}^2 = 19.92$, $p < 0.005$) for sugar maple. Preference ratios reflected the $\underline{E}_i$ values for sugar maple; the preference ratio for trunk-bark feeding was greater than for total feeding (Table 4). Thus, sugar maple, the most common hardwood in the sampling area, appeared to be used in proportion to its widespread occurrence in the area; porcupines did not seek out sugar maple specifically when compared with overall use of all species fed upon. However, the trunk bark of sugar maple indeed appeared to be a highly selected food item. Sugar maple accounted for 0.66 of the bark feeding on trees at HRSNA (Table 2). The average proportion of trunk bark removed from individual sugar maple trees was 0.07 (Table 5). However, as much as 0.67 of the trunk bark was removed from an individual tree; in this instance, nearly the entire tree appeared girdled. Thus, the porcupines in HRSNA seemed to be selective in use of individual maple

Table 2. Availability of tree species and use as feed trees by porcupines at HRSNA, winter-spring 1988. Data are proportions of all trees available (sampled in vegetation transects, _n_ = 609), total feed trees (_n_ = 96), trunk-bark feed trees (_n_ = 47), limb-bark feed trees (_n_ = 60), and foliage feed trees (_n_ = 45) listed in descending order of abundance.

Species	Proportion				
	Available	Total Feed Trees	Trunk Bark	Limb Bark	Foliage Feed Trees
Sugar maple (*Acer saccharum*)	0.396	0.489	0.659	0.450	0
Paper birch (*Betula papyrifera*)	0.128	0.021	0.042	0.033	0
White spruce (*Picea glauca*)	0.102	0	0	0	0
Yellow birch (*B. lutea*)	0.087	0	0	0	0
Aspen (*Populus* sp.)	0.076	0	0	0	0
White cedar (*Thuja occidentalis*)	0.061	0.146	0	0	0.351
Balsam fir (*Abies balsamea*)	0.059	0	0	0	0
Ironwood (*Ostrya virginiana*)	0.044	0	0	0	0
Red Oak (*Quercus rubra*)	0.021	0.010	0	0.017	0
White pine (*Pinus strobus*)	0.010	0.271	0.234	0.433	0.513
American basswood (*Tilia americana*)	0.010	0	0	0	0
Eastern hemlock (*Tsuga canadensis*)	0.006	0.062	0.064	0.067	0.135

Table 3. Electivity indices[a] for total feeding, trunk-bark feeding, limb-bark feeding, and foliage feeding by porcupines at Hemlock Ravine Scientific and Natural Area during winter-spring 1988.

Species	Total Use	Trunk-bark Feeding	Limb-bark Feeding	Foliage Feeding
Sugar maple	+0.38	+1.05 ***	+0.22	-----
White pine	+3.60 ***	+3.45 ***	+4.34 ***	+4.95 ***
White cedar	+0.97 ***	-----	-----	+2.15 ***
Eastern hemlock	+2.40 ***	+2.36 ***	+2.38 ***	+3.19 ***
Paper birch	-1.92 **	-1.21 @	-1.45 *	-----
Red oak	-0.75	-----	-0.25	-----

---

[a] Electivity indices tested for statistical significance as described in text. ***, $\underline{p} < 0.005$; **, $0.005 < \underline{p} < 0.01$; *, $0.01 < \underline{p} < 0.05$; @, $0.05 < \underline{p} < 0.10$

Table 4. Preference ratios for all feeding, trunk-bark feeding, limb-bark feeding, and foliage feeding by porcupines at Hemlock Ravine Scientific and Natural Area during winter and spring 1988.

Species	All feeding	Trunk-bark feeding	Limb-bark feeding	Foliage feeding
Sugar maple	1.18	1.64	1.14	0
White pine	29.20	23.90	43.30	51.30
White cedar	2.39	0	0	5.75
Eastern hemlock	10.33	10.83	11.17	22.50
Paper birch	0.16	0.33	0.26	0
Red Oak	0.48	0	0.81	0

Table 5. Proportion ($\bar{x}$ ± S.D.) trunk-bark removed for the four trunk-bark feed tree species at Hemlock Ravine Scientific and Natural Area, winter 1987-88. Ranges in parentheses.

Species	Number	Proportion Trunk bark Removed
Sugar maple	31	0.068 ± 0.136 ($0.0005\overline{2}$-0.667)
White pine	11	0.017 ± 0.015 ($0.0002\overline{4}$-0.035)
Eastern hemlock	3	0.009 ± 0.011 ($0.0013\overline{2}$-0.028)
Paper birch	2	0.042

trees; although these data do not consider the quantity of bark removed from each particular tree, some sugar maple trees were highly used relative to others.

White vine.-- White pine occurred in the diet more frequently than expected on the basis of its availability it accounted for similar proportions of all feed trees and trunk-bark feed trees (Table 2). Eis ($p < 0.005$) and preference ratios both indicated strong selection by porcupines for this species as .a component of all trees fed upon and as a source of trunk bark (Tables 3 and 4). Although proportional trunk-bark removal from individual white pine trees averaged only 0.02 with a maximum of 0.035 (Table 5), most, of the trunk-bark removal from white pine was in the crown. The effect of this feeding was accentuated by its concentration in a relatively small area of the tree; considerable portions of some white pine crowns were girdled.

Eastern hemlock.- Availability of hemlock was lower than for all other species occurring along the transects at HRSNA. Total feeding and trunk-bark feeding on hemlock was slight relative to that on sugar maple and white pine (Table 2). However, $\underline{E}_i$s and preference ratios showed strong selection by porcupines for hemlock as a component of the total feed trees and for trunk-bark feed trees (Tables 3 and 4). An average of 0.009 of the trunk bark was removed from hemlocks, with a maximum proportion of

0.02$ on any one tree (Table 5). In no instance was complete girdling of the bole observed on a hemlock, and unlike white pine, the area of trunk bark removed was not concentrated in a small area of the tree. Six of the 11 hemlock trees in the study area were fed upon.

Northern white cedar.-- White cedar was moderately abundant in the study area but made up a proportionately greater, number of the total trees fed upon by porcupines and was significantly selected as a food source (Tables 2-4). Porcupines did not use white cedar bark during this study, nor have they been recorded using white cedar bark as a food source elsewhere; thus the sole contribution of this species to the porcupine's diet is in the form of foliage.

Other species.-- Paper birch occurred infrequently in the diet relative to its availability in the areas this species was the second most abundant species in the study area (Table 2). However, the $\underline{E}_i$ value for total. use indicated significant selection against this species by the porcupines ($p < 0.01$); porcupines selected against paper birch as a source of trunk-bark at the 0.10 level (Table 3). Preference ratios far paper birch in these two categories were <l, also indicating selection against this species. Only two paper birch trees were used for trunk-bark feeding in the study area (Table 5).

Red oak occurred infrequently in the study area and also made up a small proportion of the total feed trees used by porcupines. In no instance was trunk-bark feeding observed on red oak (Table 2). The $\underline{E}_i$ value for red oak, though negative, did not indicate significant selection against this species (Table 3): likewise, the preference ratio for this species was slightly <1 (Table 4).

White spruce and yellow birch, 3rd and 4th in availability, never appeared in the diet. Likewise, balsam fir, common at HRSNA, was never fed upon. These three species lacked visible scars indicating that porcupines have not used these species in recent years in HRSNA.

Limb-bark Feeding

Sugar maple.-- The proportion of sugar maple trees used for limb-bark feeding was slightly greater than the proportion of sugar .maple trees in the study area (Table 2). E1 values and preference ratios indicated that the porcupines did not significantly select sugar maple as a source of limb bark (Tables 3 and 4). An average of 3.5 limbs per sugar maple tree were fed upon; most were in the light and moderate category (Table 6).

White dine.-- White pine made up a large proportion of the trees used for limb feeding, especially relative to its availability in the area (Table 2). $\underline{E}_i$ values and preference ratios indicated strong selection by porcupines for white pine limb bark (Tables 3 and 4).`White pine had

Table 6. Number of trees in which porcupines fed on limb-bark, the mean (± standard deviation) number of branches per tree showing light, moderate, and heavy feeding, and the total number of branches fed upon per tree. Parenthetical values are the mean (± standard deviation) proportions of limb-bark feeding recorded as light moderate, and heavy. Data were collected at Hemlock Ravine Scientific and Natural Area, February-May 1988.

