# HIERARCHICAL HABITAT SELECTION BY NORTH AMERICAN PORCUPINES (*Erethizon dorsatum*) in Parc National du Bic, Québec, Canada

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#### ABSTRACT

Hierarchical habitat selection was studied in the North American porcupine (*Erethizon dorsatum*) in Parc National du Bic, Quebec, Canada. To establish the study population, 150 porcupines were captured and immobilized using a mixture of ketamine and xylazine. Different drug doses and injection techniques were tested. Best results were obtained by injecting in the tail muscles, which allowed a 50% reduction in dose relative to reported dosage. Hierarchical analysis of habitat selection revealed that although porcupines are generalists at the landscape scale, they display habitat selection at the home range and individual tree scales. Human-used land and conifer forests were least preferred features of home ranges. Trembling aspen was found to be preferred over other deciduous trees, except for fruit-producing trees, which came out as being even more preferred at the tree scale. This study shows the importance of a multi-scale approach that includes fine-scale selection.

### Résumé

La sélection hiérarchique de l'habitat a été étudiée chez le porc-épic d'Amérique (*Erethizon dorsatum*) au Parc National du Bic, Québec, Canada. Pour établir une population d'étude, 150 porcs-épics ont été capturés et immobilisés avec un mélange de kétamine et de xylazine. Différentes doses d'anesthésiants et techniques d'injection ont été testées. Des résultats optimaux ont été obtenus par injection dans les muscles de la queue, ce qui a permis une réduction de 50% de la dose prescrite. L'analyse hiérarchique de sélection de l'habitat a révélé que malgré que les porcs-épics étaient généralistes à l'échelle du paysage, ils étaient sélectifs aux échelles du domaine vital et de l'arbre. Les milieux anthropiques et les forêts de conifères étaient moins préférés à l'intérieur du domaine vital. Le peuplier faux-tremble était préféré aux autres essences de feuillus, à l'exception des arbres fruitiers qui étaient préférés davantage. Cette étude démontre l'importance d'une approche multi-échelles incluant la sélection à l'échelle fine.

#### PREFACE

### **Contribution of authors**

This thesis consists of two manuscripts, both of which I wrote. Chapter I is a manuscript co-authored by Dominique Berteaux and myself on the methods of chemical immobilization we have elaborated for safer porcupine handling. This paper is in the format of the journal it was submitted to in June 2002, which is slightly different from the rest of the thesis. Chapter II is the marrow of this thesis, a manuscript on hierarchical habitat selection of the porcupine co-authored by Dominique Berteaux, Ilya Klvana and myself, which is soon to be submitted. Each of these manuscripts contains references pertaining to their respective subjects, which complement the literature review contained in the general introduction and conclusion.

Dominique Berteaux, my masters' supervisor and co-author of both manuscripts, provided supervision during the preparation, fieldwork, analysis and writing. He also suggested corrections to earlier versions of both manuscripts.

Ilya Klvana, co-author of the manuscript in chapter II, provided editing comments on earlier versions of the manuscript as well as extensive help on the field. Regarding fieldwork, I elaborated and fine-tuned the anaesthesia protocol. Ilya Klvana and I jointly adapted capture techniques to porcupines and to our field conditions. Telemetry was performed by two field assistants and myself.

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I called Ilya Klvana in the beginning of the project for help with the fieldwork, and eventually he joined our team to conduct his own project. This was fortunate for me, as he became an important part of this chapter of my life. Ilya, all the late-night discussions, ideas, help and friendship shared along the way were essential to me and will always be remembered.

In total I spent a whole year on the field, with an exceptional crew: Isabelle Lessard, Mathieu Charette, Cédric Daguerre, Brandee Diner (volunteers), Angie Pelletier (wildlife technician intern), and Caroline Trudeau (NSERC summer assistant). My summer 2001 crew was the best I could have dreamed of: Marie-Andrée Giroux (NSERC summer assistant) and Émilie Robert (volunteer) valiantly sought porcupines, in solitary, through day and night, dense forest, mosquitoes and rugged terrain, while Martin Riopel (volunteer), unaided, sampled the vegetation of the whole study area. Julie Roberge (wildlife technician) had the difficult task of keeping crews and camp well organized, as well as being in the field, and her meticulous work was invaluable to me.

Parc National du Bic and their staff provided logistic support, building materials for the camp, their basement for our office, communication facilities and help. Research was supported by grants from the Natural Sciences and Engineering Research Council of Canada and the Fonds pour la Formation des Chercheurs et l'Aide à la Recherche du Québec to D. Berteaux. Capture techniques and immobilization procedures were approved by the McGill Animal Care Committee (permit # 4213) and the Société de la Faune et des Parcs, Gouvernement du Québec (permit # 20000417-001-01-S-P).

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exploration of my data. Kieran O'Donovan's project on 4<sup>th</sup> order selection was also helpful in the same manner.

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#### **GENERAL INTRODUCTION AND LITERATURE REVIEW**

Conservation of biodiversity has increasingly become the centre of public concern in the last decades. Sometimes, effective actions can only be taken when a species is found to be vulnerable or in danger of extinction. These attempts, if they result in saving species, lead to populations with restricted gene pools, which are more vulnerable to environmental change. Conservation efforts would be more effective if the approach was more preventative. To achieve this, efforts should be placed, through fundamental research, into accumulating knowledge on the ecology of species and into understanding key ecological and behavioural processes at work in healthy populations. Since protecting habitat is one of the best ways to conserve a species, knowledge on habitat selection is a key element to guide conservation efforts.

### Habitat selection

Habitat use can be defined as the quantity of a resource an individual utilizes in a period of time, whether it is food, space for mating and rearing young, shelters, or other factors necessary for survival and reproduction. If an animal does not use its habitat in proportion to the availability of resources, its habitat use is said to be selective. Finally, the preference of an individual for a given component indicates the probability of that component to be chosen, given that it is as equally available as others (Johnson 1980).

Habitat selection, although it has been the subject of many studies (Schaefer and Messier 1995; Poole et al. 1996; Mysterud et al. 1999; Aberg et al. 2000; Hjermann 2000; Larivière and Messier 2000; Poole et al. 2000; Potvin et al. 2000; Rettie and Messier 2000; Rolstad et al. 2000; Kazmaier et al. 2001; McLoughlin et al. 2002; Russo et al. 2002; Courtois et al. In Press) remains a poorly understood ecological process, especially at the scale of home ranges and landscapes (Rolstad et al. 2000).

In many cases, the most obvious way that a species uses resources is by feeding on them, yet it is difficult to perceive selectivity because individuals can feed on many species simultaneously (Snyder and Linhart 1997). Four orders or scales of selection, described by Johnson (1980), are generally used in the literature. First-order selection is the selection of the distribution range of a species. Second-order selection is the process through which an individual selects its home range within the landscape. Third-order selection relates to the selection of habitat components within the home range. Finally, fourth-order selection is the selection of an item (*e.g.* a food item) amongst available ones within the habitat component selected at the third order.

