THE ROLES PORCUPINE (*Erethizon dorsatum*) POPULATIONS WITHIN A HUMAN DOMINATED LANDSCAPE

by

Joseph F. Mudge

Acadia University

March, 2005

Acknowledgments

This research was funded through a research grant from the Nova Scotia Habitat Conservation Fund and an Acadia Summer Honours Research Award. I would like to express special thanks to everyone who helped me with project design and data collection at the Morton Centre, especially Cate Trueman and Rebecca McQuaid. I would also like to thank Ron Hrushowy for his dedication to the Morton Centre and students who work there. Thanks to my supervisor, Dr. Soren Bondrup-Nielsen for his guidance and support throughout this entire process. The 2004 Environmental Science 1013 class deserves thanks for helping with sampling the exclosures. Thanks also to Marcena Croizier for helping me with Corel at the last minute.

Table of contents

List of tables

List of figures

Abstract

The winter feeding of North American porcupines over several years can also significantly influence the structure and composition of the surrounding forest. Porcupines were found to increase the structural diversity of both the canopy and understory layers of the forest. In human-dominated landscapes, however, the foraging of porcupines is not restricted to the forest, where their impacts typically go unnoticed by most people. Porcupines are often very destructive to various forms of vegetation either planted or growing naturally on people's properties. A survey of local residents shows that local attitudes towards porcupine populations are highly based on the short-term effects of these herbivores on plants, rather than their long-term effects on the surrounding forest ecosystem.

1 – Introduction

1.1 - Study area

This study was undertaken at the Morton Centre, on Heckman's Island, near Lunenburg, on the South Shore of Nova Scotia, Canada. Heckman's Island is connected to the mainland by a small bridge not more than 15 m long and there are over 100 residences on the island. Approximately half of these residences are summer cottages; the other residences are permanent dwellings. The property of the Morton Centre is 40 ha (hectares), approximately half of which is forested while the other half is hayfield and pasture land. The Morton Centre also has almost 2 km of coastline and a small amount of bog and salt marsh systems. The forest at the Morton Centre was logged extensively from the 1940's through the 1960's and can be considered secondary Acadian forest. Primary tree species in the forest are balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), white spruce (*Picea glauca*), and white birch (*Betula papyrifera*).

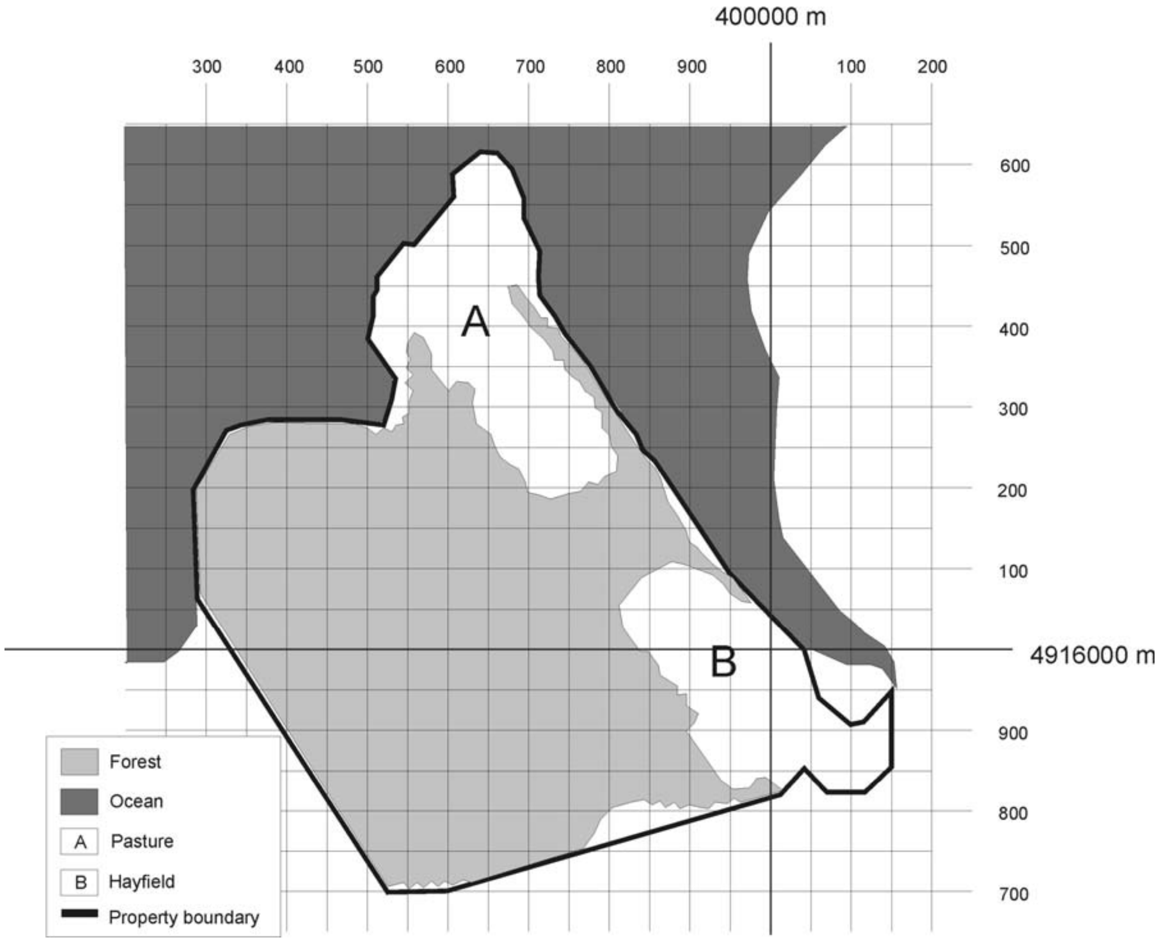

Figure 1: Map of the Morton Centre property showing the forest, hayfield and pasture (Modified from Greene 2003)

1.2 - Herbivory in forest ecosystems

All forms of herbivory combined are seldom responsible for consuming more than 10% of primary production in forest ecosystems (Perry 1994). This is certainly smaller than the 30-60% of the aboveground vegetation commonly consumed by herbivores in grassland ecosystems and far smaller than many aquatic systems where nearly all of the plants and algae produced are consumed by herbivores (Ricklefs, 1997). Although this 10% of forest vegetation consumed may contain valuable reproductive organs, the daily consumption of plant material by herbivores does not generally alter plant communities to any great extent.

Invertebrates, birds, and mammals make up the majority of the herbivores in forest ecosystems. Invertebrates are the most significant consumers of plant material in forest ecosystems. The high reproductive rates, high specialization and high diversity of feeding strategies among invertebrate species make them very efficient at consuming virtually any plant material that can provide nutrition. For this reason, invertebrates have been able to extend into every conceivable available herbivorous niche within forests. Despite their widespread occurrence within forests, it is only the large cyclic or eruptive outbreaks of herbivorous forest invertebrates that tend to reshape forest structure and composition. This is true not only for herbivorous forest invertebrates but for any forest herbivore.

The fact that invertebrates tend to consume the highest amounts of plant material in forest ecosystems does not mean that they are the only important forest herbivores. Larger, mammalian herbivores also have important influences on the plant communities of present and past forest ecosystems. The megaherbivores that roamed North America during the Pleistocene are postulated to have had major impacts on forest ecosystems and their extinction at the end of the Pleistocene is thought to have radically changed the composition of North American Forests (Owen-Smith 1987).