		Mean number of browsed branches per tree			
Species	Number of trees	Light	Moderate	Heavy	Total
Sugar maple	27	1.7 ± 1.2 (0.68 ± 0.38)	1.4 ± 0.8 (0.24 ± 0.35)	0.4 ± 0.7 (0.08 ± 0.15)	2.9 ± 2.1
Paper birch	2	1.5 (0.50)	1.0 (0.37)	0.5 (0.13)	3.0
White pine	26	4.2 ± 3.7 (0.88 ± 0.22)	1.7 ± 4.2 (0.10 ± 0.17)	0.6 ± 2.6 (0.02 ± 0.06)	6.5 ± 9.7
Red oak	1	2 (1.00)	0 (0)	0 (0)	2
Eastern hemlock	4	3.2 ± 4.6 (0.57 ± 0.54)	1.2 ± 1.4 (0.43 ± 0.54)	0	4.5 ± 4.7

the most limbs fed upon per tree ($\underline{X}$ = 6.5); of those, 0.88 were only lightly fed upon (Table 6). As was the case for white pine trunk-bark feeding, in some trees the limb-bark feeding was accentuated by its concentration in a relatively small area of the crown; girdling of some of the major limbs was apparent.

Eastern hemlock.-- Hemlock was significantly selected as a source of limb bark, although it was used proportionately less than some of the other species used for limb-bark feeding (Tables 2-4). An average of 0.045 limbs per hemlock were fed upon, but feeding intensity was moderate for a substantial proportion of these trees and no limbs were fed upon heavily (Table 6). In contrast to white pine, in no instance was limb-bark feeding concentrated in an area of a particular hemlock, nor was complete girdling of a major hemlock limb observed.

Other, species.-- Paper birch and red oak both made up a small proportion of the trees used for limb-bark feeding (Table 2). Paper birch was significantly selected against for this type of feeding; red oak was not selected for or against (Tables 3 and 4). The mean number of branches browsed per tree was low in both instances (Table 6).

Foliage Feeding

Foliage feeding (a category applicable only to conifers) was most extensive on white pine (Table 2). For several pines, this type of feeding was the only feeding observed, and in those trees the crown was noticeably defoliated. The $\underline{E}_i$ values and preference ratios reflect the extensive use of this species for foliage feeding (Tables 3 and 4).

Hemlock accounted proportionately for the smallest number of trees used for foliage feeding; however, foliage feeding (as opposed to trunk or limb bark feeding) was the most common type of feeding on this species (Table 2). $\underline{E}_i$s and preference ratios indicated strong ($p < 0.005$) selection by porcupines for hemlock foliage (Tables 3 and 4). Unlike foliage feeding on white pine, substantial defoliation of an individual hemlock tree was not observed during this study.

White cedar accounted for 0.35 of foliage feeding; it was significantly selected by porcupines in this feeding category (Tables 2-4).

Selectivity for Tree Size

Porcupines at HRSNA did not use white spruce, yellow birch, aspen, balsam fir, or ironwood for any form of feeding despite the relatively high frequency of occurrence of these species in the study area. These results do not compare to those of other studies in the north-central and northeastern portion of the range where porcupines do select these species out of a variety of different food items available (Curtis and Kozicky 1944; Shapiro 1949: Krefting et al. 1962; Speer and Dilworth 1978; and Tenneson and Oring 1985). There is some evidence that porcupines select food items, in part, on the basis of tree dimension (e-.g., Harder 1980); thus these contrasting results may be explained by discrepancies in tree size among different areas. White spruce, yellow birch, and balsam fir trees in HRSNA averaged smaller in height and/or diameter than trees of these species used by porcupines elsewhere. Conversely, aspen and ironwood trees, commonly used elsewhere in the northeastern portion of the range, may have been larger in HRSNA than trees of these species selected by porcupines in other areas (Table 7).

Individual trees of species used by porcupines tended to be larger than the average for these species in the area. The mean height and dbh of sugar maple feed trees (for all types of feeding combined) were significantly greater than the overall mean for sugar maple in HRSNA (for height, $t = 1.747$, $df = 47$, $p < 0.0005$: for dbh, $t = 3.705$, $df = 53$, $p < 0.0005$; Table 8). Sugar maples used for trunk-bark feeding were larger than overall (for height, $t = 6.734$, $df = 44$, $p < 0.0005$: for dbh, $t = 3.943$, $df = 58$, $p < 0.0005$). Likewise, sugar maple trees used for limb-bark feeding were significantly larger than the mean for sugar maple in the area (for height, $t = 3.004$, $df = 30$, $p < 0.005$; for dbh, $t = 2.643$, $df = 30$, $p < 0.01$).

Table 7. Species, number, height (m), and DBH (cm) of trees occurring in the vegetation transects at Hemlock Ravine Scientific and Natural Area (HRSNA) that were not used recently by porcupines as feed trees. Data are from winter and spring 1988 and are compared to mean height and DBH of trees used as feed trees in other areas. DBH and height for HRSNA are means and standard deviations.

	HRSNA			Other areas	
Species	Total	Height	DBH	Height	DBH
Balsam fir	36	7.69 ± 4.29	9.53 ± 5.33	18[a]	33[a]
Yellow birch	53	10.25 ± 4.36	15.92 ± 14.06		30-35[a] 25-36[b]
Ironwood	27	9.78 ± 5.72	12.37 ± 9.11	7-10[c]	5-8[c]
Spruce sp.	62	9.89 ± 6.68	15.47 ± 12.93	13-26[a]	20-41[a] 25-36[b]
Aspen	46	9.07 ± 5.48	9.93 ± 8.51	3-5[c]	3-5[c]
American basswood	6	7.33 ± 2.26	6.00 ± 2.30	2-13[c]	3-13[c]

a, Shapiro 1949
b, Krefting et al. 1962
c, Curtis 1941

Table 8. Comparison of size ($\overline{X}$ ± SD) of all feed trees, trunk-bark feed trees, and limb bark-feed trees to the size of trees in the vegetation transects for the four major species used as food by porcupines. Values are dbh (cm) except for sugar maple, in which height also was compared. Sample sizes in parentheses.

Species	All Feed Trees	Trunk-bark Feed Trees	Limb-bark Feed Trees	Vegetation Transect Trees
Sugar maple				
height (m)	10.9±3.4 (47)*	10.7±2.7 (30)*	10.3±3.5 (27)*	8.8±3.6 (241)
dbh (cm)	15.5±11.1 (47)*	13.4±4.5 (30)*	15.4±9.8 (27)*	9.8±8.2 (241)
White pine	49.4±17.2 (26)	44.3±16.3 (11)	51.6±15.3 (26)	38.2±19.9 (6)
E. hemlock	33.5±11.2 (6)*	30.3±18.4 (3)	33.5±13.0 (4)*	8.5±6.7 (4)
W. cedar	29.4±11.0 (14)*	-----	-----	24.4±11.2 (37)

*, $p < 0.05$

The mean diameters of white pine and white cedar feed trees were greater than for all trees of these species in ~IRSNA. White pine trees were larger as a component of total use as well as for trunk-bark and limb-bark feed trees, but the differences were not significant ($p > 0.10$, 0.25, and $p > 0.05$, for overall, trunk-bark, and limb-bark, respectively; Table 8). White cedar trees used for foliage feeding had a mean diameter significantly greater than the mean for this species in the area ($t = 1.747$, $df = 24$, $p < 0.05$).

The mean diameter of all hemlocks used as feed trees was greater than the mean for the 14 hemlocks in the area ($t = 4.397$, $df = 8$, $p < 0.005$: Table 8). Diameters of hemlocks used for trunk feeding also were greater than overall, but not significantly so ($0.05 < p < 0.10$). Mean dbh for hemlock trees used for limb feeding was significantly larger than the mean for the 14 trees ($t = 3.512$, $df = 4$, $p < 0.025$)

The 14 hemlocks at HRSNA included three saplings 3-6 m high and 4-7 cm dbh, and 11 canopy trees 11-20 m high and 15-45 cm dbh (Table 9). Calcote (1986) reported that during his study a porcupine damaged a sapling, and foliage of two canopy trees were fed upon: he observed porcupines in these trees on one or more occasions. In the present study, five of the six hemlocks with the largest dbh were fed upon (Table 9). In no instance was there evidence that

Table 9. Height (m) and DBH (cm) of hemlock trees at HRSNA, 1988. Trees indicated "feed" were fed upon by porcupines; those indicated "transect" were counted in the vegetation transects. Tree ID numbers indicate the transect on which the tree was located and the individual.