These orders are the basis of the concept of hierarchy in habitat selection (Johnson 1980; McLoughlin et al. 2002). The hierarchical approach defines what is considered as available at each order, based on the selection at the order below. For example, once its home range is established, an animal bases its subsequent decisions on the resources that are available in its home range. Hence selection of resources within the home range is of higher order than (*i.e.* depends on) selection of the home range within the landscape. Furthermore, usage data on a particular tree species is compared to the availability of other tree species within the habitat patch the animal is in.

Taking coarse-scale selection only as the basis of research and management decisions, while ignoring fine-scale patterns (*i.e.* single-scale approach) might give a misleading portrait of patterns of habitat selection for a given species (McLoughlin et al. 2002). Hence much effort has to be dedicated to exploration of habitat selection as a multi-scale, hierarchical process (Wiens 1989; Aberg et al. 2000).

### The North American Porcupine: Ecology and habitat selection

The North American porcupine (*Erethizon dorsatum*) is a 5-13 kg rodent, strictly herbivorous, which crossed the Isthmus of Panama in the Pleistocene and spread throughout North America afterwards (Banfield 1974). The species occupies many ecosystems of North America (Banfield 1974) but is mostly found in forests. Their whole body is covered with a characteristic armour of quills. Females are on average smaller than males. Porcupines mate in the fall, and a single young is born after 209 to 217 days of gestation, twins being rare (Banfield 1974). Juvenile porcupines are precocial, they weight around 500g at birth, and are born with their eyes open and soft quills grown. Quills quickly harden as they dry. They reproduce at two and a half years of age.

The porcupine is a useful subject for habitat selection studies for several reasons. First, literature on its summer habitat preferences is limited (Griesemer et al. 1998), hence there is much to learn from this study. Even if habitat selection of porcupines is not well known, there are several studies providing background information, although most were done during winter and at the tree level. During summer, porcupines feed on leaves of

trees such as linden (*Tilia Americana*), largetooth aspen (*Populus grandidentata*), trembling aspen (P. tremuloides), beech (Fagus grandifolia), white ash (Fraxinus americana), red oak (Quercus rubra), white oak (Q. alba), paper birch (Betula *paperifera*), red maple (*Acer rubrum*) and sugar maple (*A. saccharum*) (Roze 1989; Griesemer et al. 1998). To fulfill their winter food needs, they feed on the bark of trees such as paper birch, white pine (Pinus strobus), and tamarack (Larix laricina) (Curtis 1941, 1944; Spencer 1964; Gill and Cordes 1972; Speer and Dilworth 1978; Harder 1980; Roze 1984; Payette 1986; Sullivan et al. 1986; Roze 1989; Snyder and Linhart 1997; Zimmerling and Croft 2001). The species is a feeding generalist at the population level, but that individuals may specialize on certain food items (Snyder and Linhart 1997). Snyder and Linhart (1997) also suggest that feeding patterns of porcupines may be influenced by biochemical and genetic variability of potential food trees, meaning that there is at least some level of selective herbivory. Porcupine use existing cavities (e.g. rock cavities, tree stumps, hollow trees, culverts, underneath buildings) as dens in winter (Marshall et al. 1962; Roze 1984, 1987; Griesemer et al. 1996, 1998). Dens are sometimes shared between two or more individuals, and potentially allow predator avoidance, social interactions, and have a thermal function (Griesemer et al. 1996). Den location presumably plays a role in the porcupine's pattern of tree utilization in winter (Roze 1987; Griesemer et al. 1996; Snyder and Linhart 1997; Griesemer et al. 1998; Zimmerling and Croft 2001). Complementarily, Zimmerling and Croft (2001) have shown that porcupines use within-site variation in tree species to select den sites with a higher proportion of desired tree species. Preliminary observations suggested that porcupines in our study area use dens in the summer more than previously reported in the literature.

Secondly, the porcupine is the only arboricolous-folivorous mammal in North America. Since porcupines are tree dwelling, their "food item" is easily defined as each tree they feed on. This is particularly useful in 4<sup>th</sup> order selection, because we can easily ensure what species an individual is using, which could be more difficult with other non-arboreal herbivores (*e.g.* animal grazing in a meadow where a variety of plants grow).

Third, this species is slow moving, allowing direct observations to be performed using radio-telemetry on foot. In addition to being cost effective relative to aircraft-based telemetry, we can collect highly precise data from direct observations. When 4<sup>th</sup> order selection is determined after an animal's position was estimated using triangulation, habitat use can only be estimated from a sample collected *a posteriori* (*e.g.* Lesage et al. 2002).

The objectives of this study are to 1) improve existing chemical immobilization procedures for the North American porcupine 2) test whether porcupines exhibit different patterns of habitat selection at three spatial scales during summer, 3) investigate the potential divergence in habitat selection between sexes as well as patterns of den use. As a whole, this thesis will contribute to our limited knowledge of porcupine ecology.

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# CHAPTER I: IMMOBILIZATION OF NORTH AMERICAN PORCUPINES (*Erethizon Dorsatum*) Using Ketamine And Xylazine

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## IMMOBILIZATION OF NORTH AMERICAN PORCUPINES (*Erethizon Dorsatum*) Using Ketamine And Xylazine

#### ABSTRACT

We performed 345 immobilizations on 150 North American porcupines (Erethizon dorsatum) using a mixture of ketamine hydrochloride and xylazine hydrochloride. A subsample of 184 immobilizations performed on 124 individuals from 04 May to 07 November 2000 and from 22 January to 30 April 2001 is thoroughly analyzed. In contrast to published procedures, we found that injecting drugs in the tail muscles was more effective than in the longitudinal muscles of the lower back, since tail injections decreased the need of multiple injections by 26%. Using tail injections, we were able to reduce the dose by 50% from other published reports without significantly affecting induction, immobilization, standing or recovery times. We recommend that injection of 5 mg KH/kg and 2 mg XH/kg in the tail become the standard procedure to immobilize North American porcupines. Body mass significantly affected the induction and standing times for single injections performed in the tail, irrespective of dose or sex. Sex, dose, and mass had no effect on the quality of immobilizations and the respiration rate of individuals during immobilization. We report a 0.87% mortality rate using a mixture of ketamine hydrochloride and xylazine hydrochloride, and suggest ways to further decrease this rate.

*Key words*: North American porcupine, *Erethizon dorsatum*, immobilization, ketamine, xylazine, injection site, dosage, mortality risks

### **INTRODUCTION**

Capture and immobilization of North American porcupines (*Erethizon dorsatum*) present unique challenges because the species is defended by a dense armour of quills, which makes manipulations potentially dangerous for both porcupines and investigators. In addition, porcupines are often found in dens and trees, which requires special safety measures for immobilized or recovering individuals, as sub-optimal procedures can result in individuals falling from trees or suffering from respiratory obstruction in dens.

