PORCUPINE-EASTERN HEMLOCK INTERACTIONS AT HEMLOCK RAVINE SCIENTIFIC AND NATURAL AREA

Final Report to the

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November 1, 1988

INTRODUCTION

The North American porcupine, Erethizon dorsatum, is a large rodent found throughout much of the continent (Hall, 1981). It inhabits boreal forests in the northern and eastern portions of its range. This species is well known for its habit of feeding primarily on the inner bark and branches of trees in winter. Winter feeding by porcupines has important economic impact on valuable timber because scarring, girdling, and pruning of branches may permanently damage or kill trees (Brander and Stearns, 1963; Curtis, 1944; Curtis and Kozicky, 1944; Curtis and Wilson, 1953; Faulkner and Dodge, 1962; Gabrielson, 1928; Krefting et al.,1962; Rudolph, 1949; Shapiro, 1949; Storm and Halvorson, 1967; vanDeusen and Myers, 1962). Winter feeding by porcupines also may have substantial aesthetic impact. 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 occurring as low elevation Krummholz in southern Alberta. Tenneson and Oring (1985) investigated whether porcupine feeding threatened the few remaining virgin white pines in Itasca State Park in northwestern Minnesota. Thus, there has been substantial interest in winter feeding ecology of porcupines.

Eastern hemlock, Tsuga canadensis, is a highly preferred winter food of porcupines over much of the area where the two species co-occur (Brander, 1973; Brander and Stearns, 1963; Curtis, 1944; Curtis and Kozicky, 1944; Krefting et al., 1962; Roze, 1984; Shapiro, 1949; but see Spear and Dilworth [1978] for conflicting information). Eastern hemlock (hereafter, "hemlock") reaches the western-most limit of its range in northern Minnesota, and has been designated a "special concern" species in the state (Smith, 1988). The number of mature trees may be as low as 34; fourteen of these (11 canopy trees and 3 saplings) plus about 100 seedlings are located in Hemlock Ravine Scientific and Natural Area (HRSNA), adjacent to the northwest corner of Jay Cooke State Park in Carlton County, Minnesota. HRSNA is virtually the only site in Minnesota where there is significant hemlock regeneration, and represents the greatest concentration of hemlocks in the state (Calcote, 1986). Because porcupines feed so intensively and extensively on hemlocks in the eastern portion of the range of this tree species, it is important to determine whether porcupine feeding has an important effect on the hemlocks at HRSNA.

The present study was conducted to assess damage by porcupines to the hemlocks in HRSNA and to determine feeding patterns, selectivity for hemlocks and other tree species, and other aspects of the winter feeding ecology of porcupines in this area. This information is perhaps an especially critical prerequisite to porcupine management at special designation sites, where controlling porcupines by killing may not be compatible with conservation values.

STUDY AREA AND METHODS

Porcupine Transects. Preliminary surveys of the area and transect location began in mid-January 1988. Eight transects, four on either side of the ravine, were marked with flagging. Transects were spaced so the entire area could be surveyed for porcupine feeding activity: one transect was placed on either side of the ravine across the level top slope well away from the ravine edge, two transects were placed on the midslope, and one transect was placed on the bottom slope along the creek on either side of the ravine. The total length of the eight transects was approximately 1800 meters. Topography and, to a lesser extent, such obstacles as windthrown trees determined transect placement.

Transects directly intercepted 7 of the 14 mature hemlocks. Unfortunately, 2 adult hemlocks and 3 saplings grow in a steep side-ravine with numerous hemlock seedlings scattered about. These transects were abandoned when it became apparent that walking on this slope could cause erosion detrimental to hemlock regeneration. Thus, these 5 hemlocks as well as two other mature hemlocks growing independently on the northwest slope of the main ravine were spot-checked regularly for signs of feeding activity and porcupines.

Data were collected weekly from 31 January 1988 to 1 May 1988. The objective was to walk all eight transects at least every two weeks, observing and flagging feed trees, drawing scars of bark removal, noting presence on the ground of gnawed twigs and branches, and searching for den sites and porcupines. Feed 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 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. Limb feeding was designated slight (<10% bark removal), moderate (10-50% bark removal), and heavy (>50% bark removal). Twig feeding was noted as slight, moderate, or heavy on a subjective scale depending on the amount of accumulation beneath the feed tree. Deer frequently feed on twigs dropped by porcupines (Shapiro, 1949). Trees also were considered feed trees if 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. We attempted to mark porcupines with spray paint and succeeded in marking one individual with orange on the right rear flank. Other porcupines when located were either high in trees and inaccessible or marking was confounded by frozen paint.