Tree	Height	DBH	Feed or Transect
301	19	45	feed
803	17	39	feed
606	12	36	feed
308	17	35	feed
Z-line	14	32	------
310	20	31	feed
F-line	18	28	------
D-line	14	25	------
C-line	11	18	------
919	12	17	transect
605	16	15	feed
738	6	7	transect
736	6	6	transect
733	4	4	transect
$\overline{x}$	14.17	26.75	
SD	5.49	12.86	

porcupines used the saplings.

Seasonal Feeding Patterns

At the time the study began in mid-January, about 37% of the season's total sugar maple trunk-bark and about 25% of the total sugar maple limb-bark, already had been removed by porcupines at HRSNA. About 54°s of trunk bark and 18% of limb bark of white pine had been removed by this time (Figs. 2 and 3). For these two species, feeding activity progressed at about the same rate throughout the season (for both species, r^2 for the relationship between sampling period and cumulative proportion bark removal > 0.95).

Bark removal from hemlock was noted initially on 21 February but increased dramatically after 8 April (Fig. 2). Limb feeding on hemlock was noted for the first time on 25 March and increased sharply after 2 April (Fig. 3). Average weekly temperature was above 0°C for the first time that year during the week of 2 April. Therefore, there appeared to be a seasonal shift by porcupines toward use of hemlock coinciding with milder spring temperatures. However, when the amount of bark removed from each species was compared to the amount of weekly temperature change over the 3-month period, there was no significant correlation among any of the three major species used in bark feeding (r = 0.52, 0.55, 0.32 for sugar maple, white

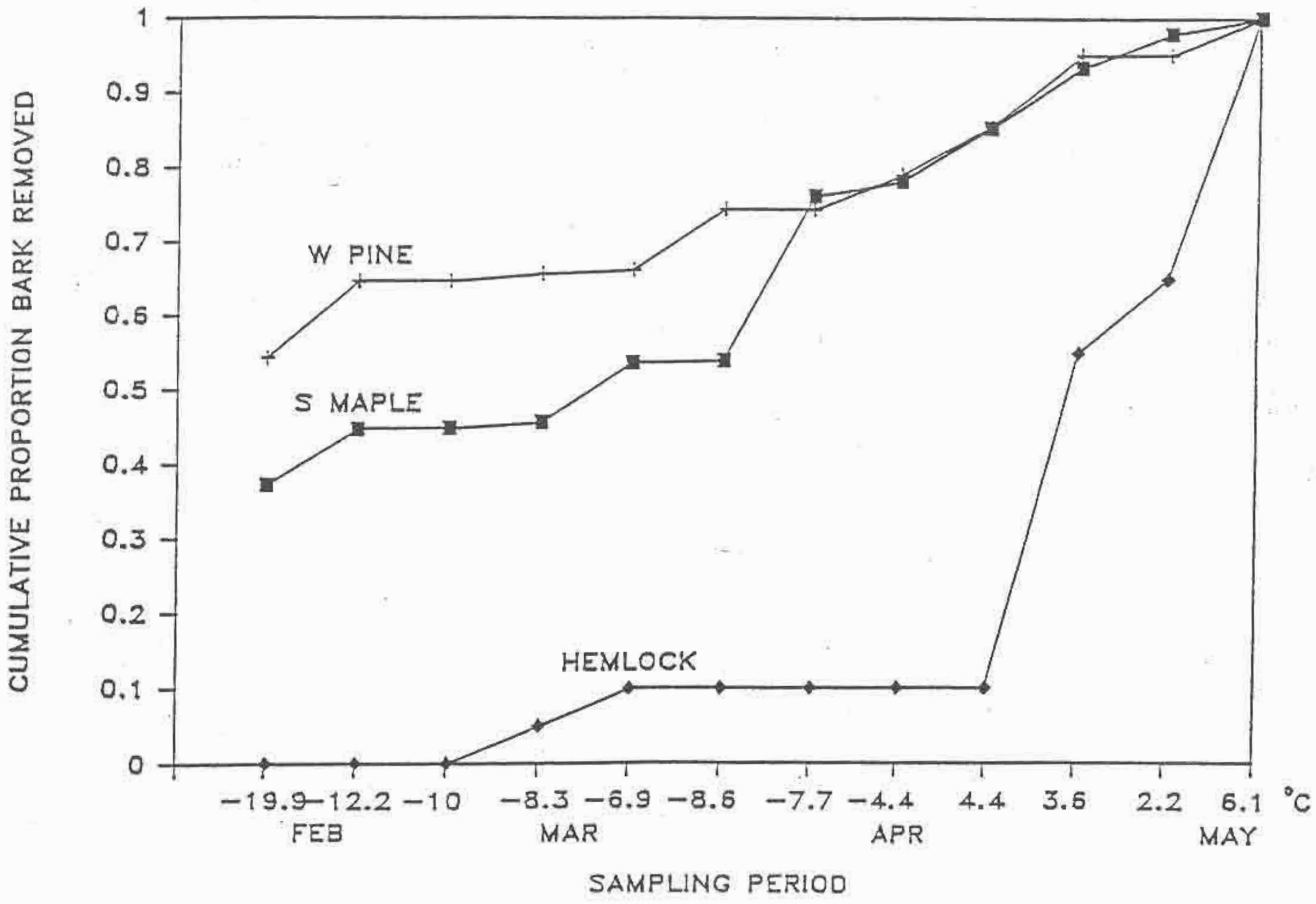


Figure 2. Cumulative proportion of trunk bark removed from major feed-tree species at Hemlock Ravine Scientific and Natural Area, 1988. Data presented are means computed from cumulative removal data for all feed trees of each species plotted against sample period and average weekly temperature (°C).

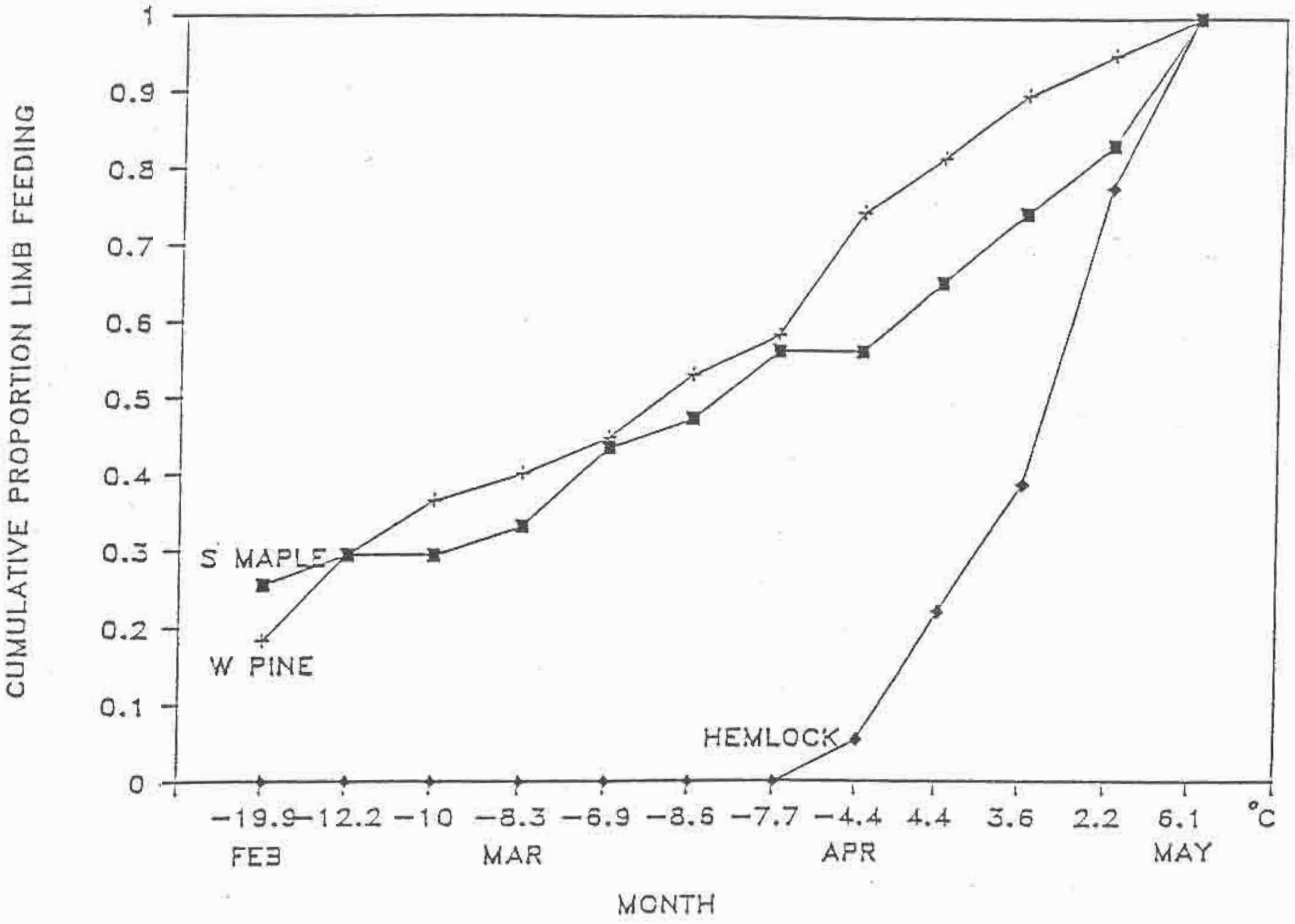


Figure 3. Cumulative proportion of limb-bark feeding on major feed-tree species at Hemlock Ravine and Scientific and Natural Area, 1988. Data presented are means computed from cumulative number of limbs fed upon for all feed trees of each species, plotted against sample period and average weekly temperature (°C).

pine, and hemlock, respectively).