Techniques currently used to immobilize porcupines are varied and some confusion is found in the literature concerning which technique should be used. Roze (1987) used ketamine hydrochloride (KH) (10mg/kg). Sweitzer (Sweitzer, 1996; Sweitzer and Berger, 1998) used a mixture of KH (10mg/kg) and xylazine hydrochloride (XH) (4mg/kg), but Sweitzer and Berger (1992), which was based on the same fieldwork as Sweitzer (1996) and Sweitzer and Berger (1998), incorrectly reported a dosage 10 times higher than the dosage they used in reality. Hale et al. (1994) used Telazol® (a 1:1 mixture of tiletamine hydrochloride (HCl) and zolazepam HCl) at doses varying from 7mg/kg to 10mg/kg. Recovery periods using Telazol® were excessively long, and some porcupines were still stumbling 250 minutes after injection (Hale et al. 1994). More recently, Zimmerling and Croft (2001) used KH (10mg/kg) combined with XH (1mg/kg).

Ketamine HCl has been widely used on many species of carnivores and herbivores (Pond and O'Gara 1996). Some of its side effects are apnea, excessive salivation, and hypothermia. Administered alone, it can also cause convulsions, muscle rigidity and violent recoveries. However, KH is often given in combination with other drugs such as XH, in order to reduce its adverse effects (Lumb and Jones 1984b; Pigozzi 1987; Pond and O'Gara 1996; Mudappa and Chellam 2001). Administered via intramuscular injection, the KH-XY mixture induces rapid non-cumulative anesthesia while insuring a wide margin of safety (Pigozzi 1987), an attribute that is critical in fieldwork.

In 2000, we started a long-term study of a porcupine population that required marking all individuals in our study area. We therefore needed to find a safe way to repeatedly immobilize individuals. This need was exacerbated by the increasing attention paid by Animal Care Committees to procedures involving wild animals. Published reports allowed us to exclude the use of Telazol®, given the excessively long recovery periods

(Hale et al., 1994) that were incompatible with our intense capture schedules. We therefore used a KH-XY mixture and, given the diversified procedures reported in the literature, collected data to answer four specific questions: 1) what is the most appropriate site of injection for immobilization of porcupines, 2) what are the effects of dosage of KH-XH on the different parameters of anesthesia, 3) what is the optimal dosage of KH-XH that should be administered given that three common constraints to wildlife immobilization are to minimize induction time, recovery time, and cost of immobilization, and 4) what are the mortality risks when immobilizing North American porcupines with KH-XY.

#### MATERIALS AND METHODS

### **Study Area**

Porcupines were captured and immobilized in Parc National du Bic (68°46W, 48°21N), Québec, Canada. One hundred and fifty individuals were captured 735 times and immobilized 345 times. Detailed data were recorded for a subsample of 184 immobilizations (124 individuals: 60 females, 64 males), which form the basis for the current analysis. Immobilizations were carried out from 04 May to 07 November 2000 and from 22 January to 30 April 2001. All immobilizations were necessary to ear-tag, measure, or radio-collar the animals.

### Immobilizations

Immobilizations for which we gathered detailed data (n=184) were performed during night capture sessions. Most of the time (n=146), individuals were captured while feeding or traveling on the ground using a modified dip net (3.5 cm mesh-size). Thirtyeight immobilizations were performed after porcupines where captured using one of the following methods: dip net while porcupine was in a tree, gloved hands (PVC coated gloves with leather work gloves underneath), noose pole, vertical trap (3 or 4 live traps (Tomahawk Live Trap Co, Tomahawk, Wisconsin, USA) strapped against tree trunk), or guiding porcupine down trees using long aluminum or fibreglass tent poles. Once captured, animals were weighed in a net to adjust the dose to their body mass. Injections were administered intramuscularly at one of two sites: 1) longitudinal muscles (*Longissimus dorsi*) than run along the vertebral column in the lower back (called "back" hereafter) or 2) muscles at the base of the tail halfway between the spinal column and the edge of the tail ("tail"). Injections were performed using a hand-held syringe while porcupines were restrained in the net (back) or grabbed by the tail with one gloved hand (tail).

Porcupines were administered a mixture of 100 mg/ml KH (Vetalar® (100 mg/ml) Vetrepharm Canada Inc., London, ON, Canada) and 20 mg/ml XH (Anased® (20 mg/ml) Novopharm Limited, Toronto, ON, Canada) at a 1:2 ratio. Following the procedures used by previous authors, we initially injected doses of 10 mg KH/kg and 4 mg XH/kg. This dosage will be referred to as "full dose" hereafter. During our study, we lowered the doses in order to determine the lowest dose compatible with safe manipulation (tagging or radio-collaring). We always used the 1:2 KH-XH ratio. A second dose was administered after 15 minutes if there was no sign of drug effect or if the individual was not immobilized sufficiently for manipulations to be safe. If necessary, a third dose was administered 15 minutes after the second dose.

### **Measured parameters**

*Induction time* is defined as the time lapse between injection of the drug and its induction, when the animal could be handled safely, which usually corresponded to the animal rolling down to its side. This state is also referred to as loss of righting reflex (Pond and O'Gara 1996) or cumbancy (Belant, 1991). *Immobilization time* is the time elapsed between induction and the time when the porcupine first lifts its head. *Standing time* is the amount of time elapsed from the end of immobilization to recovery of righting reflex, that is when the porcupine first stands on its four legs. *Recovery time* is the amount of time elapsed between the time when the porcupine first stands on its four legs and the time when all signs of intoxication disappear.

During immobilization procedures, we collected data on induction time, respiration rate, immobilization quality, immobilization time, standing time, and recovery time. Immobilization quality was classified as deep (animal perfectly still during manipulations), intermediate (slight movements or muscle tremors, and/or vocalizations), and shallow (movements in response to stimuli, animal difficult to manipulate because state of immobilization never fully reached). During our first field season (May to November 2000), animals were attended until completely recovered. After we gained confidence in our immobilization techniques (January to April 2001), porcupines were left to fully recover by themselves once they were able to defend themselves against potential predators by erecting their quills and striking their tail.

### Statistical analysis

A G-test (Fowler et al. 1998) was used to test whether the number of injections required to immobilize the animals differed between the two sites of injection. A series of ANCOVAs with induction, immobilization, standing, or recovery times as the dependent variable, body mass and dose as covariates, and the effect of sex were performed. When needed, data were log-transformed prior to the ANCOVA to respect the assumption of normality. All differences in means between two groups were tested using Mann-Whitney U tests since the normality assumption was always violated (Fowler et al. 1998). A G-test adjusted with Williams' correction factor (Fowler et al. 1998) was used to test if dose had an impact on the need for multiple injections. Tests were performed using SYSTAT version 9 (SPSS Inc. 1998). Significance level was set at 0.05.