Perry (1994) described a series of five factors that, when combined, are responsible for regulating herbivore populations. These factors are the nutritional quality of the plant tissues, the toxic or indigestible secondary chemicals contained within the plant tissues, the predators and pathogens of the herbivore, the abundance of food at different spatial scales, and weather. Changes in any of these regulating factors can potentially cause large increases or decreases in herbivore populations regardless of whether they are invertebrate or vertebrate populations. These changes may occur cyclically or irregularly with different frequencies or probabilities. Predators and pathogens of the herbivore and weather are variables influencing herbivore populations that operate at short time scales. The abundance of food at different spatial scales is a variable that influences herbivore populations on an intermediate time scale. The nutritional quality of plant tissues and the toxic or indigestible secondary chemical contained within plant tissues are variables affecting herbivore populations at longer time scales. The combinations of these fast and slow variables determine the frequency, probability and magnitude of herbivore population eruptions and their resulting effect on the ecosystem.

1.3 - Herbivory and vertical stratification within forests

Forests are commonly classified into several different levels of vertical strata. Herbivory within the different levels of vertical strata affects the forest in different ways. The overstory is the highest layer of vegetation within a forest and is composed of the mature trees that form the forest canopy, for this reason it is also commonly called the canopy layer. The understory is the layer of vegetation growing beneath the cover of the forest canopy. The canopy and understory are often divided up into several more specific levels of vertical stratification but for this study it is only necessary to distinguish between the canopy layer and the understory layer.

Herbivory in the canopy layer increases light availability to the understory layer. Competition between individual mature trees for light typically produces a closed forest canopy layer, allowing very little light to penetrate the canopy layer and reach the understory layer beneath. Plants growing in the understory layer must therefore be somewhat shade tolerant and/or concentrate their growth to areas where there are gaps in the canopy layer and light is able to penetrate to the forest floor. These canopy gaps are naturally produced when mature trees die, lose their leaves or needles, and eventually break or fall over. Canopy gaps are also produced when herbivores kill or defoliate trees. Canopy gaps are eventually filled in not only by branches of neighbouring trees but also by immature understory trees that are able to grow rapidly into mature trees with the increased light exposure. Forests with many small canopy gaps tend to have higher biodiversity values in the understory layer than forests that have fewer canopy gaps (Meier et al. 1996).

Herbivory in the understory layer decreases the ability of some plants to capitalize on the light penetrating through the canopy layer. There is usually intense competition for light between different individual plants within the understory layer. Many of these plants could potentially grow into canopy gaps and become a part of the future canopy layer of the forest. The plants with the most light are able to grow into the canopy gaps the fastest and shade out other potential competitors. Herbivory affects which plants are able to capture the most light by eating the photosynthetic portions of plants. High levels of preferential feeding within the understory can decrease biodiversity of the understory and future overstory layers (deCalesta 1997).

1.4 - Herbivory and structural heterogeneity within forests

Forest structural heterogeneity refers to the variability within the three-dimensional physical organization of the forest. An increase in complexity within the forest overstory and understory layers means an increase in forest structural heterogeneity. Ultimately, it is the dead and alive mature trees of the canopy layer and the dead and alive immature trees, shrubs and herbaceous vegetation of the understory layer that make up the structure of a forest. Structural heterogeneity is therefore composed of a combination of variables such as size diversity, condition diversity, and species diversity, density of mature trees, immature trees, shrubs and herbaceous vegetation. Forests with higher levels of structural heterogeneity tend to have higher species richness and abundance values for invertebrates, birds and mammals than forests with lower levels of structural heterogeneity (Berg 1997, Halaj 2000 and Ecke et al. 2002).

Forest canopy herbivores have the ability to affect forest structural heterogeneity by influencing the size diversity, condition diversity, species diversity and density of mature trees. Canopy herbivores sometimes kill or compromise the condition of certain species of mature trees. This act can increase the diversity of mature tree conditions in the forest because it can create trees with dead portions as well as snags, which eventually break and fall over. This act can also increase the size diversity by allowing smaller trees to grow into the gaps created by larger trees that were damaged by herbivores. Species diversity of mature trees can be decreased by canopy herbivores if they damage particular tree species more than others. The creation of canopy gaps by forest canopy herbivores also temporarily decreases the density of mature trees in the immediate area of the canopy gap.

Forest understory herbivores have the ability to affect forest structural heterogeneity by influencing the size diversity, condition diversity, species diversity and density of immature trees, shrubs and herbaceous vegetation. Herbivory within the understory layer can increase the diversity of conditions of immature trees and shrubs the same way that it does in the canopy layer. Understory herbivores tend to have a different effect on size diversity than canopy herbivores; their feeding tends to decrease the height of vegetation within the understory layer (Schmitz and Sinclair 1997). Intense understory herbivory can also decrease the species diversity and density of immature trees, shrubs and herbaceous vegetation.

1.5 - Porcupines as a forest herbivore

Porcupines inhabit a wide variety of ecosystems across North America including forest, grassland, desert and tundra ecosystems (Roze, 1989). In order to survive in these very different areas, their feeding strategies must differ widely between different ecosystems. This makes them an ultimate generalist herbivore. Their feeding strategies are also highly differentiated by season in many areas where there is high seasonal weather variation (Batchelder 1948). There is also evidence for different food preferences between individual porcupines in the same region at the same time of year (Roze, 1989).

In general, the summer diet of porcupines in the forests of northeastern North America is very similar to the diet of deer in the same region; porcupines feed primarily on herbaceous plants found in open fields, forests and along the banks of streams or lakes during the summer months (Jones 1973, Krefting et al. 1962, Roze 1989). Jones (1973) studied porcupines in Nova Scotia and found that although porcupines sometimes fed on the twigs and new leaves of maple (*Acer* spp.), beech (*Fagus grandifolia*), aspen (*Populus* spp.) and red oak (*Quercus borealis*) trees during the summer, they primarily fed on ground vegetation. Herbaceous plants consumed by porcupines in the summer in Nova Scotia included wild carrot (*Daucus carota*), dandelion (*Taraxacum officinale*), clovers (*Trifolium* spp.), plantain (*Plantago* sp.), violets (*Viola* sp.), asters (*Aster* sp.) and common elders (*Sambucus canadensis*). Porcupines also fed on fruit such as strawberries (*Fragaria virginiana*) and blueberries (*Vaccinium* sp.), as well as aquatic plants such as water lilies (*Nymphaea odorata*), bloodroot (*Sanguinaria canadensis*), and arrowhead (*Sagittaria latifolia*).

There are two characteristics of porcupines that allow them to feed on forest vegetation that deer cannot feed on; they have the ability to climb trees and they have specialized teeth that allows them to chew through tree bark. These adaptations allow them to modify their feeding strategy during the winter months when ground vegetation is covered by snow. The winter food preferences of porcupines have been well studied (Curtis 1944, Batchelder 1948, Shapiro 1949, Krefting et al. 1962, Gill and Cordes 1972, Jones 1973, Harder 1979 and 1980, Tenneson and Oring 1985, Sullivan et al. 1986, Roze 1989 and Griesemer et al. 1998) but are highly varied between different regions. The reason that porcupine winter feeding habits are so well studied is due to the fact that porcupines have the potential to significantly damage or even kill mature trees by feeding on their inner bark during the winter. James (1973) studied porcupine winter feeding in Nova Scotia and reported that porcupines fed primarily on the bark and foliage of softwoods and the bark of hardwoods and that species consumed depended largely upon what was available in the immediate surroundings.

Individual territorial behaviour has been observed in porcupines (Roze 1989) and they are generally regarded as solitary animals. Instances of overlapping home ranges and high porcupine densities have also been reported (Jones 1973) especially in areas disturbed by man. Evidence for this has been observed at the Morton Centre during the summer of 2003, when seven porcupines were found feeding in the hayfield after the hay had been harvested in July. Before this study took place, it was unknown whether porcupines at the Morton Centre commonly occur in such high densities year round, or whether porcupines occupy separate home ranges most of the time and only congregate in the field when food is extremely abundant.