Den Sites and Roost Trees

Five den sites were discovered in HRSNA. One of these seemed to be little more than a temporary shelter beneath a fallen tree, and another, in a hollow log at the top of the east slope, did not appear occupied during the study; there were no fresh feces in it or trails leading directly to it. The other three den sites were occupied during the study; one of these was beneath a large fallen white pine, a second was in a large hole on the midslope, and a third was in a large hollow log. All five dens were on the east slope of the ravine. The maximum number of porcupines observed at one time during the study was three (Table 10). Based on observations of the marked porcupine and the absence of trails leading in and out of the area, three probably is a reliable estimate of porcupine numbers at HRSNA. This yields a density of one porcupine per 6.75 hectares (ha) for the area. Roze (1984) reported about 1 porcupine per 10 ha and Krefting et al. (1962) reported densities of 1 porcupine per 3.9 ha, 0.77 ha, and 1.2 ha in three adjacent study areas.

Porcupines were observed roosting in nine different trees, all of which were used as feed trees (Table 10). Six of the nine roost trees were large white pines, two were large hemlocks, and one was a large white cedar. Five

Table 10. Porcupine locations in HRSNA on a weekly basis from 13 February - 1 May 1988. X = a porcupine located in its den; W = a porcupine located in a white pine; C = a porcupine located in a white cedar; H = a porcupine located in a hemlock. The Ws connected by a dashed line indicate the porcupine was observed in the same white pine tree on successive sampling dates.

	FEB			MAR				APR				MAY
	1	2	3	4	5	6	7	8	9	10	11	12
DEN	X	X					X					
TREE	W---	W		W	W	W		W	H	W		
			W---	W---	W---	W---	W	C				
						H		H				
TOTAL NUMBER OF PORCUPINES	2	2	1	2	2	3	2	3	1	1	0	0

of the nine trees, including one of the hemlocks, were closely associated with den sites. That is, trails led directly between the dens and the roost/feed trees. The mean distance, measured along the porcupine trails, from den to the feed/roost tree was 33.7 m (range = 16-45 m). This measure is comparable to the "mean cruising radius" of Brander (1973) and Faulkner and Dodge (1962), the one-way distance measured from den to feed tree and considered to be the approximate range of activity for an individual in winter. Mean cruising radii in these studies were 8 m and 90 m, respectively. The remaining four roost/feed trees were located on the west side of the ravine, away from den sites. In one of these instances, I believe the porcupine was using the roost tree as a den site or "station tree" (terminology of Curtis and Kozicky [1944]). From this station tree there were a number of trails leading to nearby trees that showed evidence of having been fed upon. Apparently the porcupine ventured out and back to the station tree numerous times, judging by the worn appearance of the trails.

No porcupines were observed in the stand on or after 22 April 1988. However, new feed scars were observed on 1 May, the last sampling date. Maximum temperatures reached the mid-to-upper teens (°C) in the 2 weeks before the animals left the vicinities of roost trees and den sites.

Assessment of Adjacent Habitat

The survey at HRSNA and the adjacent ravine on 22 April indicated that feeding activity was very similar in the two areas. The number of feed trees was comparable in the two areas or possibly less in HRSNA than in the adjacent ravine. There also appeared to be similar relative proportions of feed scars among the species. One porcupine was visible in the adjacent ravine at this time. As no porcupines were observed in HRSNA on this date, it is possible that this individual came from HRSNA.

Other Observations

Porcupines were present in the study area for a number of weeks before mid-January, when the study began, judging by the amount of feeding activity that had already occurred in the area. Roze (1986) reported that den occupancy in the state of New York began on 27 October 1983 and 10 November 1984 and lasted until 5 April of one year and 30 April of another year. Brander (1973) reported that in Michigan, bark consumption was noted on a yellow birch on 20 September while the tree. was fully leaved. "About" October in Michigan, porcupines dispersed into winter habitat, and by mid-October all the porcupines were on a bark diet (Brander 1973). 1 visited HRSNA on 17 October 1988 and found evidence that a den from the previous season was occupied. On that date one porcupine was seen roosting in a large white pine, and white pine twigs on the ground showed evidence of feeding. Bark removal on sugar maple also had already begun before that visit.

T also visited the study site in May 1989: At that time I noted substantial defoliation by twig feeding in a mature hemlock. This tree was one of those used by porcupines as a feed/roost tree during winter 1988. Many branches were pruned and large gaps appeared in the crown: this foliage-feeding was more extensive than any foliage-feeding observed in hemlocks during the study. On this day I also observed a white pine that was fed upon slightly in winter 1988 but had been used extensively for trunk-bark feeding in the following season-(1988-89). I visited HRSNA again in early November 1989. At this time I observed a small (< 10 cm dbh) red oak tree with substantial portions of the trunk bark removed. Only two red oaks were fed upon during the study season and these were very large, mature trees. These observations indicate that porcupines vary their food habits within an area from one season to the next, thus only tentative conclusions about food habits can be drawn from short-term studies.

DISCUSSION

In this study T attempted to draw conclusions about the winter feeding ecology of porcupines in Hemlock Ravine Scientific and Natural Area during the winter and spring of 1988. This area was used by a consistent number of porcupines during the study, had a small, isolated population of eastern hemlocks (a highly desirable food source), and is located close to the edge of the geographical range of many, if not all, of the tree species occurring there (USDA 1960). The practical intent of this study was to determine if porcupines posed a threat to the continued existence of the hemlocks in HRSNA (or if the hemlocks were drawing unusual numbers of porcupines to the area), and additionally, to contribute to the natural history information on this animal, especially in regard to the northern hardwoods-hemlock forest communities in which it resides.

There is much regional variation in porcupine food habits and diet selectivity (Curbs 1941), and for this reason it is difficult to generalize about winter .food habits over the porcupine's range. Roze (1984) noted that, in a particular habitat, porcupines are specialists regarding their choice of winter foods, and show considerable behavioral flexibility in response to local conditions. This behavioral trend was apparent in the porcupines occurring in HRSNA. There are, however, some consistencies in food selection by porcupines in northern hardwood-hemlock forests across the continent. In these forest communities, hemlock often emerges as a highly selected winter food item, often in conjunction with sugar maple, a species frequently associated with hemlock. For example, Roze (1984) recorded a relative preference for hemlock in the Catskill Mountains in New York; hemlock had the highest preference ratio of all species sampled but had the second and third lowest relative density and basal area, respectively, for all tree species. In that study sugar maple had the third highest preference ratio but also had the second and third highest basal area and relative density, respectively. In Upper Michigan, hemlock was the most highly selected winter food relative to the number of trees present; sugar maple was selected with second greatest frequency (Brander 1973). In northeastern Wisconsin, 26 of 54 porcupine stomachs contained a mixture of hemlock and sugar maple in approximately a 2-to-1 ratio. When food preferences were weighted according to relative abundance, hemlock was first and sugar maple third in overall preference (Krefting et al. 1962). In Maine, hemlock and sugar maple were used heavily for bark feeding (Curtis 1941) and in another instance hemlock foliage was preferred above all other food items (Curtis and Kozicky 1944). Curtis and Kozicky (1944) stated that sugar maple bark was a preferred winter food throughout New England. However in the latter two studies it is not possible to determine whether hemlock and sugar maple were positively selected because data on the amount of bark removed and/or twig feeding were not recorded; the information was based on tree counts and casual observation only.