### RESULTS

### Site of injection

A single injection was sufficient to safely immobilize porcupines in 94% of cases when drugs were injected in the tail (n = 80, Table 1). In contrast, a single injection was sufficient to safely immobilize porcupines in only 74% of cases when drugs were administered in the back (n = 104, Table 1). These two proportions are significantly different (G = 14.97, P < 0.01, df = 2). A third injection was never required when injecting drugs in the tail, but a third injection was necessary in 3.9% of cases when drugs were injected in back. To understand the origin of the difference in efficiency of drugs between the two injection sites, we compared the initial KH dose (XH always given in constant proportion to KH) that was given in each case. Mean initial dose of KH was significantly lower for tail than for back injections (Tail: N = 80, mean =  $6.52 \pm 1.95$  mg KH/kg; Back: N = 104, mean =  $9.46 \pm 1.57$  mg KH/kg; Mann-Whitney, U = 7158.00, P < 0.001, Table 1), indicating that the higher efficiency of tail injection was obtained despite a lower average dosage. Initial KH dose was significantly lower for immobilizations that required multiple (two or three) injections than for immobilizations reached after a single injection (Tail: single  $6.64 \pm 1.95$  mg/kg, multiple  $4.75 \pm 0.37$  mg/kg, Mann-Whitney U = 317.5, P = 0.01; Back: single  $9.67 \pm 1.44$  mg/kg, multiple  $8.84 \pm 1.77$ , Mann-Whitney U = 1375.5, P = 0.013).

Reaching a safe level of immobilization after a single injection was our priority. A preliminary analysis of our results had suggested that tail injections were the most effective. We therefore focused our efforts on tail injections from 13 July to 07 November 2000 and from 22 January to 01 April 2001. The following results deal only with immobilizations that required a single injection and were performed in the tail.

### Effect of dosage on measured parameters

Immobilizations that required a single injection and were performed in the tail (n = 75) were done on 28 females and 47 males, with respective average body masses of  $7.05 \pm 1.76$  kg (range = 3.50 - 10.55) and  $7.98 \pm 1.74$  kg (range = 4.30 - 10.60). Mean induction time was  $5.2 \pm 2.8$  min (range: 0.5 - 14.8, n = 71), mean immobilization time was  $31.6 \pm 13.1$  min (range: 8.5 - 77.0, n = 49), mean standing time was  $9.4 \pm 7.5$  min (range: 0 - 29, n = 46), and mean recovery time was  $29.5 \pm 16.8$  min (range: 11.8 - 98.3, n = 27). The 0 values obtained for standing time correspond to two individuals that woke up suddenly and stood up. Mean respiration rate during the immobilization period was  $48.3 \pm 20.9$  inspirations per minute (range = 18 - 120, n = 67). ANCOVAs showed that a higher body mass (m) resulted in a longer induction (i) (F = 16.27, P < 0.001) and standing (s) (F = 6.478, P = 0.015) times. Mass had no effect on immobilization and recovery times, while sex and dose had no effect on induction, immobilization, stand and recovery times. The relations between mass and induction and standing times can be described by log(i) = 0.067m + 0.136 and log(s) = 0.170m + 0.70. There was no effect of sex, dose or mass on the quality of immobilization or the respiration rate of individuals during immobilization.

### **Optimal dosage**

Our initial results indicated that injection in the tail was more appropriate than injection in the back, and that there was no effect of dosage on the standard descriptive measures of immobilization. Accordingly, we focused subsequent investigation on injections performed in the tail and we compared immobilizations performed with 29%-49% of the full dose to those performed with 50-114% of the full dose. Multiple injections occurred more often at doses less than half of full dose. A second dose was necessary in 4 cases when the initial dose was inferior to 50% of full dose, as opposed to 1 case when a dose greater or equal to 50% of full doses (n=18) were not as constantly effective as doses greater or equal to 50% of full dose (n=62) ( $G_{aid} = 6.99$ , P < 0.01, df = 1).

### Mortality

Over a total of 345 immobilizations, three porcupine deaths (0.87%) were likely attributable to immobilization. Here we describe the context of each death in order to help future investigators to further refine our procedures. The first porcupine received a dose of 7.0 mg KH / kg + 2.8 mg XH / kg (body mass = 5.7 kg). On 07 March 2001, after being radio collared, it was left partially recovered under the low branches of a conifer tree. The next day the porcupine was found dead, head first in one of our snowshoe tracks, 5 meters from where it was left recovering. The temperature during immobilization was -8°C and reached -13°C during the following night. This porcupine had previously been immobilized twice (25 May 2000 with 10.7 mg KH/kg + 4.3 mg XH/kg (body mass = 7.5 kg); 28 June 2000 with 3.7 mg KH/kg + 1.5 mg XH/kg (body mass = 8.1 kg)) and had shown a normal response to drugs.

The second porcupine to die had received a dose between 10 mg KH /kg + 4 mg XH /kg and 5 mg KH / kg + 2 mg XH / kg (body mass = 5.9 kg; exact dose not recorded) on 11 May 2001. The porcupine stood up before the end of the tagging procedures. After being tagged, but before having fully recovered from the immobilization, it was placed in a rock cavity, with its back and tail facing out. The porcupine was found in the same position one week later. The physical condition of this animal was very poor, as shown by

inspection of the bone marrow of one femur that contained virtually no fat. This porcupine had been immobilized for the first time.

The third porcupine died during the induction phase. It received a dose of 6.3 mg KH/kg + 2.5 mg XH/kg (body mass = 9.45 kg) on 16 June 2001. The animal seemed stressed before injection. This porcupine had previously been immobilized twice (3 May 2000, 10.3 mg KH/kg + 4.1 mg XH/kg (body mass = 7.8 kg); and 05 June 2000, 10.1 mg KH/kg + 4.0 mg XH/kg (body mass = 8.9 kg), and had responded to drugs with unusually short induction times of 0.5 and 2 minutes.

### DISCUSSION

Our results show that for North American porcupines, administration of KH/XH in the tail requires multiple injections less frequently and require a lower dosage than in the back.

### **Mechanics of injection**

When the KH-XH mixture was administered in the back, a significantly higher dose was required to safely immobilize the animal than when injection was performed in the tail. For both sites of injection, however, the initial dose used was significantly higher for single than for multiple injections.

Injections in the back yield a higher probability to miss muscles because they can be very thin, especially in late winter and spring when porcupines have exhausted most of their fat and protein reserves. Autopsies of road-killed animals at this time and throughout our field season clearly revealed how easily a needle can go straight through back muscles and result in an intraperitoneal injection. Since the doses we used were intended for intramuscular injection, their intraperitoneal effectiveness is likely lower. An additional reason to avoid back injections resides in the risk of peritonitis associated with back injections.

On the other hand, the tail of porcupines is highly muscularized, since it is used as a prop when porcupines climb trees and as a defence weapon against predators. Tail muscles can hardly be missed during injections, as long as care is taken to avoid the bones. Inserting the needle at a 45° angle from the vertical while holding the tail from underneath is a safe way to perform intramuscular injections. Tail muscles of porcupines do not atrophy as much as back muscles in late winter, which is another reason to favour tail injections.