1.6 - Human interactions with porcupines

Porcupines are not protected from hunting at any time in most parts of North America (Roze 1989) since they are commonly viewed as a pest species throughout most of their range. During the twentieth century, many areas have even offered bounties for killing porcupines and/or began poisoning programs for porcupines. Currently in Nova Scotia, porcupines may be taken or killed without a license or permit at any time of year for the purpose of preventing damage to property (NSDNR 2004). There are four possible areas of conflict between porcupines and humans that lead them to be considered to be pest species. First, the porcupine's sodium deficiency causes it to constantly seek sources of salt, gnawing on anything that might contain it, such as treated wood or the underside of cars in the spring (Roze 1989). Second, porcupines often harm curious domestic animals by swatting them with their tail in an act of self defence. Third, porcupines can wreak havoc on gardens, fruit trees, and agricultural crops by feeding on them during the summer months. Finally, throughout the winter, porcupines feed on the inner bark of a number of species of trees that people often highly value on their property, an act that can kill or seriously damages the trees. On Heckman's Island, some residents have come into conflict with porcupines in the second, third and fourth ways. Salt is not an issue for porcupines living so close to the coast; porcupines get their salt from consuming plants in the intertidal zone in this area rather than damaging residents' properties in search of salt.

1.7 - Overview and objectives

Over several years, the winter feeding of North American porcupines can significantly influence the structure and composition of the surrounding forest. In human populated areas, however, the foraging of porcupines is not restricted to the forest, where their impacts typically go unnoticed by most people. Porcupines are often very destructive to various forms of vegetation, either planted or growing naturally on people's properties.

The overall objective of this study is to investigate the relationships between the different feeding habits of porcupines, the damage they cause to people's properties, their impacts on forest structure and dynamics, and people's resulting attitudes towards them. Specific objectives are:

- to estimate the density of the porcupine population in the region and to determine whether porcupines exhibit territorial behaviour within the region.
- to estimate the contribution of porcupine winter feeding habits to forest structural heterogeneity and canopy composition and density
- to quantify the damage caused to residents' properties by porcupines and to determine if residents' perceptions towards porcupine populations are correlated with their influences on the forest.

2 - Methods

2.1 - Porcupine population density and social behaviour

In order to estimate porcupine population density and determine whether individual porcupines exhibit territorial behaviour, a radio-telemetry study of porcupines was undertaken. The number of porcupines located and collared at the Morton Centre could be used as a 'minimum number alive' population estimate (Krebs 1989). The positions and behaviour recorded from a series of locations of individual porcupines can illustrate whether there is evidence that they are territorial in this region.

2.2 - Capturing porcupines

Because porcupines are generally not responsive to baiting techniques, porcupines were initially located by chance sightings. Despite the fact that porcupines are more active and mobile at night, due to visibility issues, searches for porcupines were conducted during daylight hours. Porcupine sightings were still difficult, however, because porcupines are more likely to be concealed in rest trees during the daylight hours. The musky warning odour emitted by porcupines when they are disturbed was used as a hint to tell when a porcupine was resting in a nearby tree.

Upon sighting a porcupine in a tree, the potential escape routes of the porcupine were noted and a 6 foot fence was constructed around all possible trees that the porcupine could climb down using rebar and chicken wire. The fence was constructed so that the porcupine could not reach the fence from any tree it was in, nor could it reach an outside tree through the fence and climb up and over the fence. The fence was pinned to the ground by placing nearby large rocks or logs on top of it and also by inserting short pieces of rebar into the ground through the chicken wire at an angle. An 80x25x30cm Havahart live trap was baited with an apple and inserted into a small opening that was cut into the fence. The porcupine was then left alone in the tree. The trap was checked every 2 hours.

After the porcupine was found to have descended the tree and entered the trap, the porcupine in the trap was transported to a nearby equipment shed. The porcupine was weighed and sexed while still in the trap. The porcupine was then removed from the trap by lifting it up by its tail (Shadle 1950, Spencer 1964, Tenneson and Oring 1985, Craig and Keller 1986, and Griesemer et al. 1999) and its body was wrapped in a thick blanket with its head and neck exposed. This procedure was a necessary protection measure from the porcupine's quills. The porcupine was straddled on the ground with light pressure applied to its back to keep it from attempting to run away. A second person was responsible for clipping the ends of the quills around the porcupine's neck and fitting a Holohil PD-2C 4.0 g radio-transmitter collar snugly around its neck but loose enough that two fingers could be inserted between the collar and the neck. The porcupine was then persuaded into a wooden capture cone like apparatus (Shadle 1950), within which it was transported back to the area where it was found and released. The fence around the tree that the porcupine was originally sighted in was then disassembled.

2.3 - Locating porcupines

The collared porcupines were each located daily over a period of three weeks in June 2004. Porcupines were located at dusk, when they have been reported by Roze (1989) to stop resting and become more active. Porcupines were approached to a distance where their behaviour could be observed but where the porcupine would not be disturbed. For each time a porcupine was located, the porcupine's GPS position, and behaviour was recorded. Weather conditions including whether it was sunny or rainy and whether it was windy were also recorded for each sighting. Recorded behaviour included whether the porcupine was found in a tree or on the ground, whether it appeared to be sleeping, feeding, or moving and its interactions with any potential nearby porcupines.

2.4 - Porcupine winter feeding habits

Forest transects were surveyed for tree species, DBH, condition and porcupine damage in order to estimate the effects of porcupine winter feeding habits at the Morton Centre. Thirty 50 m by 50 m forested grid squares were randomly selected without replacement from a possible 129 forested grid squares within a virtual grid of the Morton Centre set up by Greene (2002). At each grid square selected, a point was randomly chosen within 10 m North/South and within 10 m East/West of the centre of the square. This point designated the centre of a 30 m transect orientated in a random direction.

At each transect, all trees rooted within 2.5 m of either side of the transect were counted. Data recorded for each tree included species (or genus if species was not discernable), diameter at breast height (DBH), tree condition, presence or absence of porcupine bark damage, and whether it was likely that porcupines were responsible for contributing to the current condition of the tree. Possible tree conditions included standing-alive, leaning-alive, broken-alive, fallen-alive, alive-dead top, standing-dead, leaning-dead, broken-dead, and fallen-dead (Roberts-Pichette and Gillespie 1999). In some cases it was necessary to record a combination of two tree conditions for a single tree. For example, a tree could simultaneously be broken-dead and leaning-dead. In these cases, one condition was recorded as the primary condition, and the other was recorded as the secondary condition. Porcupine bark damage was determined with the aid of binoculars in cases where there appeared to be damage near the tops of trees. Porcupine bark damage is distinguishable from other types of bark damage by the pattern of damage and the tooth marks left in the wood. It was considered likely that porcupines were responsible for contributing to the current condition of the tree in situations where a porcupine had eaten a ring of bark off a tree (cutting off its branches from its roots), as well as in situations where part of a tree was either broken at or dead above a point that had sustained substantial porcupine bark damage.

2.5 - Residents' interactions, perceptions, and attitudes towards porcupines

In order to better understand the attitudes and perceptions of Heckman's Island residents towards the porcupine population and also to better understand the nature of the interactions between porcupines and people on the island, a 4 page survey (including instructions) was delivered to the door of each dwelling on Heckman's Island in mid-August 2004. Residents were asked to complete this 5 minute survey and mail it back to Acadia using the envelope and postage stamp provided. The survey included questions on residents' land use, their attitudes towards porcupines, their knowledge of the feeding habits of porcupines, the impact of porcupines on their property and their control measures used against porcupines.