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 previous feed scars was noted.

Assessment of Adjacent Habitat. On 22 April 1988 a survey of the ravine adjacent to HRSNA was done 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. To calculate preference ratios and electivity indices a survey of vegetation in the ravine and adjacent top slopes was conducted. Sample plots 10 m long and 6 m wide centered on the porcupine transects were located at 20-m intervals for the entire length of each of the eight transects (Roze, 1984). In addition to the porcupine transects, a vegetation transect was located in the previously abandoned side ravine. Vegetation also was sampled on the opposite side of this ravine and midslope along the northwest side of the main ravine where previously only spot-checking was conducted of the hemlocks located there. Every tree >3 cm dbh was measured with a dbh tape. Tree heights were estimated to the nearest 1 m and occasionally a clinometer was used to check accuracy of estimates. No "shrubs" >3 cm (e.g. mountain maple, alder) were included in the survey; there was no indication that porcupines fed on bark or twigs of these plant species.

Data Analysis. Surface area of bark removed was calculated based on the area of a cylinder; no adjustment was made for taper. 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 were calculated as:

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

where ri= the proportion of food type i in the diet and pi= the proportion of type i among foods available. A positive electivity value indicates selection for a food item, a negative electivity value indicates selection against a food item. Preference ratios were calculated as r_i/p_i. A preference ratio greater than one indicates selection for a food item and a ratio less than one indicates selection against a food item. Jacobs (1974) shows that the electivity index may be more appropriate than the preference ratio, ri/pi, when available food types differ in abundance.

RESULTS AND DISCUSSION

Feeding Preferences. In the ravine and adjacent top slopes porcupines utilized sugar maple (*Acer saccharum*) and white pine (*Pinus strobus*) with greatest frequency (Table 1). Other studies have shown sugar maple to be a preferred winter food (Brander, 1973; Curtis, 1944; Curtis and Kozicky, 1944; Krefting et al., 1962; Shapiro, 1949). White pine is apparently utilized less frequently, but a high incidence of white pine feeding was found in studies around the Lake states (Curtis, 1944; Tenneson and Oring, 1985) and in New Brunswick (Speer and Dilworth, 1978). In these studies sugar maple tends to be high in availability and white pine relatively low

Table 1. Availability of tree species and use as feed trees by porcupines at HRSNA, February-May 1988. Data are proportion of all trees sampled in vegetation transects and of all feed trees, respectively.

Species	Available	Used
Sugar maple *Acer saccharum*	0.396	0.469
White pine *Pinus strobus*	0.010	0.290
White cedar *Thuja occidentalis*	0.061	0.146
Eastern hemlock *Tsuga canadensis*	0.006	0.062
Yellow birch *Betula lutea*	0.087	0.021
Red oak *Quercus rubra*	0.021	0.010
White birch *B. papyrifera*	0.128	0
White spruce *Picea glauca*	0.102	0
Aspen *Populus* sp.	0.076	0
Balsam fir *Abies balsamea*	0.059	0
Ironwood *Ostrya virgiana*	0.044	0
American basswood *Tilia americana*	0.010	0
	n=609	n=96

in availability, as is the case at HRSNA (Table 1). Sugar maple occurred in the diet in proportions roughly the same as its occurrence in the study area. Conversely, white pine occurred in the diet much more frequently than its availability would have indicated (Tables 1 and 2). The electivity values and preference ratios for these two species indicate weak selection by porcupines for sugar maple and very strong selection for white pine (Table 3).

Hemlock made up a very small proportion of overall tree availability (Table 2). Electivity values and preference ratios for hemlock were second highest for the six species utilized as food (Table 3). Therefore, even though feeding appeared slight relative to that of white pine and sugar maple, porcupines selected hemlock as a food source with a frequency far exceeding its proportional occurrence in the area. It should be emphasized, however, that even though the preference ratios and electivity values are high, the amount of damage done to hemlocks at HRSNA was miniscule (details below). From an ecological point of view these values are of interest in that they indicate that porcupines are able to preferentially seek out certain foods as opposed to feeding at random in an area.