Drugs can also be administered in the thigh muscles to immobilize porcupines (Hale et al. 1994). We did not include this injection site in our methods, as we find that the tail is a safer injection site for the following two reasons: 1) the hind leg is a more complex anatomical member with major blood vessels, tendons and nerves that can potentially be damaged by a needle, especially if the animal is attempting to escape, 2) injecting in the tail requires the investigator to hold the tail, hence decreasing the risks of porcupine attack.

### **Optimal dosage**

Porcupines with a greater body mass took longer to reach a safe level of immobilization and to stand on their four legs after they woke up. Since there was no significant effect of dose on induction time, there is no reliable means of overcoming this potential difficulty. Although the drug is induced more slowly in larger animals, they will stay immobilized for the same period and fully recover within the same period.

The dose of KH-XH did not affect immobilization parameters within the dose range we tested, indicating that a dose lower than the published full dose of 10 mg KH/kg + 4 mg XH/kg (Sweitzer, 1996; Sweitzer and Berger, 1998) can be used without affecting immobilization quality. Focusing on injections in the tail, we established that doses inferior to 5 mg KH/kg + 2 mg XH/kg have a greater chance of requiring a second dose. Therefore we suggest that doses half those reported in the literature are just as effective, while they increase safety and decrease costs of immobilization. Our results contrast with Plumb (1999) who indicates that an increase in KH dosage should increase the duration of immobilization (but not the intensity). The KH-XH mixture might behave differently than KH alone, or porcupines might handle the drug differently than animals treated in veterinary practice as referred to by Plumb (1999).

The fact that doses lower than 50% of the full dose were less effective than doses 50-100% of the full dose, and that we detected virtually no effect of dosage in the parameters of immobilization lead us to use 5 mg KH/kg and 2 mg XH/kg (50% of the full dose) as a standard for North American porcupine immobilization.

### Mortality

We were not able to determine the cause of mortality for the three individuals that died during or following our immobilizations, but hypothermia or drug hypersensitivity (Lumb and Jones 1984a) may be involved. One may have died from respiratory obstruction due to an unfavourable positioning. All three individuals had received their injections in the tail. The second porcupine to die was in poor physical condition, which probably made this individual more susceptible to immobilization complications, although we have immobilized many other individuals in similar condition. The third individual had exhibited a high degree of sensitivity to KH-XH on two occasions before the fatal dose, as shown by the short induction times leading to previous immobilizations. These were perhaps warning signals of a predisposition to complications, and we suggest researchers should be vigilant about these cues. Plumb (1999) reported cardiac arrest and respiratory depression as adverse effects for ketamine, and reduced respiratory rate and bradycardia for xylazine. Although these effects were observed in domestic animals such as dogs, cats and horses, they may also occur in porcupines.

The 0.87% mortality rate we observed in this study is not particularly surprising. Mortality has been observed in other studies using KH-XH (12% on crested porcupines (*Hystrix cristata*) n=17, Pigozzi (1987); 1% on domestic dogs (*Canis familiaris*), n=200, Lumb and Jones (1984b)), Telazol® (1.5% on North American porcupines, n=66, Hale et al. (1994)), or XH (2.1% on mountain goats (*Oreamnos americanus*), n=141, Haviernick et al. (1998)). Some studies have experienced no mortality using KH-XH (on fishers (*Martes pennanti*) n=6, Belant (1991); on coypus (*Myocastor coypus*), n=8, Bó et al. (1994), on common genets (*Genetta genetta*), n=15, Palomares (1993)), and using medetomidine and KH (on California sea lions (*Zalophus californianus*), n=51, Haulena et al. (2000)). Although these references are representative rather than comprehensive, it does show that the mortality rate we described is within the lower range of observed mortality rates.

Our procedures could be improved in two ways. First, XH could be injected alone followed 10 min later with KH, as mentioned by Lumb and Jones (1984b) and tested by Pigozzi (1987). Second, a specific antagonist, Yohimbine, can partially reverse the effects of a KH-XH anesthesia, as it is fully effective against XH but not totally against KH (Plumb 1999). This latter option was suggested by Belant (1991), and could help to shorten recovery time and perhaps prevent mortality when complications arise.

Mortalities are always possible during anesthesia even when all precautions are taken. Consequently, reducing the dose should always be a goal for field biologists. As an example, the dose used to immobilize crested porcupines was progressively reduced from 27 mg KH/kg (Alkon 1984) to 11 mg KH/kg (Pigozzi 1987) to 10 mg KH/kg (Sonnino 1998). Similarly, for the North American porcupine, the dose can be reduced from 10 mg KH/kg + 4 mg XH/kg (Sweitzer, 1996; Sweitzer and Berger, 1998) to 5 mg KH/kg + 2 mg XH/kg as our study shows.

#### CONCLUSION

We propose a new injection site for the immobilization of North American porcupines. Injection of the drugs in the tail dramatically reduces the need for multiple injections compared to injection in the back. In addition, this procedure requires the investigator to hold the porcupine's tail (its best weapon), making manipulations safer. We also show that KH doses can be reduced to 50% of the doses previously reported in the literature (Sweitzer and Berger, 1998) without significantly changing induction, immobilization, standing and recovery times. This reduction in dose has management implications due to the enhanced safety for animals and field workers and the reduced monetary cost of immobilization. We hope attempts will be made to validate similar safety enhancements for other wildlife species.

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### TABLE

Table 1. Initial doses of Ketamine Hydrochloride and Xylazine Hydrochloride administered to porcupines at two sites of injection, and consequences of total number of injections required to safely immobilize the animal. Results based on 184 immobilizations performed in Parc National du Bic, Québec, Canada, from 1 May 2000 to 30 April 2001.

Site of Injection	Number		Ketamine HCl (mg/kg)			Xylazine HCl (mg/kg)				
	of n injections needed	n	Mean	±	SD	Range	Mean	±	SD	Range
Back						4.5 -				1.8 -
	1	77	9.7	$\pm$	1.4	11.4	3.9	±	0.6	4.6
						5.4 -				2.2 -
	2	23	8.7	$\pm$	1.8	10.6	3.6	±	0.7	4.2
						7.4 -				3.0 -
	3	4	9.5	±	1.5	10.7	3.8	±	0.6	4.3
Tail						2.9 -				1.2 -
	1	75	6.6	±	2.0	10.9	2.6	±	0.8	4.3
						4.3 -				1.7 -
	2	5	4.8	±	0.4	5.3	1.9	±	0.1	2.1
	3	0	-		-	-	-		-	-

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### FROM METHODS TO APPLICATION

The habitat selection study presented in chapter II is part of an ongoing long-term study of porcupine ecology that began in 2000.

The methods described in chapter I establish new standards for porcupine chemical immobilization. They can also be useful to researchers or veterinarians using ketamine and xylazine on other animal species, who could reduce doses administered. These techniques allowed us to safely immobilize and radio-collar a sample of animals in our study area in order to study how they use their habitat and whether or not they exhibit patterns of habitat selection. Chapter II presents the details of this effort to describe porcupine habitat selection, using a hierarchical and multi-scale approach.