3 - Results and discussion

3.1 - Radio-telemetry

Five porcupines were sighted, 3 were captured, and 2 were radio-collared (one male and one female) using the capture method described earlier. Two porcupines were not captured because they consisted of a mother and a juvenile. These porcupines were not sighted at the Morton Centre until August, when they were observed while they were feeding in an apple tree near the hayfield (Figure 1). They were only sighted on the property on the one occasion. Another porcupine was captured while feeding in an apple tree near the hayfield late in the summer, but had a large open wound on the back of its neck from an unknown cause. This porcupine was not collared out of concern for aggravating the wound. The porcupine was sighted on one other occasion in the hayfield.

Other radio telemetry studies involving porcupines used some form of drug to immobilize individuals when fitting the porcupines with radio-collars (Craig and Keller 1986, Griesemer et al.1998, Hale et al. 1994, Roze, 1987). This study successfully fitted 2 porcupines with radio-collars without the need to administer immobilization drugs. Wrapping a captured porcupine in a thick blanket is a sufficient safeguard against the porcupine's quills. Using headlamps, straddling the porcupine and fitting the porcupine with its radio-collar in the dark also seem to calm the porcupine and keep it from struggling excessively.

The minimum number of porcupines alive at the Morton Centre during the summer of 2004 was 5. Five porcupines over an area of 40 ha yields a porcupine population density of 12.5 porcupines/km^2. This estimate is likely accurate for the Morton Centre property, but it is a very rough estimate for the entire island due to the large amount of area extrapolation. Porcupines may be living at higher or lower population densities on other parts of the island. Because only 2 of 5 porcupines found at the Morton Centre were fitted with radio-collars and repeatedly located, it is not known how much time the other 3 porcupines spent on the property, what their home ranges were, and whether their home ranges overlapped with the collared porcupines' home ranges. Since only 2 porcupines were sighted at the Morton Centre for most of the summer and the other 3 appeared late in the summer after the hayfield was hayed and the apples were becoming ripe, it seems likely that 2 porcupines have their home ranges on the Morton Centre while the other 3 moved to the Morton Centre when food in the hayfield and on the apple trees was very abundant. If this is true, the density of porcupines in the area becomes 2 porcupines over an area of 40 ha, which translates to 5 porcupines/km^2.

The collared porcupines tended to occupy distinct and separate home ranges during the summer at the Morton Centre (Figure 2). The female porcupine was consistently found either on the west end of the Morton Centre or on other properties west of the Morton Centre. The male porcupine was consistently found on the eastern and northern areas of the property and was never located off the Morton Centre Property. There were two instances where the two collared porcupines were located in trees adjacent to each other. In both of these cases the porcupines were fixated on one another and paid no attention to my presence. In these two instances both the male and female porcupine made chattering sounds with their teeth interspersed with louder vocalizations that sounded slightly like a parrot.

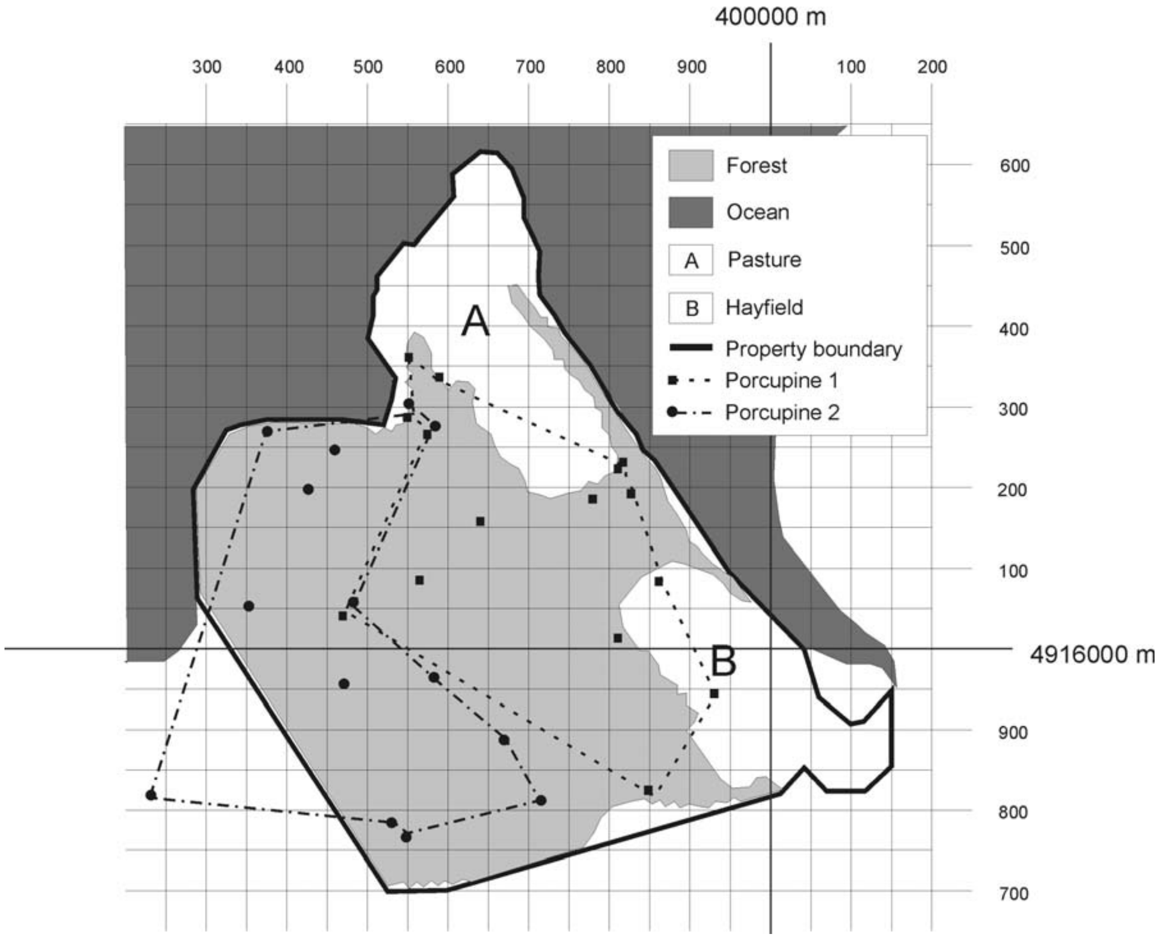

Figure 2: Property map of the Morton Centre with summer home ranges of 2 porcupines overlain (Modified from Greene 2003)

It was impossible for this study to determine the winter ranges of the porcupines sighted at the Morton Centre. Two porcupines were found in winter dens on the property during February 2005 but 5 previously used winter dens have been located on the property. Since porcupines have been found to occupy more than one den during any given winter and since porcupines have been observed to occupy different summer and winter ranges (Roze 1989 and Griesemer et al. 1998), it is not known whether the 3 porcupines sighted at the Morton Centre in the late summer overwintered on the property.

Despite these uncertainties evidence from the 2 radio-collared porcupines suggests that they exhibit territorial behaviour and occupy different home ranges.

3.2 - Porcupine bark consumption

While porcupine damage was generally easily distinguishable from other forms of bark damage, there were some instances where it was difficult to tell whether a tree had sustained porcupine damage or not. The most difficulty arose when searching for porcupine damage on large, tall trees with dense branching. In many of these cases, a clear view of the crown of the tree with binoculars was obscured by the lower branches of the tree and other surrounding trees. Some of these trees had scratch marks on the trunk, suggesting that a porcupine had climbed the tree, but climbing is not necessarily evidence of feeding. Trees for which presence or absence of porcupine damage could not be determined from the ground were recorded as having no evidence of porcupine damage. Since climbing trees to check for porcupine damage was not feasible due to safety concerns, the estimated proportions of porcupine feeding on larger trees are likely to be slightly conservative.