Feeding activity was recorded in three categories: trunk bark removal (bark feeding), primary and secondary limb-bark removal (limb feeding), and twig feeding. Sugar maple accounted for 65% of the bark feeding while white pine accounted for 24% of bark feeding (Table 2). In some instances, bark feeding was so pronounced that substantial portions of boles (maple) or crowns (pine) appeared stripped of bark. For maples, the average amount of bark removal was about 4% (Table 4). However, as much as 24% of trunk bark was removed per individual tree. White pine averaged about 1% trunk bark removal with a maximum of 3%. Most of this bark removal was in the crown, concentrated in a relatively small area of the

Table 2. Species distributions of feed trees at HRSNA. Proportions are frequencies of occurrence of feed-tree species in vegetation transects (available) and of all feed trees, trunk-bark-fed trees, limb-bark fed trees, and twig-fed trees.

	Proportion				
Species	Available	Total Feed	Bark Fed	Limb Fed	Twig Fed
Sugar maple	0.396	0.469	0.652	0.450	0
White pine	0.010	0.292	0.239	0.433	0.513
White cedar	0.061	0.146	0	0	0.351
Eastern hemlock	0.006	0.062	0.065	0.067	0.135
Yellow birch	0.087	0.021	0.043	0.033	0
Red Oak	0.021	0.010	0	0.017	0

Table 3. Preference ratios and electivity indices for total feeding, bark feeding, limb feeding, and twig feeding by porcupines at Hemlock Ravine Scientific and Natural Area during winter 1987-88.

Species	Total use	Bark feeding	Limb feeding	Twig feeding
Preference Ratios				
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
Yellow birch	0.24	0.49	0.38	0
Red oak	0.48	0	0.81	0
Electivity Indices				
Sugar maple	+0.298	+1.052	+0.223	-----
White pine	+3.723	+3.453	+4.342	+4.664
White cedar	+0.970	-----	-----	+3.163
E. hemlock	+2.311	+2.356	+2.380	+2.125
Yellow birch	-1.500	-0.740	-1.017	-----
Red oak	-0.728	-----	-0.252	-----

Table 4. Species, number, height (m), and DBH (cm) of all porcupine feed trees and trunk-bark feed trees at Hemlock Ravine Scientific and Natural Area, February-May 1988, and estimated proportion of trunk bark removed by porcupines. Computation of proportional bark removal described in text. Height, DBH, and proportion bark removal are means and standard deviations.

	All Feed Trees			Trunk-Bark Feed Trees			Proportion Trunk Bark Removed
Species	Number	Height	DBH	Number	Height	DBH	
Sugar Maple	45	10.9 ± 3.4	15.5 ± 11.1	30	10.7 ± 2.7	13.4 ± 4.5	0.039 ± 0.064
Yellow Birch	2	12.5	18.5	2	12.5	18.5	0.031
White Pine	28	21.5 ± 7.4	49.4 ± 17.2	11	22.1 ± 8.8	44.3 ± 16.3	0.011 ± 0.012
Red Oak	1	23	54	--	----	----	---
White Cedar	14	11.1 ± 2.3	29.4 ± 11.0	--	----	----	---
Hemlock	6	17.5 ± 1.8	33.5 ± 11.2	3	18.3 ± 2.6	30.3 ± 18.4	0.005 ± 0.005

tree. Hemlock had only 0.5% of the trunk bark removed, with a maximum value of 0.9% on any one tree.

Limb feeding was divided about equally between sugar maple and white pine (Table 2). Again, bark removal was so complete in some instances that entire limbs appeared devoid of bark. White pine had the highest average number of limbs fed upon per tree; however, 88% were in the "light" category (Table 5). Hemlock had an average of 4.5% of limbs fed upon, but a substantial proportion of these were in the "moderate" category. An average of only 1.2 branches per hemlock tree were fed upon moderately and no branches were fed upon heavily.