# CHAPTER II: HIERARCHICAL HABITAT SELECTION BY NORTH AMERICAN PORCUPINES IN SOUTHERN BOREAL FOREST

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#### ABSTRACT

In habitat selection studies, a multi-scale approach is considered necessary to ensure that all elements of selection are depicted and management decisions accurately reflect the needs of the species under study. We examined hierarchy in summer habitat selection in North American porcupines (*Erethizon dorsatum*) in Eastern Canada at landscape, home range, and tree scales. We used radio telemetry to find and observe animals visually in order to record their behaviour and exact location in the habitat. Den use in summer was unexpectedly high for some of our animals, which forced us to use a restricted data set for comparison among scales. Although porcupines are generalists at the landscape level, selection patterns appear at the home range and tree levels. Humanused land and conifer forests were least preferred features of home ranges, while trembling aspen-dominated deciduous forests and mixed forests were most preferred. At the tree scale, trembling aspen was found to be preferred over other deciduous trees. However, fruit-producing trees were even more preferred. This study shows the importance of a multi-scale approach that includes fine-scale selection.

**Keywords:** North American porcupine, *Erethizon dorsatum*, hierarchical habitat selection, radio-telemetry, scale ecology, direct observation, den

### **INTRODUCTION**

Issues of scale and hierarchy have become a primary focus in ecological research (Wiens 1989), and have been increasingly considered in habitat selection studies (*e.g.* Johnson 1980; Schaefer and Messier 1995; Rettie and Messier 2000; Rolstad et al. 2000; Chamberlain et al. 2002). Habitat selection, defined as the use of a habitat component disproportionately to its availability, was broken down and ordered by Johnson (1980). First-order selection is the selection of the distribution range of a species. Second-order selection is the process through which an individual selects its home range within the landscape. Third-order selection relates to the selection of the habitat components within the home range. Finally, fourth-order selection is the selection of an item (*e.g.* a food item) amongst available ones within the habitat component selected at the third order. These orders are hierarchical because what is available at each order depends on use at the order above.

The North American porcupine (*Erethizon dorsatum*) is one of the largest rodents of North America (5-13 kg), and is strictly herbivorous. Their body is covered with a characteristic armour of quills. Females are on average smaller than males, and must cope with a long gestation period (209-217 days) and summer-long care of young. The species occupies many ecosystems but is mostly found in forests (Banfield 1974).

Porcupines constitute a unique study model for several reasons. They are the only arboricolous-folivorous mammals in North America, and therefore do not need to cope with interspecific competition for food. In addition, food items chosen by porcupines can easily be identified. Also, being relatively slow moving, then can be precisely localized using radio-telemetry on foot. Finally, knowledge on their patterns habitat selection in summer is limited.

Habitat use by porcupines has been studied throughout North America (*e.g.* Marshall et al. 1962; Gill and Cordes 1972; Harder 1980; Roze 1987; Snyder and Linhart 1997; Griesemer et al. 1998; Zimmerling and Croft 2001), but never in a boreal forest ecosystem. Furthermore, habitat use studies have focused on tree selection, and some on home range size of the porcupine, with most relating to winter. The porcupine is described as a generalist herbivore at the species level, exhibiting selective herbivory at the individual level (Snyder and Linhart 1997). They select trees that differ in their chemical composition and genetically from other trees of the same species (Roze 1989; Snyder and Linhart 1997). Porcupines use existing cavities (e.g. rock cavities, tree stumps, hollow trees, culverts, underneath buildings) as dens in winter (Marshall et al. 1962; Roze 1984, 1987; Griesemer et al. 1996, 1998). Dens are sometimes shared between two or more individuals, and potentially allow predator avoidance, social interactions, and have a thermal function (Griesemer et al. 1996). Habitat selection by the porcupine at the landscape, home range or stand level has rarely (*e.g.* Harder 1980) been examined. Accordingly, the link between habitat selection at various levels remains to be understood for this species. Such an integrative study will contribute to our understanding of spatial scales in habitat selection.

Taking coarse-scale selection as the only basis for research and management decisions, while ignoring fine-scale patterns may give a misleading portrait of patterns of habitat selection for a given species (McLoughlin et al. 2002). Although Rolstad et al. (2000) state that habitat selection "remains a poorly understood ecological process, especially at the scale of home ranges and landscapes", we need to direct further research towards a hierarchical approach integrating many scales of selection simultaneously (Wiens 1989; Aberg et al. 2000). Such a multi-scale approach allows us to compare patterns of habitat selection depicted at each scale, and to understand the hierarchy between them, *i.e.* to see if patterns are constant throughout scales or if they differ. If the habitat selection patterns are different between scales, then it becomes essential to integrate them all to fully understand what habitat components are crucial to fulfill the needs of a given species.

Our objective was to test whether porcupines exhibit different patterns of habitat selection at three spatial scales during summer. Our approach was to assess habitat selection at the 2<sup>nd</sup>, 3<sup>rd</sup> and 4<sup>th</sup> orders of selection simultaneously. To ensure accuracy of our data in space, we used direct observations of radio-tagged individuals instead of triangulation (Garshelis 2000). This approach also allowed us to record the behaviour of animals at each location and its position within in the microhabitat. We further investigated the potential divergence in habitat selection between sexes as well as patterns of den use, because preliminary observations suggested that porcupines in our study area used dens in summer more intensively than previously reported in the literature.

### **MATERIALS AND METHODS**

### **Study Area**

Fieldwork was conducted in Parc National du Bic (68°46W, 48°21N), on the south shore of the St. Lawrence river estuary, Québec, Canada (Figure 1). The 2-km<sup>2</sup> study area is characterized by its rugged topography and a high porcupine density (*ca.* 40 individuals  $/ \text{ km}^2$ ) (D. Berteaux, unpublished).

Habitat is fragmented into small patches ranging from cultivated fields to deciduous, mixed and coniferous forests. This type of mosaic is typical for the region, which accommodates predominant agriculture and forestry industries that have fragmented and modified the landscape with time. Present human activities (tourism) are concentrated along roads, bike trails, and the park administration buildings, which together represent 2.0% of our study area. Trembling aspen (*Populus tremuloides*, hereafter called aspen), eastern white cedar (*Thuya occidentalis*, hereafter called cedar), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*) are the dominant tree species respectively representing 28, 16, 16 and 15% of the total basal area. The presence of serviceberry (*Amelanchier sp.*) and American mountain ash (*Sorbus americana*) along forest edges is noteworthy as porcupines in our study site are fond of their fruit. Our study area belongs to the eastern balsam fir-yellow birch (*Betula alleghaniensis*) ecological domain, in the mid-Appalachian hills ecological region (Grondin et al. 1999).