The age of the bark damage occurring on a tree can be measured by counting the growth rings on a section of the tree where the damage is starting to heal. This study did not collect data on the age of the damage on each damaged tree that was observed. This would have been valuable for determining the amount of damage that porcupines cause to trees over a single winter and possibly even for estimating the relative population sizes of porcupines on the property for past winters. It was not feasible to age the damage that was observed because much of the bark damage that porcupines are responsible for occurs near the crowns of trees. Aging the damage would have involved climbing many trees, which would have been a safety concern. Aging the damage is not, however, necessary for determining the contribution of porcupine winter feeding habits on forest structural diversity and canopy layer composition and density.

Among the 30 transects sampled for porcupine winter feeding, the mean proportion of trees showing evidence of bark damage caused by porcupines was 6% with a standard error (SE) of 1.34.

Red spruce and balsam fir make up the majority of porcupines' winter diets at the Morton Centre (Table 1), however porcupines' tree species preferences can be more accurately determined using the ratios of each tree species percentage of the total number of trees observed with porcupine bark damage to that species percent occurrence in the forest. A ratio greater than 1 means that porcupines feed on that tree species proportionately more than it occurs in the forest, while a ratio less than 1 means that porcupines feed on that tree species proportionately less than it occurs in the forest. Porcupines tend to selectively feed on the bark of beech, tamarack (*Larix laricina*), and red spruce, while avoiding white spruce and all hardwoods other than beech. The bark of balsam fir is consumed in proportion to its abundance in the forest. The proportion of beech bark consumed by porcupines is 13.3 times the occurrence of beech in the forest, making it the most preferred species for bark feeding. The proportion of red spruce and tamarack bark consumed by porcupines are both between 2 and 3 times the occurrence of these species in the forest, making them secondary preferred species for bark feeding. Balsam fir bark is consumed in the same proportion that it occurs in the forest, meaning that it neither prefers nor avoids the species. No evidence of porcupine feeding was found in many of the less common hardwood species in the forest, nor in the 2 most common hardwood species, white birch and yellow birch (*Betula alleghaniensis*), meaning that these species are avoided when feeding on bark. Porcupines were, however, observed feeding on the twigs and new leaves of yellow birch and white birch during the spring. This feeding could not be quantified within the transects because the damage was not easily observable at the time when the transects were sampled, in the summer after the leaves were back on the trees. White spruce is also generally avoided because it makes up 17% of the forest, but only makes up 4% of the porcupines bark diet.

Table 1: The percentages of different tree species that have evidence of porcupine bark damage and their relative abundances in the forest

	% of trees occuring within 50x50m grid squares			% of trees with porcupine damage within 30x5m transects			% feeding / % occurrence
tree species	mean	SE	n	mean	SE	n	ratio
balsam fir	39	1.93	106	39	8.62	22	1.0
beech	0.3	0.08	106	4	3.54	22	13.3
red spruce	22	1.63	106	49	6.75	22	2.2
tamarack	2	0.51	106	5	4.55	22	2.5
white spruce	17	1.91	106	4	1.97	22	0.2

The sampling scheme for this study was designed with no previous knowledge as to what particular tree species porcupines prefer to feed on during the winter in this specific region. This sampling design gives a reasonable estimate of what types of bark porcupines are eating in the forest, and in what proportions. However, as a result of this sampling design, a large amount of data was collected about hardwood trees that never showed signs of porcupine damage. These data did not end up being useful to the study and were, therefore, not analyzed. It is recommended that future studies of porcupine winter feeding on bark should be undertaken in two parts. The first part should determine the tree species that porcupines consume the bark of during the winter. Secondly, if the study concerns the effect of porcupine damage on trees, it should focus only on the tree species whose bark porcupines in the area have consumed during past winters. It was known from observations of individual trees in the forest at the Morton Centre and other locations on Heckman's Island that local porcupines also feed on the bark of eastern hemlock and red and white pine. These species were not captured in the transects that were sampled because these species are very rare in the forest at the Morton Centre. High proportions the individual eastern hemlock, white pine and red pine trees sighted at the Morton Centre appeared to have evidence of porcupine damage on them. Also, because tamarack and beech are also relatively rare on the property, only a few individual tamarack and beech trees were included in 2 of the transects. This meant that they had to be excluded from more detailed analysis concerning the size and condition of damaged trees because of the large degree of error associated with the small sample sizes. If the sampling had been designed to focus only on the tree species that porcupines consume the bark of during the winter, the sampling unit would have been individual trees, meaning eastern hemlock, white pine, red pine, tamarack and beech could have been more easily included in the analysis.

One hindrance encountered during data collection was that since many spruce trees with evidence of porcupine bark damage were dead, it was impossible to tell whether the trees were red spruce or white spruce. Because it was impossible to identify these trees to the species level, many dead spruce trees were classified simply as “spruce.” An attempt was still made to classify all other trees to the species level. To estimate the percentage of porcupine damage occurring on red spruce and white spruce, the relative proportions of living red spruces and living white spruces sustaining porcupine damage was applied to the total proportion of spruce trees (living and dead, red and white) that showed evidence of porcupine feeding. This estimate was necessary because there is a clear distinction between the proportions of living red and white spruces fed on by porcupines. Living red spruce trees were fed on by porcupines much more often than living white spruce trees. This estimate is, however, likely to overestimate the proportion of red spruce fed on by porcupines and underestimate the proportion of white spruce fed on by porcupine because red spruces are more resilient than white spruces (Cogbill 1996), and may be less likely to die as a result of porcupine damage. More detailed analysis of size and condition with respect to porcupine feeding habits focuses on balsam fir and spruce; the trees most often used as feeding trees by porcupines during the winter and the trees for which the most data was collected. A distinction was not made between red spruce and white spruce for this analysis because of the significant number of trees that were classified simply as “spruce” when the data was collected.

Porcupines were found to feed selectively on mid-sized balsam fir and spruce with diameter at breast height (DBH) of between 10 and 20 cm (Table 2), while avoiding immature trees with DBH between 1 and 10 cm. Larger fir and spruce trees were also selectively fed on, but comprised a smaller proportion the total number of damaged trees. Porcupine feeding on balsam fir trees seemed to be concentrated on small to medium size trees while porcupine feeding on spruce trees seemed to be concentrated on medium to large size trees.

Table 2: Distribution of DBH classes of balsam fir and spruce within the forest and among trees with evidence of porcupine bark damage

		1.0 - 10.0 cm DBH			10.1 - 20.0 cm DBH			> 20.1 cm DBH		
	tree type	mean	SE	n	mean	SE	n	mean	SE	n
% occurrence in forest	Balsam fir	61	2.49	104	29	1.98	104	11	1.01	104
	spruce	47	2.10	104	31	1.17	104	22	1.67	104
% of porcupine damage	Balsam fir	40	12.1	14	45	12	14	15	8.48	14
	spruce	15	6.85	17	47	9.06	17	38	9.92	17

3.3 - Effect of porcupine bark damage on trees

The mean proportion of trees showing evidence that porcupine bark damage has altered the condition of the tree within the transects was 4% (SE = 1.00, n = 30).

Porcupines are likely responsible for altering the condition of 4% (SE = 1.45, n = 29) of balsam fir trees in the forest at the Morton Centre. Only 46% (SE = 5.09, n = 29) of balsam fir trees in the forest at the Morton Centre are of the condition “standing alive,” meaning they are alive and healthy trees (Table 3). A significant amount of balsam fir trees at the Morton Centre are in the condition classes “standing dead” (24%) and “fallen dead” (15%). The remaining six condition classes collectively only make up 15% of balsam fir trees on the property. Porcupine damage only contributes to the “alive dead top” and “standing dead” tree condition classes of balsam fir trees at the Morton Centre. Porcupines are likely responsible for around 7% (SE = 3.78, n = 24) of standing dead balsam fir trees and around 50% (SE = 11.39, n = 14) of alive balsam fir trees with a dead top in the forest at the Morton Centre.