Twig feeding was heavily weighted in favor of white pine (Table 2). In several instances, twig feeding was the only feeding observed in a particular pine. In these cases the crown appeared noticeably defoliated. White cedar (Thuja occidentalis) accounted for 35% of twig feeding, but no bark removal was noted for cedar. Hemlock accounted for 13% of twig feeding; this type of feeding on twigs, rather than trunk or limb bark, was proportionately most common for this species. The preference ratios supported this; the electivity values, however, indicated that selectivity for twigs as a food source is less than that for other types of feeding on hemlocks (Table 3).

White spruce (Picea glauca) and balsam fir (Abies balsamea), although common at HRSNA, never appeared in the diet. This constrasts with results from other studies, in which one of these two conifers was used slightly (Curtis and Kozicky, 1944; Krefting et al., 1962; Shapiro, 1949; Tenneson and Oring, 1985) or abundantly (Speer and Dilworth, 1978). Likewise, two species (Betula lutea and B. papyrifera) which appeared very infrequently or not at all in the diet of porcupines at HRSNA, but occurred frequently in the vegetation sampling, are known to be preferred food in other areas (Curtis and Kozicky, 1944; Shapiro, 1949; Krefting et

Table 5. 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.

Species	Number of trees	Mean number of branches per tree: 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
Yellow 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
Hemlock	4	3.2±4.6 (0.57±0.54)	1.2±1.4 (0.43±0.54)	0	4.5±4.7

al., 1962). Several other deciduous tree species on the area showed no indication of feeding by porcupines (Table 1).

The fourteen hemlocks at HRSNA consist of 3 saplings ranging from 3-6 m high and 4-7 cm dbh, and 11 canopy-size trees ranging from 11-20 m high and 15-45 cm dbh (Table 6). Calcote (1986) reported that during his study a porcupine damaged a sapling and that two of the canopy trees were twig-fed upon and porcupines were observed in these trees on one or more occasions. In the present study, 5 of the 6 hemlocks with the largest dbh were fed upon (Table 6). Five of the six also had some bark removed, either on the trunks or primary limbs, although this removal was slight relative to the size of the tree, and relative to bark removal on other tree species (Tables 4 and 5). In no instance was there evidence that porcupines utilized the saplings.

Considering all feed trees, the average size classes for sugar maple and white cedar were slightly greater than the average size for these two species in the area. White pines used as feed trees had an average diameter about 10 cm greater than the average for white pines in the area (Tables 4 and 7). Average size classes of feed trees with only trunk-bark removal were also above the average for the area, although these differences are not as great as for all feed trees of these species.

At the time the study began in mid-January the porcupines had removed about 30% of the bark on trunks and limbs of sugar maple and about 20% of the bark on trunks and limbs of white pine (Figures 1 and 2, p. 16). For these two species feeding activity progressed at about the same rate throughout the season. Bark removal on hemlock was noted initially on 21 February but did not increase dramatically until after 8 April. No limb-feeding was noted before 25 March at which time it increased very rapidly. Therefore, there appeared to be a seasonal shift by porcupines toward use of hemlock coinciding with milder spring temperatures.

Table 6. Height (m) and DBH (cm) of hemlock trees at HRSNA, 1988. Trees indicated "feed" were fed upon by porcupines; those indicated "veg" were counted in the vegetation transects.

Tree	Height	DBH	Feed or Veg
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	veg
605	16	15	feed
738	6	7	veg
736	6	6	veg
733	4	4	veg
x	14.17	26.75	
SD	5.49	12.86	

Table 7. Species, number, height (m), and DBH (cm) of all trees occurring in the vegetation transects at Hemlock Ravine Scientific and Natural Area during the winter 1987-88 season. Height and DBH are means and standard deviations.