### **Study Design**

Animal needs vary in time and habitat selection is season-dependent. We worked during the summer season, and defined summer biologically according to the porcupine's life history in our region. Preliminary observations in 2000 showed that porcupines feed predominantly on aspen leaves in summer. Aspen leaves open in late May, which defined the start of summer for this study. In late August, porcupines shift a portion of their diet to the fruits of mountain ash, so we defined the end of the summer period as the third week of August.

### Capture and marking

Porcupines were captured from 19 January to 21 May 2001 throughout our study area and immobilized by intramuscular injection in the tail of a mixture of 5 mg/kg ketamine hydrochloride (Vetalar® (100 mg/ml) Vetrepharm Canada Inc., London, ON, Canada) and 2 mg/kg xylazine hydrochloride (Anased® (20 mg/ml) Novopharm Limited, Toronto, ON, Canada). Details about capture and immobilization methods are described in Morin and Berteaux (in review). All animals were ear tagged and equipped with a Lotek SMRC-5RB VHF transmitter (Lotek Wireless Inc., Newmarket, ON, Canada, L3Y 7B5) mounted on a leather collar.

#### Telemetry

Telemetry locations were performed at regular intervals during the study period to prevent autocorrelation and to provide an unbiased representation of habitat use (Aebischer et al. 1993). Our sampling scheme was equally distributed around the circadian cycle for each individual.

Each time an animal was located using telemetry, the signal was followed to the individual and a visual observation of the porcupine was performed. UTM coordinates were obtained from a hand-held Global Positioning System (GPS). If the animal could not be seen because it was in a deep den or in a tree with a dense foliage, we could still ascertain its geographic position within a 5-10 m radius with our telemetry equipment. This allowed us to record which microhabitat an animal was using (underground or in a tree) whether the animal could be seen or not. Each time a porcupine was located in a den, a unique number was assigned to the den. We recorded den type (rock crevice, tree stump, hollow tree, culvert or building) and assigned a depth category as an index of den quality (category 1 = porcupine can be reached by hand, category 2 = porcupine can be seen but not reached, category 3 = porcupine cannot be seen). We assumed that deep dens were of highest quality because they offer a better protection against predators, biting flies, and temperature extremes.

#### Habitat description

Forest maps from the Ministère des Ressources Naturelles du Québec (MRN), which are intended for forestry purposes, are often used in wildlife studies in Quebec (Ministère des Ressources Naturelles 1995). MRN forest maps provide biologists with a wide range of data such as tree species, tree density, age class, slope class, regeneration, disturbances, origin, surface deposits, and defoliation. The minimum mapped area varies between 2 ha for unproductive land, 4 ha for small timber harvest patches or forest patches within them, or 8 ha for forest stands (Potvin et al. 1999). These forest maps were found to be suitable for wildlife studies by Dussault et al. (2001) and Potvin et al. (1999). However, because of their low resolution and complex habitat classification, both studies concluded that MRN maps are unsuitable for wildlife studies if habitat features that reflect the species' requirements are not defined by these maps, which is most likely the case for species that are not wide-ranging and when the forest mosaic is composed of small patches. Both studies recommended to ground proof MRN maps at the stand level *a priori* to verify its suitability to each case.

Preliminary observations suggested that the MRN map did not have a sufficient resolution to represent the habitat patchiness perceived by porcupines. Porcupines are primarily tree-dwelling animals, using trees almost exclusively when feeding or resting outside of their dens. They largely base their choice of food largely on tree species (Griesemer et al. 1998; Zimmerling and Croft 2001). They use ground vegetation only when they venture out of the forest to feed in adjacent fields. Therefore, we concluded that an accurate knowledge of tree species dominance would be adequate for our purposes. Consequently, we created a forest map with a high cartographic resolution to represent the high forest heterogeneity, but we used a relatively simple classification of vegetation.

To create our map, we used a 1:3000 scale aerial photo taken in 1993 (Photocartothèque Québécoise, Ministère des Ressources Naturelles du Québec, <u>http://photocartotheque.mrn.gouv.qc.ca</u>) scanned at high resolution. This image was imported into Cartalinx software (Clark Labs 1999), where we outlined all the zones of different tree cover. For our 1.82 km<sup>2</sup> study area, we obtained 146 polygons (mean area = 1.25, SD = 1.7 ha, range = 0.014-1.43 ha), which suit the heterogeneity of the landscape closely.

To ground-proof this map and determine the proportion of tree species for each polygon, we sampled 90 of the 112 forest polygons outlined in our study area. The

remaining 22 forest polygons were assigned with a vegetation class based on the aerial photo and our knowledge of the landscape. Species and basal area of trees with a diameter at breast height (DBH) greater than 9 cm (Potvin et al. 1999) were measured using a factor-2 prism (Grosenbaugh 1952) at two stations 20 m apart for each sampling point. The 34 remaining polygons did not require sampling as they were either fields, roads, trails, or buildings.

Since trembling aspen is by far porcupine's preferred food source (Roze 1989; pers. observation), we based our habitat classification on this species (Table 1, Figure 1).

#### **Data Analysis**

We imported the vegetation polygons and the vegetation survey data into Idrisi32 GIS software (Clark Labs 2000) to create the vegetation map. To calculate 100% Minimum Convex Polygons (MCP) (Mohr 1947), we used the ANIMAL MOVEMENTS extension (Hooge and Eichenlaub 1997) to ArcView (Environmental Systems Research Institute Inc. 1998). We outlined our study area by taking the MCP of all locations. This method assumes that all animals have equal access to all these resources, which may not necessarily be the case (Garshelis 2000). Nevertheless, we chose the MCP because it is an objective method, widely used in habitat selection studies, which facilitates comparison with other studies.

Individual home ranges were outlined using the MCP method. Girard et al. (2002) found that the MCP method consistently underestimated home ranges, as opposed to kernel and cluster estimators that tend to overestimate home ranges to varying degrees. As recommended by Stone et al. (1997), we used topographic home ranges, which were computed using the SURFACE TOOLS FOR POINTS LINES AND POLYGONS extension (Jenness 2001). The XTOOLS extension (DeLaune 2001) was used to extract information, such as vegetation data within home ranges, from the different maps.

At the scale of the study area (2<sup>nd</sup> order), we compared the proportion of each habitat type within individual home ranges to the availability of these habitats within the entire study area. At the home range scale (3<sup>rd</sup> order), we compared the proportion of locations in each habitat type for each porcupine to the relative availability of habitat types within its home range. For 4<sup>th</sup> order selection, we analyzed selection by comparing tree species used by porcupines at each observation to the availability of all tree species in

the vegetation polygon it was in. We had to redefine available resources at this scale, because in the classification shown in Table 1 a single species can be in more than one category. Consequently, we used the percent availability of the following species or group of species at the 4<sup>th</sup> order: aspen, cedar, conifer (all conifers species except cedar), fruit-bearing trees (serviceberry and American mountain-ash), deciduous (all deciduous species except aspen and fruit trees). Note that we created a specific category for *Thuya occidentalis* because we suspected this species to be used as a refuge against biting insects during summer (Marshall et al. 1962).