The electivity values and preference ratios for hemlock and sugar maple at HRSNA reflect patterns of diet selectivity similar to those in the above studies. Although the data indicated strong selection only for trunk bark of sugar maple and not other parts of this tree, the porcupines in HRSNA relied heavily on this species. However, porcupines sought and selectively used the hemlock trees at HRSNA for all forms of feeding during the winter and spring of 1988. The animals probably comprehended the location of the 14 mature trees and the saplings with the possible exception of the two trees ("919" and "Z-lane", Fig.1, Table 9) located to the north of the annual stream on the west slope. Six of the other 12 hemlocks were fed upon and at least two of the six were used as roost trees (porcupines were observed in them during the day). The distribution of these six trees (three on the east slope and three on the west slope) indicates that porcupines were familiar with all of the trees in these two areas within HRSNA. The three hemlocks used on the west side of the ravine were separated from one another topographically and were not associated with major feeding on adjacent trees of other species. This indicates further that the porcupines knew the locations of the individual hemlock trees and were not feeding fortuitously on hemlocks in association with other feed trees. The three hemlocks used on the east side of the ravine were among a group of five, hemlocks growing together in association with northern white cedar, white pine, and sugar maple trees that were heavily fed upon. In addition, a large hollow log that served as a den for part of the season also was associated with this area. This den contained an old porcupine. skull indicating that the site was familiar to porcupines in the area. However, it is not known if the presence of the hemlock trees caused the den site to be attractive or the reverse.

The most significant type of feeding on hemlock was foliage feeding (Tables 2-4). Though porcupines positively selected hemlock trunk and limb bark, these forms of feeding appeared to have minimal impact on the individual trees; no complete girdling of the trunk or major limbs was observed. Although many hemlock branches were pruned by porcupines in the 1988 winter season, I did not observe marked defoliation, i.e., there were not observable gaps in any of the crowns of trees used by porcupines. However, in spring 1989 I observed that a porcupine had removed many branches on one or more primary limbs from a hemlock that was-used in the previous season; this resulted in a noticeably sparse crown. This type of feeding may affect the survivial of the tree; Curtis (1941) observed several dead hemlocks that were nearly stripped of foliage. due to repeated porcupine browsing in successive years.

Northern white cedar foliage also was a highly selected winter food in HRSNA as it is in other areas (Curbs and Kozicky 1944 Ferguson and Merriam 1978 Spear and Dilworth 1978). The occurrence of moderate numbers of white cedar in HRSNA may have influenced the presence of porcupines at this site. Perhaps of greater interest in terms of the long-term impact on this area is the extensive use of white pine in all feeding categories (Tables 2-4). In some instances, repeated bark feeding in individual pines during successive years caused either death of the crown or of the entire tree. It is not known whether porcupines have been active at HRSNA for a long period of time or if the amount of activity observed there is a recent phenomenon. However, given the relatively low frequency of occurrence of white pine in HRSNA, and the intensity of porcupine feeding on this species, it seems that porcupine damage may alter the character of the stand through time as the large pines die off. Porcupine feeding in white pine prompted concern for the few remaining old-growth trees in northwestern Minnesota. Tenneson and Oring (1985) found that white pine was the most preferred winter food in Itasca State Park, and that the occurrence of the mature white pines was an important factor in location of porcupine home ranges in that area. It is likely that there was a similar association at HRSNA between large white pines and porcupine home range because the four areas of concentrated activity centered around one (or more) large white pine trees. However, three of these areas also contained active den sites; it is not absolutely clear whether the white pines were the focal point of activity or coincidental with den use.

During the winter of 1988, a minimum of three porcupines inhabited HRSNA; that is, a maximum of three porcupines were observed on a given day. However, it is reasonable to assume that four porcupines used the area. Brander (1973) acknowledged that because porcupines are solitary in winter it is possible to use their sign as a reliable indicator of numbers of individuals. At HRSNA the four areas of concentrated activity associated with large white pines were analogous to the "damage pockets" in a study by Spencer (1964). Damage pockets are areas of concentrated activity that allow one to reliably estimate the number and distribution of porcupines in an area during winter months (Spencer 1964). These pockets may be associated either with den sites or roost trees: at HRSNA three were associated with dens and one with a "station tree" (Curtis and Kozicky 1944). In addition to their association with white pines all four of these areas also were associated with northern white cedar trees, and in the case of the hollow log den, with hemlocks. Curtis (1941) . observed that the percent of gnawed stems on all species decreased with distance from den sites. This situation also applied in HRSNA except that sugar maple stems were fed upon in all portions of the study area.

Paper birch, second in overall species availability at HRSNA, was significantly selected against (Tables 2-4). These results are in accordance with those of other studies in which paper birch was used little or not at all as a food source (Curtis 1941; Curtis and Kozicky 1944; Brander 1973; Speer and Dilworth 1978; Roze 1984; Tenneson and Oring 1985). Perhaps of greater interest is the lack of selection for species such as yellow birch, white spruce, and balsam fir. These species, present in HRSNA, were not used by the porcupines, but are frequently used for feeding in other parts of the range. It is not possible to determine from the statistical methods used whether porcupines in HRSNA are strongly selecting against these species or are indifferent to them, because the $\underline{E}_i$ and preference ratio values for these species are undefined. However, my subjective impression is that porcupines selected against these species in HRSNA.

It is difficult to determine which of the many variables (e.g., nutritional requirements, plant species composition, microclimatic factors, water availability) affect a porcupine as it makes a decision about which food items to select. Models have been developed that attempt to predict vertebrate feeding strategies (e.g., Emlen 1968; Schoener 1971; Westoby 1974; Freeland and Janzen 1974; Ellis et al. 1.976: Senft et al. 1987). Most models of optimal foraging, in particular, require that food dietary items be ranked in terms of energy gained per unit time spent foraging (Schoener 1971). Thus, Schoener (1971) suggested that animals feed in a manner that either maximizes the energy obtained from the diet, or minimizes the time spent foraging. There are, however, instances in which net energy gained may not be the precise goal of a foraging animal. For example, Ellis et al. (1973) suggested that because herbivores consume plant material that is generally abundant but variable between species and/or phenological stages, energy demands may not be associated closely with nutritional requirements. This discrepancy between sufficient energy and insufficient nutrients especially in winter, has been linked to selective harvesting of vegetation by meadow voles (Microtus pennsylvanicus; Grant 1978). It is possible that selective feeding by porcupines also may be linked to a disparity between energy and nutrient requirements. Alternatively, because plant foods are abundant, energy expenditure may not be crucial to an herbivore attempting to satisfy nutritional requirements (Ellis et al. 1973). During winter, porcupines have been observed (e.g, this study: Brander 1973) remaining in the crown of a particular tree for many days at a time, and also travel relatively short distances on the ground. Thus, it appears that energy expenditure is not extensive for individuals of this species in winter. For the porcupine and other herbivores it follows that the necessity of a balanced diet may dictate that these animals underselect foods with the greatest energy yield if these foods are deficient in other nutrients or contain large amounts of toxic compounds (citations in Schoener 1971;.Bryant et al. 1988).

The variety of plant species used by porcupines among different areas, and particularly the selection of plant species with low availability in a forest community such as HRSNA, might be explained by the optimization model of Westoby (1970. This model for generalist herbivores predicts that a food is chosen on the basis of its nutritional qualities rather than on its availability. Therefore, proportions of food in the diet should not correlate directly with availability. The percent use of a species should be inversely related to availability; thus, the less abundant plant species may be used more intensely by a generalist herbivore. Indeed, the electivity values and preference ratios of food items selected by porcupines at HRSNA, particularly those for eastern hemlock, white pine, and paper birch may be reflected in this model.

Of further consideration when interpreting dietary selection is the role of plant secondary compounds. The best measure of food quality may depend more on the absence of secondary chemicals and other negative attributes than on the presence of nutrients (Crawley 1983). Defensive chemicals, in addition to or in conjunction with the need to balance nutritional requirements, force an herbivore to eat a variety of food types and may be the actual basis upon which browsing herbivores select food (Freeland and Janzen 1974). Studies of plant secondary compounds in juvenile versus mature-growth shoots of subarctic woody vegetation revealed a disproportionately large amount of secondary compounds in juvenile shoots; consequently mountain hares (Lepus timidus), when given a choice, consistently fed upon mature-growth shoots (Tahvanainen et al. 1985). Furthermore, relatively slow-growing woody species on resource-limited sites are less palatable to herbivores than fast-growing species that quickly grow beyond the level of herbivore browsing (Coley et al. 1985, Bryant et al. 1983).