Porcupines are likely responsible for altering the condition of 8% (SE = 2.31, n = 30) of spruce trees in the forest at the Morton Centre. There are higher proportions of alive and healthy spruce trees than balsam fir trees at the Morton Centre. Around 59% (SE = 4.96, n = 30) of spruce trees in the forest at the Morton Centre are in the condition class “standing alive”. There is also a significant amount of spruce trees at the Morton Centre in the condition classes “standing dead” (16%) and “fallen dead” (11%). The remaining six condition classes collectively only make up 14% of spruce trees on the property. Porcupine damage significantly contributes to the “alive dead top,” “standing dead” and “broken dead” tree condition classes of spruce trees at the Morton Centre. Porcupines are likely responsible for around 23% (SE = 6.94, n = 23) of standing dead spruce trees, around 88% (SE = 12.50, n = 8) of alive spruce trees with a dead top, and around 20% (SE = 9.85, n = 11) of broken dead spruce trees in the forest at the Morton Centre.

Table 3: The proportions of Balsam fir and spruce trees of different conditions that porcupines are responsible for causing

		% of tree type in each condition			% of condition caused by porcupine damage		
Condition	tree type	mean (%)	SE	n	mean (%)	SE	n
Standing Dead	Balsam fir	24	2.94	29	7	3.78	24
	spruce	16	2.29	30	23	6.94	23
Leaning Dead	Balsam fir	6	1.46	29	0	0	16
	spruce	3	0.90	30	4	3.85	13
Fallen Dead	Balsam fir	15	4.05	29	0	0	20
	spruce	11	3.65	30	0.7	0.7	18
Broken Dead	Balsam fir	3	0.84	29	0	0	14
	spruce	2	0.63	30	20	9.85	11
Standing Alive	Balsam fir	46	5.09	29	0	0	28
	spruce	59	4.96	30	0	0	28
Leaning Alive	Balsam fir	2	1.16	29	0	0	9
	spruce	5	1.79	30	3	3.33	15
Fallen Alive	Balsam fir	0.4	0.31	29	0	0	2
	spruce	0.3	0.28	30	0	NA	1
Alive Dead Top	Balsam fir	4	1.26	29	50	11.39	14
	spruce	3	1.70	30	88	12.50	8
Broken Alive	Balsam fir	0.03	0.03	29	0	NA	1
	spruce	0.3	0.24	30	50	50.00	2

The balsam fir and spruce trees on the property that fell into the tree condition classes that porcupines were found to cause were analyzed by size to determine if larger or smaller trees were more susceptible to particular changes in condition as a result of porcupine feeding. These results are provided in Table 4b. The distribution of condition classes in the forest by tree size and tree type are provided for comparison in Table 4a. Porcupines are responsible for the death of 6% of small standing dead balsam fir trees, 5% of mid-size standing dead balsam fir trees, and 3% of large standing dead balsam fir trees on the property. Porcupines are responsible for killing the top of 49% of small, alive balsam fir trees with a dead top, 56% of mid-size alive balsam fir trees with a dead top, and none of large alive balsam fir trees with a dead top. Porcupines are responsible for the death of 4.7% of small, standing dead spruce trees, 50% of mid-size standing dead spruce trees, and 27% of large standing dead spruce trees. Porcupines are responsible for causing the break in none of the small, broken dead spruce trees, 33% of mid-size broken dead spruce trees, and 17% of large broken dead spruce trees. Porcupines are responsible for killing the top of all of the small, alive spruce trees with a dead top, 75% of mid-size alive spruce trees with a dead top, and all of the large alive spruce trees with a dead top.

Table 4a: Distribution of Balsam fir and spruce trees of 3 different conditions (that porcupines may cause) among DBH classes

		1.0 - 10.0 cm DBH			10.1 - 20.0 cm DBH			> 20.1 cm DBH		
condition	tree type	mean	SE	n	mean	SE	n	mean	SE	n
standing dead	Balsam fir	63	5.94	24	23	3.69	24	14	5.18	24
	spruce	50	8.75	23	25	6.44	23	25	7.98	23
broken dead	Balsam fir	42	10.87	14	49	9.64	14	7	4.85	14
	spruce	23	12.36	11	41	12.69	11	37	13.22	11
alive dead top	Balsam fir	32	12.41	14	58	12.69	14	10	7.35	14
	spruce	38	15.67	8	38	15.67	8	25	16.37	8

Table 4b: Proportions of different conditions caused by porcupines of Balsam fir and spruce trees in each DBH class

		1.0 - 10.0 cm DBH			10.1 - 20.0 cm DBH			> 20.1 cm DBH		
condition	tree type	mean	SE	n	mean	SE	n	mean	SE	n
standing dead	Balsam fir	6	4.14	22	5	2.88	19	3	3.33	10
	spruce	5	2.51	15	50	12.97	13	27	13.17	10
broken dead	Balsam fir	0	0	9	0	0	11	0	0	2
	spruce	0	0	3	33	16.67	6	17	16.67	6
alive dead top	Balsam fir	49	20.72	5	56	15.47	9	0	0	2
	spruce	100	0	4	75	25.00	4	100	0	2

3.4 - Survey of local residents

A survey was given to each household on Heckman's Island, both permanent and summer. A total of 90 surveys were handed out. Of the 48 competed surveys that were submitted back, 23 were submitted by summer residents and 25 were submitted by permanent residents, yielding a 53% response rate overall. General survey results are presented first, followed by a discussion of the differences in responses between summer residents and permanent residents.

Residents of Heckman's Island generally see porcupines somewhere between yearly and even less frequent than yearly. The perceived population sizes for porcupines on Heckman's Island ranged from 0 to 150 with a median of 25. Residents felt that the porcupine population has remained relatively the same size over the past 10 years. Residents stating that they valued the presence of porcupines on the island made up 38% of respondents. Only 24% of respondents stated that they value the presence of porcupines on their property. Common reasons why residents stated that they value the presence of porcupines on the island included: that porcupines are natural on the island, that they have very few or no interactions with porcupines and that porcupines are enjoyable to see. Common reasons why residents stated that they do not value the presence of porcupines on the island included: that porcupines damage vegetation, that they are worried about porcupines harming their pets and that they don't care about porcupines one way or another. In general, residents of Heckman's Island never take pictures of porcupines. Porcupines generally don't damage the man-made possessions of Heckman's Island residents. The survey suggests that porcupines are having an impact on the vegetation of Heckman's Island since 58% of respondents stated that porcupines are having an impact on the vegetation on their property. Respondents stated that this impact occurred on a yearly basis. Respondents react to this impact on the vegetation on their properties by using control measures to prevent porcupines from impacting their vegetation. Some form of control measure is used by 58% of residents, with 15% of respondents using relocation as a control measure for porcupines and 6% using extermination as a control measure for porcupines.

Residents were asked to state the total cost of all control measures used against deer and porcupines on their property. Some respondents stated this number in terms of cost per year while others stated it in terms of total absolute cost. The sum of all of the costs stated by respondents of the survey was $18,600 over the past year. This number represents a minimum value for the total costs of control measures used against deer and porcupines over the past year on Heckman's Island. This is an underestimate of the true total cost of control measures to Heckman's Island residents because 47% of residents did not complete the survey and many residents who did complete the survey did not specify the cost of the control measures that they used. It is, however, important to note that much of the money spent on control measures came from a single respondent who spent $15000 on a fence to protect their property from deer and porcupine foraging.