Species	Total	Height	DBH
Balsam fir	36	7.69 ± 4.29	9.53 ± 5.33
Sugar maple	241	8.83 ± 3.63	9.79 ± 8.16
Yellow birch	53	10.25 ± 4.36	15.92 ± 14.06
White birch	78	14.69 ± 2.98	18.64 ± 7.05
Ironwood	27	9.78 ± 5.72	12.37 ± 9.11
White spruce	62	9.89 ± 6.68	15.47 ± 12.93
White pine	6	20.00 ± 8.46	38.17 ± 19.86
Aspen	46	9.07 ± 5.48	9.93 ± 8.51
Red oak	13	12.31 ± 4.87	20.85 ± 18.78
White cedar	37	11.38 ± 3.91	24.43 ± 11.17
Eastern hemlock	4	7.00 ± 4.00	8.50 ± 6.70
American basswood	6	7.33 ± 2.26	6.00 ± 2.30

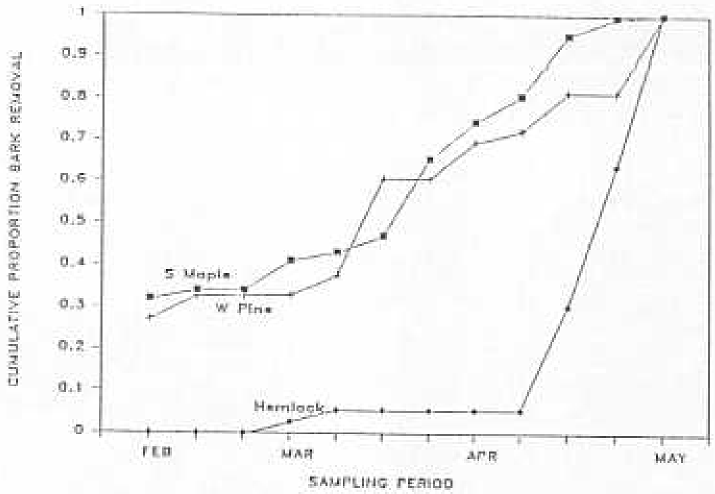

Fig. 1. Cumulative proportion of trunk bark removed over time from major feed-tree species at Hemlock Ravine Scientific and Natural Area, 1988. Data presented are means computed from cumulative removal data for all feed trees of each species.

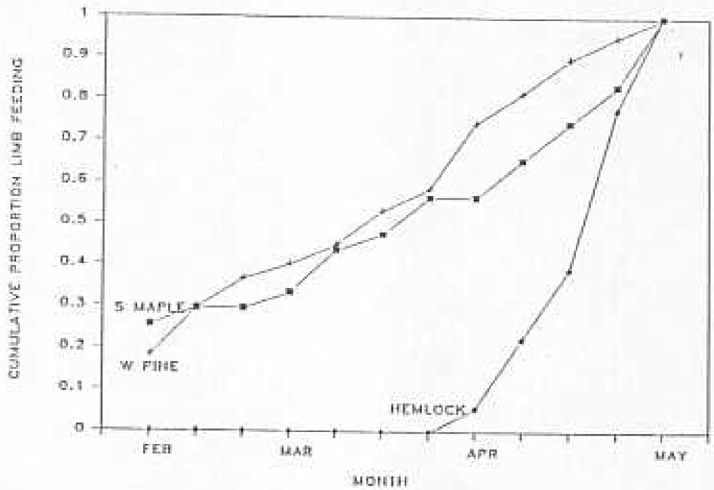

Fig. 2. Cumulative proportion (over time) of limb-bark feeding on major feed-tree species at Hemlock Ravine Scientific and Natural Area, 1988. Data presented are means computed from cumulative number of limbs fed upon for all feed trees of each species.

Den Sites and Roost Trees. Five den sites were discovered in HRSNA. One of these appeared to be little more than a temporary shelter beneath a fallen tree and another, in a hollow log on the eastern top slope, did not appear occupied during the study, i.e., 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 side of the ravine. The maximum number of porcupines observed on any given day was three. Based on observations of the marked porcupine and the absence of trails leading in and out of the area, we believe that three is a reliable estimate of porcupine numbers at HRSNA. This gives 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 utilized as feed trees. Six of the nine roost trees were large white pines, two were large hemlocks, and one was a large white cedar. Five of the nine trees including one of the hemlocks were closely associated with den sites. That is, trails led directly to and from the dens to the roost/feed trees. Four of the roost trees were located on the western side of the ravine, away from den sites. In three of these instances, we believe the porcupine was utilizing the roost tree as a den site or "station tree" (terminology of Curtis and Kozicky [1944]). The average distance from den to the feed/roost tree = 33.7 m (range = 16-45m). 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.