Although in the present study data were not collected on secondary compounds of plant species at HRSNA, there is the possibility that the lack of use of certain species (e.g., balsam fir, white spruce, yellow birch) may in part be related to the presence of secondary compounds. Many of the white spruce and balsam fir trees at HRSNA grow on the railroad grade embankment. These trees might accumulate carbon photosynthate in the form of secondary compounds because trees on this site probably were not light-limited but may have been nutrient-limited. Therefore, these trees may store greater amounts of defensive chemicals than trees of the same species growing in more shaded parts of the ravine (see Bryant et al. [1988] and citations therein for a detailed explanation of the occurrence of plant secondary compounds). Additionally, average tree size of white spruce, balsam fir, and yellow birch is smaller at HRSNA than in areas where these or similar species were recorded as porcupine food items (Table 7). If tree size and growth rate indeed affect palatability, this may explain the use of trees significantly larger than the average for the study area. A detailed study of plant secondary compounds of trees growing in HRSNA needs to be done to address these conjectures.

Harder (1980) suggested that porcupines select diets on the basis of plant community structure as opposed to selecting individual plants of certain species present in the community. His ideas may indirectly relate to the foraging theories based on the role of plant chemistry. Specifically, he suggested that porcupines favor a certain size of tree, particularly one in which the tree is exhibiting maximal vigor. Thus, porcupines select areas (communities) in which to reside rather than particular species to feed upon (Harder 1979: 1980). In stands with fairly homogeneous size structure, trees of the appropriate. dimensions would be available for only a short period relative to the forest age; thus, intensity of porcupine use in such an area would be expected to peak and decline. If these assumptions are accurate they might help explain the cyclic occurrence of porcupines over many years in Mesa Verde National Park in Colorado (Spencer 1964). HRSNA has been a protected area only since 1982 and to my knowledge no previous biological surveys have been conducted in this area, therefore, only long-term observation will reveal. whether use of the area by porcupines fluctuates periodically. Porcupines are known to exhibit a strong degree of site tenacity; Curtis (1941) observed five dens in a Massachussetts forest that were occupied for more than 20 years, and Brander (1973) also noted dens that were used year after year in northern Michigan.

In summary, food preferences of porcupines at HRSNA may be explained partly by learned behavior (Jenkins 1980, Bryant and Kuropat 1980) and by palatability of individual trees (Emlen 1973). These factors in turn depend upon associations of plants in the community (Bryant and Kuropat 1980) and on the production of secondary chemicals (Freeland and Janzen 1974; Bryant and Kuropat 1980; Coley et al. 1985; Tahvanainen et al. 1985; Bryant et al. 1988). Porcupines at HRSNA appeared to "sample" the habitat; certain individual trees had very small amounts of bark removed while others were persistently fed upon. This observation is, in accordance with foraging strategy that predicts that an animal must continuously sample a variety of plants while it feeds on a set of "staples" (Freeland and Janzen 1974). Repeated feeding by porcupines on certain trees also has been observed in other studies (Curtis 1941; Shapiro 1949; Van Deusen and Myers 1962; Brander and Steams 1963). However, once a tree is selected and a large patch of bark removed, the porcupine in effect may increase both the palatability and nutritional status of the tree. Baldwin (1934) found that 1 year after the girdling of sugar maple the sugar content in the phloem layer above the scar was 20-300 times that below. Therefore, porcupines may provide themselves with optimum forage and nutrition by altering their food source toward maximum nutrient content.

CONCLUSION

It is apparent from this study that a low frequency of occurrence does not prevent the most desirable food species from escaping selection by a porcupine during winter feeding. The porcupine, though considered a generalist herbivore, is a specialist in terms of the species it selects in an area. Additionally, for a particular tree species, these animals are selective about the individual trees they feed upon. Based on the relative proportions of species used versus their availability, electivity indices, and preference ratios, it appears that porcupines are specializing on food items in HRSNA. However, it is not entirely clear whether porcupines return to the same feed tree areas year after year because of greater nutritional value (or absence of secondary chemicals) of the trees in these areas, or simply because they occur in the vicinities of highly desirable den sites. According to Shapiro (1949), availability of den sites is not of primary importance to porcupines in selection of winter feeding areas. In contrast, Brander (1973) stated that the winter range of porcupines depends on food availability near the den site. It seems intuitive that den sites influence in some way the occurrence of porcupines in an area. The three active dens in HRSNA were spaced approximately equidistant from one another along the slope of the ravine, and separated "nuclei" of feeding activity with relatively little feeding activity in between.

The porcupines at HRSNA appeared to recognize and seek out hemlocks specifically. The relatively high electivity, values and preference ratios support the hypothesis that porcupines preferentially used hemlock trees for food and roosting above that predicted on the basis of this species abundance in the area. However, the impact of porcupine feeding on hemlock was minimal in HRSNA during the winter of 1988 the potential threat that porcupines pose to hemlocks does not appear eminent in HRSNA at this time. Additionally, the hemlocks at HRSNA do not appear to be attracting large numbers of porcupines to this area or radically influencing their behavior, i.e., porcupine densities, the travel distances around den sites, and use of station trees are all comparable to situations in other areas. Yet, a change in the habitat at HRSNA may .occur in a relatively short period of time dud-to porcupine feeding on white pine. This feeding will probably cause substantial decadence in trees of this species unless food preferences change in the coming seasons.

Factors limiting porcupine density at HRSNA remain unknown. Based on comparisons of porcupine densities in other areas, it is probable that the number of porcupines observed at HRSNA is near capacity for the area. Porcupine density at this site is probably limited by the number of suitable den sites and station tree areas in the ravine. It would be interesting to investigate the history of the HRSNA vicinity to determine if the observed winter activity of porcupines in HRSNA is relatively recent. It is possible that human disturbance is somewhat responsible for the amount of porcupine activity in this area. Gill and Cordes (1972) maintained that the elimination of porcupine predators such as fisher (Marten pennanti), mountain lion (Felis concolar), and coyote (Canis latrans) after European settlement caused porcupine numbers to increase in southern

Alberta. It is only recently that porcupines have been feeding in stands of Krummholz limber pine so intensively that the existence of this community in southern Alberta is threatened. If porcupine numbers in HRSNA have increased in recent years then the feeding patterns observed during the winter and spring of 1987-88 could shift with time as the habitat is altered by porcupine activity.

Ideally, the area should be monitored annually for changes in porcupine feeding activity. White pines should be surveyed for damage and for crown or tree mortality, and at the least, each hemlock should be checked for the presence of porcupines and for obvious increases in trunk- and limb-bark removal, and crown defoliation. Also, to ensure successful regeneration of hemlocks in this area, all seedlings should be fenced to eliminate white-tailed deer predation. At present, deer browsing on the small hemlocks appears to pose the greatest threat of all to the continued existence of this tree species in HRSNA.

LITERATURE CITED

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

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

BRANDER, R. B., AND STEARNS, F. W. 1963. Porcupine winter feeding activity in merchantable stands of northern hardwood-hemlock. U.S. Forest Service, North Central For. Exp. Sta., Research Note LS-16.

BRYANT, J. P., AND KUROPAT, P. J. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. Ann. Rev. Ecol. Syst. 11: 261-285.

BRYANT, J. P., CHAPIN, III; F. S., AND KLEIN, D. R., 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40: 357-368.

BRYANT, J. P., TUOMI, J., AND NIEMALA, P. 1988. Environmental constraint of constitutive and long-term inducible defenses in woody plants. pp. 367-389. In Chemical mediation of coevolution (K. C. Spencer, ed.) Am. Institute of Biol. Science, Washington D. C.

CALCOTE, R. R. 1986. Hemlock in Minnesota: 1200 years as a rare species. Unpub. M.S. Thesis. University of Minnesota, 55 pp.

COLEY, P. D., BRYANT, J. P., AND CHAPIN, III, F. S. 1985. Resource availability and plant antiherbivore defense. Science 230: 895-899.

COOK, D. B., AND HAMILTON, W.J. 1957. The forest, the fisher, and the porcupine. J. For. 39: 719-722.

CRAWLEY, M. J. 1983. Herbivory, the dynamics of animal-plant interactions. Studies in Ecology Vol. 10. Univ. of Calif, Press, Berkeley and Los Angeles,

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

CURTIS, J. D. 1944. Appraisal of porcupine damage. J. Wildl. Mgmt. 8:88-91.