Table 5a: Median estimated responses to questions asked to residents of Heckman's Island

	summer residents			permanent residents			all residents		
Residents' estimate of:	median	SE	n	median	SE	n	median	SE	n
number of porcupines on the island	12	6.98	13	30	9.85	18	25	6.68	31
porcupine population change over past 10	stable		19	stable		21	stable		40
cost of control measures they have used	$0	5.63	20	$100	675.44	22	$0	356.04	42

Table 5b: Proportions of Heckman's Island residents who responded positively to various questions

Residents:	summer residents %	SE	n	permanent residents %	SE	n	all residents %	SE	n
with a vegetable garden	13	7.18	23	68	9.52	25	42	7.19	48
with ornamental plants	65	10.15	23	88	6.63	25	77	6.13	48
with fruit trees	22	8.79	23	88	6.63	25	56	7.24	48
that harvest wood	30	9.81	23	52	10.20	25	42	7.19	48
that own a dog	9	6.01	23	52	10.20	25	31	6.76	48
that value porcupines on the island	35	10.94	20	43	11.07	21	39	7.71	41
that value porcupines on their property	24	10.60	17	39	10.10	21	26	7.24	38
whom porcupines affect their man-made property	5	4.76	21	4	4.35	23	5	3.18	44
whom porcupines affect the vegetation on their property	43	11.07	21	68	9.52	25	57	7.39	46
who use control measures	30	9.81	23	84	7.48	25	58	7.19	48
who use relocation as control measure	5	4.55	22	24	8.72	25	15	5.25	47
who use extermination as control measure	0	0	22	12	6.63	25	6	3.60	47
that are interested in learning more about porcupines	76	9.52	21	83	7.77	24	80	6.03	45

Table 5c: Median frequencies of different events estimated by residents of Heckman's Island

Residents:	summer residents frequency	n	permanent residents frequency	n	all residents frequency	n
view porcupines	rarely	22	yearly	25	rarely	47
take pictures of porcupines	never	19	never	24	never	43
man-made property is affected by porcupines	rarely	1	yearly	1	yearly	2
vegetation is affected by porcupines	yearly	8	yearly	17	yearly	25

The survey of Heckman's Island residents revealed some important differences between permanent residents and summer residents with respect to attitudes towards and interactions with porcupines. Permanent residents tend to use their land for a wider variety of uses that might cause interactions with porcupines. Permanent residents were more likely to tend gardens, plant ornamental plants, have fruit trees, harvest wood, and own a dog. Permanent residents see porcupines more often than summer residents and also had higher population estimates for porcupines on the island. Permanent residents are also more likely to use control measures and spend more money on them than summer residents. Permanent residents were more likely to relocate and/or exterminate porcupines. Permanent residents are also more likely to value the presence of porcupines both on the island and on their properties than summer residents.

The difference in the responses of permanent residents versus the responses of summer residents seems logical. Responses of permanent residents show that they are more likely to use their land for uses that provoke conflicts with porcupines. They therefore see porcupines more frequently, estimate higher population levels for porcupines and report more damage done to the vegetation on their property. As a result they are more likely to use control measures against porcupines and spend more money on these control measures. The only difference between the survey responses of permanent and summer residents that does not immediately seem logical is that permanent residents tend to value porcupine populations on the island more highly than summer residents. If permanent residents report more damage to their vegetation as a result of porcupine feeding, and use more control measures against porcupines, why do they value porcupines more than summer residents? The answer may be that permanent residents are more used to living with porcupine populations and have come to expect and tolerate the fact that they damage vegetation.

One survey question asked residents to circle the foods that they believed made up part of the natural diet of porcupines from a list of given options. This question was intended to be used to determine how well the residents of Heckman's Island are aware of the natural feeding habits of porcupines. The question that this survey question was intended to answer was: do residents plant certain species of plants knowing that porcupines likely find them palatable or do residents plant certain species of plants without taking porcupines into consideration and find out only later that porcupines find them desirable? This question could not be properly analyzed due to two errors in the wording of the question. Two potential food sources, needles and gardens, were not properly separated when the survey was handed out and appeared on the survey as "needlesgardens." Some respondents were confused by this error. The other error with the question was that there was no space where respondents would state whether they believe that they know what porcupines eat or not. This error meant that there was no way to tell if people didn't know what porcupines eat but felt like they should guess, or whether people felt they knew what porcupines eat and responded accordingly.

Another question that some respondents had trouble with was a question concerning the frequency with which porcupines damage any man-made items such as buildings, fences, or other non-living possessions on their property. The question was worded as follows: Do porcupines affect any infrastructure or belongings on your property? The word infrastructure was a poor word choice for this question. The intended definition of infrastructure for this survey is any of the interconnected structural elements that provide the framework for the function of a property as a place of residence. Many respondents were confused by either the word, or the definition of the word that was intended and described damage to their trees and gardens under this question. It was assumed that if a respondent had experienced an incident where a porcupine had damaged a fence, building etc. on their property, they would have understood the question. Since only 5% (%variance = 4.4) stated that porcupines have affected their infrastructure or belongings, it was assumed that porcupines have little influence on the residents of Heckman's Island's non-living components of their property.

According to the residents of Heckman's Island, porcupines on the island eat the new growth, crowns, branches, twigs, leaves, and bark of mature and immature trees. They are also reported to feed on fruit trees and vegetables in people's gardens. Specific plants reported by residents to be palatable to porcupines on the island included; pine trees, spruce trees, birch trees, hawthorne trees, tamarack, oak trees, hemlock trees, maple trees, chestnut trees, apple trees, cherry trees, quince bush, and raspberries.

4 - General discussion

4.1 - Effect of porcupines on the forest

The porcupine population on Heckman's Island may fluctuate considerably from one year to another. Seven porcupines were observed in the hayfield at the Morton Centre on one occasion during the summer of 2003 but only two were ever observed in the hayfield on a single occasion during the summer of 2004. When the porcupine population on the island elevates, some residents of Heckman's Island reportedly either exterminate porcupines that they find in their trees on their property or relocate porcupines off the island. From personal communication with Heckman's Island residents, it was determined that a minimum of 9 porcupines were either relocated from the island or exterminated between the summer of 2003 and the summer of 2004. One porcupine skeleton was also discovered near a den in the forest at the Morton Centre during the summer of 2004. This porcupine appeared to have died over the winter of 2003/2004 and there was no evidence that humans were the cause of its death.

Porcupines were found to feed on the bark of red spruce, balsam fir, tamarack, white spruce and beech (in that order) in the transects sampled for this study. Porcupine damage was also observed in eastern hemlock, white pine, and red pine on the property, although these species were not captured in the transects. The variety of species whose bark was consumed by porcupines combined with the fact that the tree species that are the most common in the forest make up the greatest percentages of its diet confirms their position as a generalist herbivore on Heckman's Island. They appear to feed on rare palatable tree species opportunistically if they happen to come across them. Their winter feeding is concentrated in the areas around their multiple winter den sites.

Porcupines are responsible for altering the condition of 4% of balsam fir trees and 8% of spruce trees; the two most abundant tree species in the forest at the Morton Centre. This means they are contributing to the structural heterogeneity of the forest, particularly with respect to the amount of small and large snags and partially dead live trees. Small snags are trees that make up the 0-10 cm and 10-20 cm DBH classes of standing dead trees within this study. Small snags provide nesting opportunities and foraging sites for many vertebrate species, especially birds (McShea and Rappole 1997). Large snags are trees that make up the >20 cm DBH class of standing dead trees within this study. Large snags are important for many species of large birds and mammals (Logsdon 1999). Partially dead trees usually have less dense crowns, which allow sunlight to penetrate to the forest floor. These small canopy gaps, and also the larger canopy gaps formed by snags, broken trees and fallen trees, promote vegetation growth within the understory layer. This provides even more structural heterogeneity, which is beneficial to many forest invertebrate, bird and mammal species, including deer (McShea and Rappole 1997).