Porcupines had been present in the stand for some time during winter 1987-88, judging by the amount of feeding activity (bark removal) that had occurred before the initial survey of this study in mid-January. 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). We visited HRSNA on 17 October 1988 and found evidence that one of last year's dens was occupied. 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 had already begun before that visit.

No porcupines were observed in the stand on or after 22 April 1988. Maximum temperatures had climbed to the low 60^{o}'s F range for the two weeks before the "disappearance" of the animals.

Assessment of Adjacent Habitat. The single-day survey at HRSNA and the adjacent ravine 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 there is a possibility that this individual came from HRSNA. There is no indication that the presence of the hemlocks in HRSNA attracts large numbers of porcupines into this localized area.

CONCLUSIONS AND RECOMMENDATIONS

There is much regional variation in porcupine food habits and preferences (Curtis, 1944). Porcupines appear to be able to utilize a wide variety of tree species in winter depending on the ecosystem type in which they occur. Within these ecotypes, however, porcupines are specialists in regards to their preferred foods (Roze, 1984). Their ability to seek out preferred foods seems to rest on a combination of "sizing up" trees on the basis of physical features (Harder, 1979) and through olfaction (Murie, 1926; Taylor, 1935). Although the precise mechanism by which a porcupine perceives its environment is not known (see

Senft et al.[1987] for discussion on large herbivore foraging strategies) the fact that it indeed discriminates between food items is well documented. In particular, frequency of occurrence and abundance do not prevent the most desirable food types from escaping selection even if those types are scarce in an area (Curtis, 1944; Roze, 1984). Speer and Dilworth (1979) reported that in 70% of porcupine feeding areas, bark was removed from one species only. Not only are porcupines specialists in terms of preferred species in an area but, for a particular tree species, they are selective about the individuals they feed upon. Curtis (1944) noted that porcupines in his study area returned year after year to the same trees, particularly larch (Larix laricina), eastern hemlock, and sugar maple. This feed-tree fidelity also was documented by Shapiro (1949) and Brander (1973).

This situation appears to prevail at HRSNA. Based on the relative proportions of species used versus their availability, preference ratios, and electivity values, it indeed appears that porcupines are specializing on food items in this area. Porcupines at HRSNA also used the same individual trees year after year as was evidenced by the presence of old scars on the majority of feed trees and by the fact that this year's feeding activity had commenced on last year's feed trees. It appeared as though porcupines travelled about the area "testing" different trees for palatability as there were many occurrences of trees with only small bits of bark removed. However, it is not clear whether porcupines return to the same feed trees year after year because of the higher nutritional value of those trees or simply because they occur in the vicinity of a highly desirable den site. Based on the observations of the marked individual in HRSNA we believe that nutritional quality may be the critical factor. This individual travelled 45 m from its den to the white pine feed/roost tree that it used for at least six weeks, by-passing in its course at least two white pines of comparable height and dbh. Also a porcupine that used the "station trees" on the western slope of the ravine where there were no den sites chose the large pines which showed heavy scarring from previous years, further indicating that den site alone does not account for feed tree selection. However, it is not known what other factors, e.g., microclimatological conditions in the various tree crowns, might be of importance in porcupine selection of feed/roost trees.

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 are spaced approximately equidistant from one another along the slope of the ravine. Interestingly, all three dens also are located at about the same contour on the slope. These three den sites appear to separate "nuclei" of activity with little or no evidence of feeding activity in between. Additionally, one of the dens contained an old porcupine skull, another indication that porcupines use the same dens year after year. Den-site fidelity has been documented by Shapiro (1949), Brander (1973), and Roze (1986).

The porcupines at HRSNA appeared to specifically seek out hemlocks. Hemlocks on the western side of the ravine, distant from den sites, also were fed upon, suggesting that porcupine use of hemlocks is not merely coincidental with use of den sites. The relatively high electivity values and preference ratios support the hypothesis that porcupines recognize hemlocks in HRSNA and preferentially use them as feed and roost trees above what their abundance in the area would predict. However, the impact of porcupine feeding on hemlock is minimal in HRSNA; means and extremes of trunk and limb bark removal were considerably less than from sugar maple and white pine. Thus it is apparent that porcupines have a much greater impact on sugar maple and white pine than on hemlocks in this area.