CURTIS, J. D., AND E. L. K0ZICKY. 1944. Observations on the caster porcupine. J. Mamm. 25:1137-146.

CURTIS, J. D., AND WILSON, A. K. 1953. Porcupine feeding on ponderosa pine in central Idaho. 'J. For. 41: 339-341.

ELLIS, J. E., WIENS,, J. A., RODELL, C. F., AND ANWAY, J. C. 1976. A conceptual model of diet selection as an ecosystem process. J. Theor. Biol. 60: 93-108.

EMLEN, J. M. 1968. Optimal choice in animals. Am. Nat. 102: 385-389.

EMLEN, J. M. 1973. Ecology: an evolutionary approach. Addison-Wesley Pub, Co. Reading, MA.

FAULKNER, C. E., AND DODGE, W. E. 1962. Control of the porcupine in New England. J. For. 60:I36-37.

FERGUSON, M. A. D., AND MERRIAM, H. G. 1978 . A winter feeding relationship between snowshoe hares and porcupines. J. Mamm. 59: 878-880.

FIENBERG, S. E. 1977. The analysis of cross-classified categorical data. The MIT Press. Cambridge, MA. and London.

FREELAND, W., AND JANZEN, D. H. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. Am. Nat. 108: 269-289.

FRELICH, L. E., AND LORIMER, G. G. 1985. Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. Biol, Conserv. 34: 99-120.

GABRIELSON, I. N. 1928. Notes on the habitat and behavior of the porcupine in Oregon. J. Mamm. 9: 33-38.

GILL, D. AND CORDES, L. D. 1972. Winter habitat preference of porcupines in the southern Alberta foothills. Can. Field-Nat. 6: 349-355.

GRANT, P.R. 1978. Dispersal in relation to carrying capacity. Proc. Natl. Acad. Sci. USA. 75: 2854-2858.

HALL, E. R. 1981. The mammals of North America. 2nd ed. John Wiley and Sons, New York.

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

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

HAZARD, E. 1982. The Mammals of Minnesota. Univ. of Minnesota Press, Minneapolis.

HIX, D. M., AND BARNES, B. V, 1984. Effects of clear-cutting on the vegetation and soil of an eastern hemlock-dominated ecosystem, western Upper Michigan. Can. J. For. Res. 14: 914-923.

JACOBS, J. 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. Oecologia 14: 413-417.

JENKINS, S. H. 1979. Seasonal and year-to-year differences in food selection by beavers. Oecologia 44: 112-116.

JENKINS, S. H. 1980 . Problems, progress, and prospects in studies of food selection by beavers. Pp. 559-579 In Worldwide Furbearer Conference Proceedings, Vol.1 (J. A. Chapman and D. Pursley, eds.). Frostburg, MD

KREFTING, L. W., STOECKELER, J. H., BRADLE, B. J., AND FITZWATER, W. D. 1962. Porcupine-timber relationships in the lake states. J. For. 60: 325—330.

NATURAL HERITAGE PROGRAM. 1984, Hemlock Ravine Scientific and Natural Area resource inventory. Unpub. Report Minnesota Department of Natural Resources. 38 pp.

NOWAK, R. M., AND PARADISO, J. L. 1983. Walker's mammals of the world. Vol, 2: Johns Hopkins Univ. Press, Baltimore and London.

PETRIDES, G. 1972. A field guide to trees and shrubs. Houghton Mifflen Company. Boston, MA

REEKS, W. A. 1942. Notes on the Canada porcupine in the maritime provinces. For. Chron. 18: 182-187.

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

ROZE, U. 1986 Denning and winter range of the porcupine. Can. J. Zool. 65: 981-986.

RUDOLPH, P. 0. 1949. Porcupines' preferences in pine plantations. J. For. 65: 981-986.

SCHOENER, T. W. 1971. Theory of feeding strategies. Ann. Rev. Eco. Syst. 2: 369-404.

SENFT, R.L., COUGHENOUR, M. B., BAILEY, D. W., RITTENHOUSE, L. R., SALA, 0. E., AND SWIFT, D. M. 1987. Large herbivore foraging and ecological hierarchies . BioScience 37: 789-799.

SHAPIRO, J. 1949. Ecological and life history notes on the porcupine in the Adirondacks. J. Mamm. 30: 247-257.

SMITH, W, 1988. Vascular plants. Pp. 33-217 In Minnesota’s endangered flora and fauna (B. Coffin and L. Pfannmuller, eds.) Univ. of Minnesota Press, Minneapolis.

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

SPENCER, D. A., 1946. A forest mammal moves to the farm - the porcupine. Trans. N. A. Wildl. Conf. 11: 195-199.

SPENCER, D. A. 1964. Porcupine population fluctuations in past centuries revealed by dendrochronology. J. Appl. Ecol. 1: 27-149.

STOECKELER, J. H. 1950: porcupine damage in a northern hardwood-hemlock forest of northeastern Wisconsin. U. S. Forest Service, Lake States Forest Expt. Sta. Tech. Note No. 326. 1 p.

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

TAHVANAINEN, J., HELLE,,E., JULKUNEN-TIITTO, R., AND LAVOLA, A. 1985, Phenolic compounds of willow bark as deterrents against feeding by mountain hare. Oecologia 65: 319-323.

TENNESON, C. AND ORING, L. W. 1985. Winter food preference of porcupines. J. Wildl. Mgmt, 49: 28-33.

UNITED STATE DEPARTMENT OF AGRICULTURE,, 1960. Silvics of forest trees of the United States. J. Handbk. No. 271. USDA, Wash. D. C.

UNITED STATE GEOLOGICAL SURVEY, 1983. Topographical map, Esko Quadranqle, Minnesota - Wisconsin. USDI, Wash. D.C.

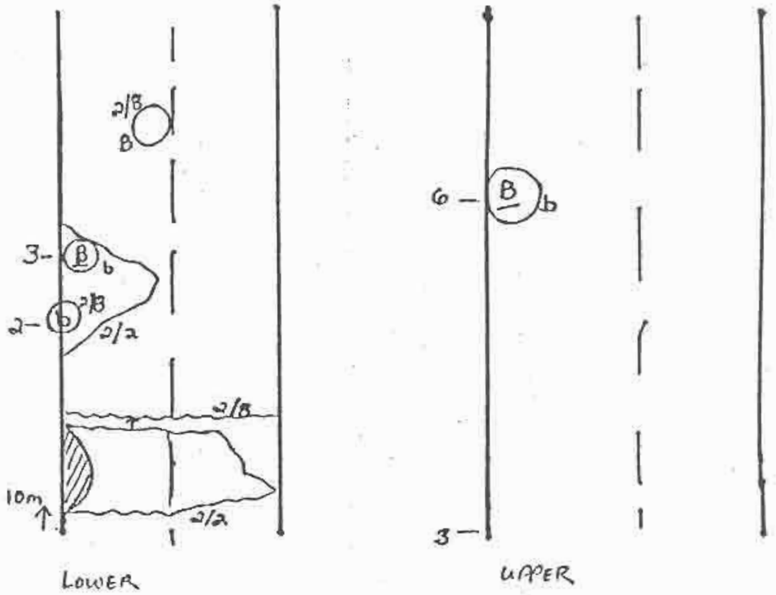
VAN DEUSEN, J. L., AND MYERS, C. A. 1962: Porcupine damage in immature stands of ponderosa pine, in the Black Hills. J. For. 60: 811-813.

WESTDBY, M. 1974. An analysis of diet selection by large generalist herbivores. Am. Nat. 108: 290-304.

Appendix I. Protocol for trunk- and limb-bark feeding data collection.

Species ______ No. ______

FEEDING DATA:



(B̲) = Heavy limb-feeding

(B) = Moderate limb-feeding

(b) = Slight limb-feeding

(B̲)$_B$ = Heavy, with heavy branch-feeding

(B̲)$_{\underline{b}}$ = Heavy, with moderate (b̲)- slight (b) branch-feeding

(b)$_B$ = Slight, with heavy branch-feeding

( )$_B$ = No limb-feeding, heavy branch-feeding

(B̲), Heavy limb-feeding = >50% of bark removed from a primary or secondary limb.

(B), Moderate limb-feeding = 10 - 50% of bark removed from a primary limb.

(b), Slight limb-feeding = Trace - 10% of bark removed from a primary limb.