4.2 - The overall impact of porcupine populations on forest dynamics

Porcupines feed on the most abundant trees within the canopy layer, sometimes creating snags and canopy gaps. Snags enhance habitat for invertebrates, birds and mammals while canopy gaps enhance habitat for understory vegetation. Enhanced understory vegetation replenishes and diversifies the canopy layer as well as further enhances invertebrate, bird, and mammal habitat.

4.3 - The overall impact of porcupine populations on local residents

The high response rate of 53% for this study suggests that porcupine populations on Heckman’s Island are a popular issue for many residents of the island. As expected, more residents value the presence of porcupines on the island than value the presence of porcupines on their property, however most residents don’t seem to value porcupines on the island in the first place, they just value them even less on their property. The fact that they are generally not valued may have something to do with the nature of the damage that porcupines tend to cause to resident’s properties. Porcupines are likely to feed on mature trees, causing (limited) long-term damage. Residents may also feel intimidated for themselves or their pets upon encountering a porcupine.

There seems very little correlation between the value that people place on porcupine populations and the role that porcupine populations have on the surrounding forest. Residents generally do not value the presence of porcupines on the island, despite the fact that they are increasing forest structural heterogeneity, which is beneficial to a wide variety of forest species.

4.4 - What should we do about it?

It is important to recognize that any management decisions regarding the population of porcupines on Heckman’s Island are dependent on value judgments concerning what someone wants the forest and/or residential community to look like. If the forest or porcupine population doesn’t fit what people think it should look like in a given environment they often decide that management is required. There is no problem with the forest; forests are dynamic systems that are continuously changing their structure and composition. There is no problem with the porcupine population, porcupines are eating the food that is available to them and reproducing healthily. It is our own activities that cause us to come into conflict with nature. Many people value forests that have high biodiversity values yet forests are commonly clear-cut and replaced with secondary forests that may never attain the same state of the original forest even if left uncut. Many people plant or selectively leave tree species on their property whose bark is eaten by porcupines during the winter and then get annoyed when porcupines eat them. Responsible management of conflicts between humans and nature would involve adapting human behaviour to resolve the conflict rather than attempting to adapt nature to best suit the needs of humans.

5 - References

Batchelder, C.F. 1948. Notes on the Canada porcupine. Journal of Mammalogy **29**: 260-268.

Berg, A. 1997. Diversity and abundance of birds in relation to forest fragmentation, habitat quality and heterogeneity. Bird Study **44**: 355-366.

Cogbill, C.V. 1996. Black growth and fiddlebutts: The nature of old-growth Red Spruce. *In* Eastern Old-Growth Forests: Prospects for Rediscovery and Recovery. *Edited by* M.B. Davis. Island Press, Washington, D.C. pp. 113-125.

Craig, E.H., and Keller, B.L. 1986. Movements and home range of porcupines (*Erethizon dorsatum*) on Idaho shrub desert. The Canadian Field-Naturalist **100**: 167-173.

Curtis, J.D. 1944. Appraisal of porcupine damage. Journal of wildlife management **8**: 88-91.

Ecke, F., Lofgren, O., and Sorlin, D. 2002. Population dynamics of small mammals in relation to forest age and structural habitat factors in northern Sweden. Journal of Applied Ecology **39**: 781.

Gill, D., and Cordes, L. 1972. Winter habitat preferences of porcupines in the Alberta foothills. Canadian Field-Naturalist **86**: 349-355.

Greene, C. 2003. Strategic environmental assessment as a tool for sustainable development: The Morton Centre model. BScH Thesis. Acadia University, Wolfville NS. 91 pp.

Griesemer, S.J., Fuller, T.K., and DeGraaf, R.M. 1998. Habitat use by porcupines (*Erethizon dorsatum*) in central Massachusetts: Effects of topography and forest composition. American Midland Naturalist **140**: 271-279.

Griesemer, S.J., Hale, M.O., Roze, U., and Fuller, T.K. 1999. Capturing and marking adult North American porcupines. Wildlife Society Bulletin **27**: 310-313.

Halaj, J., Ross, D.W., and Moldenke, A.R. 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. Oikos **90**: 139-152.

Harder, L. 1979. Winter feeding by porcupines in Montane forests of southwestern Alberta. Canadian Field-Naturalist **93**: 405-410.

Harder, L.D. 1980. Winter use of montane forests by porcupines in southwestern Alberta: preferences, density effects and temporal changes. Canadian Journal of Zoology **58**: 13-19.

Hough, A.F. 1965. A twenty year record of understory vegetational change in a virgin Pennsylvania forest. Ecology **46**: 370-373.

Jones, M.C. 1973. Ecology and life history of the porcupine (*Erethizon dorsatum dorsatum*) in Nova Scotia. MSc. Thesis. Acadia University, Wolfville NS. 146 pp.

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

Krefting, L.W., Stoeckeler, J.H., Bradle, B.J., and Fitzwater, W.D. 1962. Porcupine-timber relationships in the lake states. Journal of Forestry **60**: 325-329.

Logsdon, G. 1999. Wildlife in the Garden: how to live in harmony with deer, raccoons, rabbits, crows and other pesky creatures. Indiana University Press, Bloomington IN. 275 pp.

Martin, R.E., Pine, R.H., and DeBlase, A.F. 2001. A Manual of Mammalogy: With Key to Families of the World, Third Edition. McGraw-Hill, New York, NY. 333 pp.

Meier, A.J., Bratton, S.P., and Duffy, D.C. 1996. Biodiversity in the herbaceous layer and salamanders in Appalachian primary forests. *In* Eastern Old-Growth Forests: Prospects for Rediscovery and Recovery. *Edited by* M.B. Davis. Island Press, Washington, D.C. pp. 49-64

NSDNR. 2004. 2004 Nova Scotia Hunting and Furharvesting License and Summary of Regulations. Department of Natural Resources, Province of Nova Scotia, Halifax, NS. 32 pp.

Owen-Smith, N. 1987. Pleistocene extinctions: The pivotal role of megaherbivores. Paleobiology **13**: 351-362.

Perry, D.A. 1994. Herbivores in Forest Ecosystems. *In* Forest Ecosystems. *Edited by* D.A. Perry. John Hopkins University Press, Baltimore MD. pp. 439-475

Ricklefs, R.E. 1997. The Economy of Nature. W.H. Freeman and Company, New York, NY. 678 pp.

Roberts-Pichette, P., and Gillespie, L. 1999. Terrestrial Vegetation Biodiversity Monitoring Protocols. EMAN Occasional Paper Series No.9. Ecological Monitoring and Assessment Network, Burlington ON. 142 pp.

Roze, U. 1989. The North American Porcupine. Smithsonian Institution Press, Washington, DC.

Shadle, A.R. 1950. Feeding, care, and handling of captive porcupines (*Erethizon*). Journal of Mammalogy **31**: 411-416.

Shapiro, J. 1949. Ecological and life history notes on the porcupine in the Adirondacks. Journal of Mammalogy **30**: 247-257.

Spencer, D.A. 1964. Porcupine population fluctuations in past centuries revealed by dendrochronology. Journal of Applied Ecology **1**: 127-149.

Sullivan, T.P., Jackson, W.T., Pojar, J., and Banner, A. 1986. Impact of feeding damage by the porcupine on western hemlock-Sitka spruce forests for north-coastal British Columbia. Canadian Journal of Forest Restoration **16**: 642-647.

Tenneson, C., and Oring, L.W. 1985. Winter food preferences of porcupines. Journal of Wildlife Management **49**: 28-33.

Whitney, G.C. 1984. Fifty years of change in the arboreal vegetation of Heart’s Content, an old-growth hemlock-white pine-northern hardwood stand. Ecology **65**: 403-408.