The winter feeding activity of porcupines at HRSNA is quite similar to that observed elsewhere in the eastern portion of the range. The high selectivity for hemlock, white pine, and sugar maple, as well as travel distances around den sites, utilization of station trees, and porcupine densities in HRSNA are all comparable to situations in other areas. The hemlocks at HRSNA do not appear to be attracting large numbers of porcupines to this area or radically influencing their behavior. Factors limiting porcupine densities at HRSNA remain unknown. It is possible that numbers of porcupines observed at HRSNA are near capacity for the area and that densities are limited by the number of suitable den sites and station tree areas in the ravine.

It remains unclear why particular large white pines in HRSNA are not utilized as a food source. Porcupines are potentially capable of altering the character of the habitat at HRSNA over time, as crowns of the large white pines die due to repeated porcupine girdling (indeed, there is at least one white pine at HRSNA that has been severely girdled and is dying). As porcupines damage the white pines further it is possible that utilization of the remaining large white pines will occur or that dietary preferences will shift to other conifers (including hemlock) or to other hardwood species such as white birch.

Gill and Cordes (1972) maintained that the elimination of potential porcupine predators such as the fisher (*Martes pennanti*), mountain lion (*Felis concolor*), and the 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 is threatened. It would be interesting to investigate the recent natural history of the

HRSNA vicinity to determine if the observed winter activity of porcupines in the ravine is relatively recent. It is not known whether human disturbance has been a factor in recent porcupine occurrence at HRSNA. Therefore, it is not known whether feeding patterns observed last winter are relatively stable. If porcupine numbers have increased in recent years then the feeding patterns observed last winter could shift with time as the habitat is altered by porcupine activity.

We hesitate to draw sweeping conslusions about porcupine winter feeding ecology in an area based on one season's observations. Because it is unknown whether feeding activity observed during winter 1988 represents either year-to-year or long-term patterns, it seems important to periodically monitor the area for changes in porcupine feeding preferences. We recommend that when assessing future activity in this area, each hemlock be checked for the presence of porcupines and for obvious increases in bark and/or limb feeding. We also recommend that the white pines be surveyed for damage and for crown or tree mortality caused by porcupine girdling.

There appeared to be a shift by porcupines into the hemlocks when maximum weekly temperatures rose to about 32^{o}F. This sub-seasonal shift in feeding pattern has not been noted in the literature. This pattern suggests that future surveys should not take place before mid-March or April to avoid inaccurate assessments of porcupine use of hemlocks at HRSNA. The concentration of porcupine activity late in the season suggests that it may be feasible to monitor porcupine impact on hemlock at this site by a single late-season survey, rather than by a winter-long study.

LITERATURE CITED

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 F. W. Stearns. 1963. Porcupine winter feeding activity in merchantable stands of northern hardwood-hemlock. U. S. Forest Service, North Central For. Exper. Sta., Research Note, LS-16.

Calcote, R. R. 1986. Hemlock in Minnesota: 1200 years as a rare species. M.Sc. thesis, University of Minnesota, 55 pp.

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

Curtis, J. D., and E. L. Kozicky. 1944. Observation on the eastern porcupine. J. Mamm. 25:137-146.

Curtis, J. D., and A. K. Wilson. 1953. Porcupine feeding on ponderosa pine in central Idaho. J. For. 41:339-341.

Faulkner, C. E., and W. E. Dodge. 1962. Control of the porcupine in New England. J. For. 60:36-37.

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

Gill, D., and L. D. Cordes. 1972. Winter habitat preference of porcupines in the southern Alberta foothills. Can. Field-Nat. 86:349-355.

Hall, E. R. 1981. The Mammals of North America. 2nd ed. John Wiley and Sons, New York. 1:1-600 and 2:601-1181.

Jacobs, J. 1974. Quantitative mreasurement 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 Conf. Proc. (J. A. Chapman and D. Pursley, eds.). Frostburg, Maryland, vol. I.

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

Murie, O. J. 1926. The porcupine in northern Alaska. J. Mamm. 7:109-113.

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. O. 1959. Porcupines' preferences in pine plantations. J. For. 65: 740-743.

Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. Biosci. 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. Minnesota Press, Minneapolis, 473 pp.

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

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

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

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