B, Heavy branch-feeding = 50% of small (< secondary) branches stripped.

b̲, Slight to <u>moderate</u> branch feeding = <10% or 10 - 50% branches stripped.

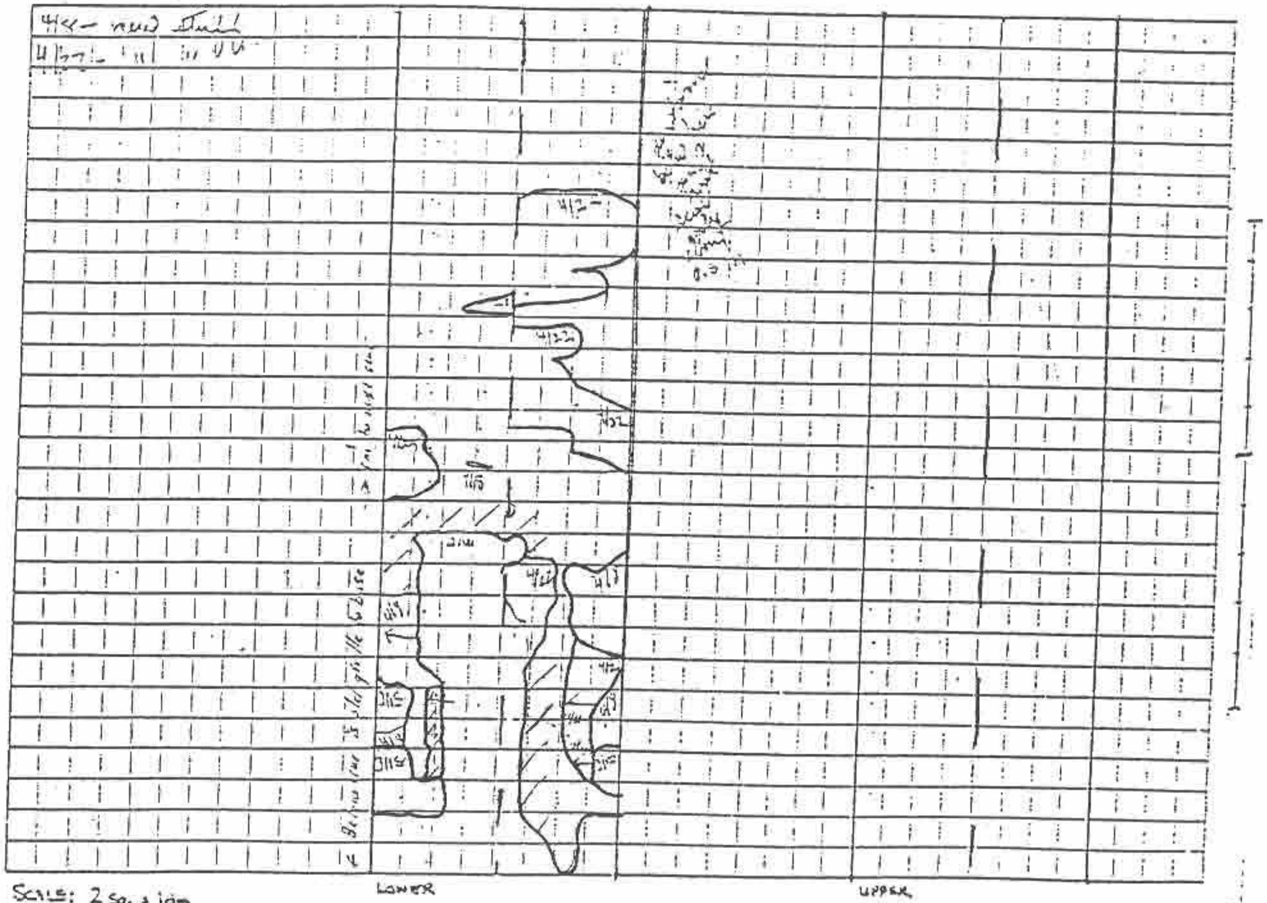
Heavy foliage feeding = Marked defoliation and/or many twigs on the ground.

Slight to moderate foliage feeding = One to a few twigs on the ground, no marked defoliation.

If possible-- Note complete girdling of trunk or main limb.

Appendix II. Sample data sheet for recording trunk and limb bark removal.

Tree sp. ACSA No. 0-5 DATE 1-5-88 (drawn) p. 1 of 2



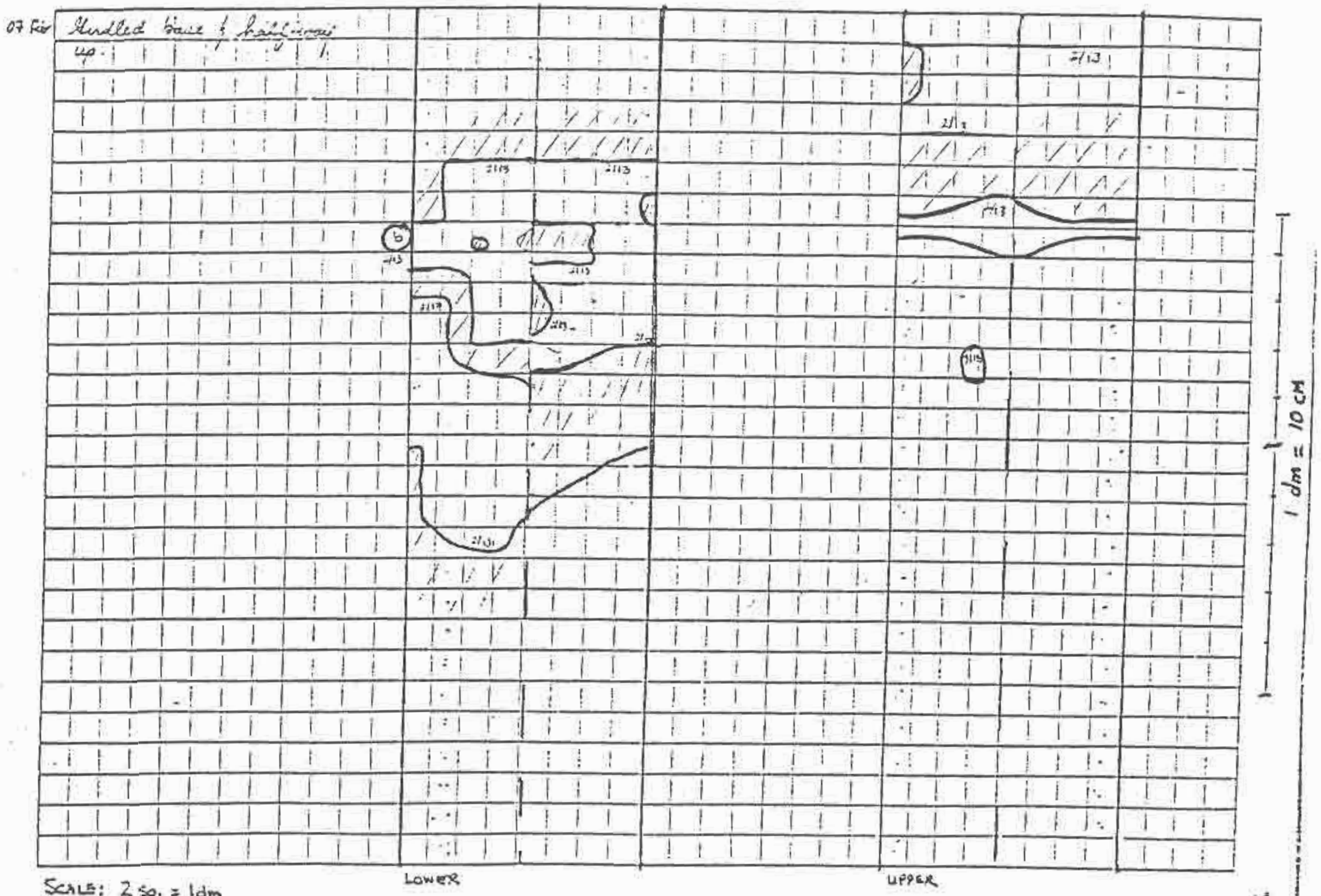
Scale: 2 sq. = 10m

Aspect: 340° — 160°

Aspect: ______ ______

Appendix II (continued)

Tree sp. ACSA No. 8-1 Date 13 Feb 88 (drawn) p. 2 of 2



Girdled base of branches up.

SCALE: 2 sq. = 1dm

Aspect: 340° 160°

Aspect: 340°