#### **Statistical analyses**

Our study design allowed us to look at habitat selection in a hierarchical manner, tackling the 2<sup>nd</sup>, 3<sup>rd</sup> and 4<sup>th</sup> orders of selection all at once. We used an adaptation of the Aebischer method (Aebischer et al. 1993), which is described in Girard et al. (2002) and Crête et al. (2001) to analyze our data and search for significant patterns of habitat selection at each level. This method uses a MANOVA, [*i.e.* Hotelling's test (SAS Institute inc. 1991)] but without the use/availability ratio transformation proposed by Aebischer et al. (1993). There is, according to Crête et al. (2001), a controversy about the effectiveness of this ratio transformation within the statistical community. Distribution of residuals was multivariate normal (Mardia 1975).

When a significant difference between use and availability was detected, one sample t-tests were used to determine which habitats were selected or avoided. The effect of sex was included in our analysis. The results obtained show selection (use superior to availability) or avoidance (use inferior to availability) of habitat types. In addition to testing for selection/avoidance of each habitat type, Hotelling's test verifies if there is a significant pattern among all habitat types. When such a significant pattern is detected, habitats can be ranked with respect to each other as suggested by Johnson (1980) and Aebischer et al. (1993). In the rankings, ">" indicates a preference for a resource over another, ">>>" indicates a significant preference for a resource over another.

Since habitat use at the 4<sup>th</sup> order was measured in terms of tree species, we could not take this measure when finding porcupines in dens. Comparison between different orders of selection was hence hazardous. To circumvent this problem, we performed our tests on a restricted data set, in which observations in dens were excluded (hereafter referred to as "no den data set"), in addition to the complete data set. The results obtained from this data set were used to compare the different orders of selection. The full data set was used only with 2<sup>nd</sup> and 3<sup>rd</sup> orders of selection, and allowed comparison with other studies.

Differences between sexes in mean home range size and proportion of observations in dens were tested with Mann-Whitney U tests since the normality assumption was always violated (Fowler et al. 1998). Throughout our analyses, we used a 0.05 significance level to reject the null hypothesis. Results are expressed as mean  $\pm$  standard deviation.

#### RESULTS

We followed 17 adult porcupines (9 females, 8 males) from 28 May 2001 to 21 August 2001 and obtained 22-31 locations per animal (n = 433, mean = 25.5, SD = 2.0). This is slightly above the minimum number recommended by Aebischer et al. (1993) for habitat selection studies. Visual contact was made for 275 of our observations (n = 433), yet we could localize and sometimes determine the behaviour of a porcupine without seeing it. Porcupines could be localized in the habitat (ground, tree, or den) under most circumstances (Table 2). Their behaviour was recorded as feeding, resting, travelling, but sometimes could not be determined (Table 2). In 83 cases, the presence of the observed appeared to disturb the porcupine behaviour (Table 2). Our results confirm that porcupines are mostly solitary in summer, as only 3.7% (n = 433) of our observations were made on individuals found to be within 5 m of another individual. Home ranges were highly variable in size. Male home ranges were on average larger (20.9 ± 16.5 ha, range = 6.0-58.4 ha) than female home ranges (15.4 ± 16.9 ha, range = 1.5-58.8 ha), but the difference was not significant (Mann-Whitney U-test = 22.00, P = 0.178).

#### Den use

Porcupines were found in a den 135 times (31.2% of locations). Consequently, the no den data set includes 298 observations. The 17 porcupines used 87 different den sites, which were all rock caverns that are present in great numbers on mountain flanks of our study area. Porcupines used of category 1 dens (low quality) 3.8% of the time, category 2 dens (medium quality) 6.9% of the time and category 3 dens (best quality) 88.5% of the

time. Overall re-use of dens was relatively low, with 63.2% of dens used only once, 25.3% used twice, 4.6% used thrice, and 4.5% used  $\ge 4$  times (n = 87). Dens were used once by the same animal 51.2% of the time, twice 38.8% of the time, thrice 7.0% of the time, and 4 times 3.1% of the time (n = 131). When we look at the proportional use of dens with respect to the individuals (Figure 2), we can see a large of variation from animals that use dens 65% of the time to porcupines that were never observed in dens. The proportion of observations in dens for males (n = 8, mean = 21.1 ± 25.2 %) and for females (n = 9, mean = 41.6 ± 21.8 %) was not significantly different (Mann-Whitney U = 53.00, P = 0.1).

## **Habitat Selection**

## 2<sup>nd</sup> order of selection

*Complete data set* – At the 2<sup>nd</sup> order of selection, no significant selection or avoidance emerged for any of the habitat types (Figure 3a). There was therefore no significant pattern among all habitat types (Wilk's  $\lambda = 0.75$ , F<sub>6,11</sub> = 0.60, P= 0.72).

*No den data set* – For the data set without den locations, human-used land was significantly avoided (t = -2.36, P = 0.031; Figure 3b), but there was no significant pattern among all habitats (Wilk's  $\lambda$  =0.58, F<sub>7,10</sub> = 1.05, P= 0.46).

## 3<sup>rd</sup> order of selection

Results at the 3<sup>rd</sup> order of selection differed from results at the 2<sup>nd</sup> order of selection as we detected significant patterns of habitat selection.

Complete data set – There was a significant pattern of selection for the complete data set (Wilk's  $\lambda = 0.21$ ,  $F_{6,11} = 7.05$ , P = 0.0028). Trembling aspen-dominated deciduous forest (t = 3.05, P= 0.0077) and mixed forest (t = 2.26, P= 0.038) were significantly preferred, and conifer forest (t = -3.11, P= 0.0067), fields (t = -3.96, P= 0.002) and human-used land (t = -4.67, P= 0.003) were significantly avoided. Deciduous forest was non-significantly preferred (t = 1.53, P = 0.15) and aspen-dominated mixed forest was non-significantly avoided (t = -0.71, P = 0.49) (Figure 4a). Since the overall pattern was significant, we could position these habitats with respect to each other to obtain the

following rank D(POTR) > M >>> D > M(POTR) >>> C > F > H (refer to Table 1 for codes).

There was no significant effect of sex on selection at this scale (Wilk's  $\lambda = 0.66$ ,  $F_{6,8} = 0.68$ , P = 0.67).

*No den data set* – For the data set without den locations, there was also a significant selection pattern (Wilk's  $\lambda = 0.27$ ,  $F_{7,10} = 3.73$ , P = 0.03): aspen-dominated deciduous forests were again significantly preferred (t = 2.32, P= 0.033), conifer forest (t = -2.76, P= 0.014) and human-used land (t= -4.32, P= 0.0005) were again significantly avoided, but fields were nearly significantly avoided (t = -2.08, P= 0.054), with deciduous (t = 1.54, P = 0.14), mixed (t = 1.34, P = 0.20) and aspen-dominated mixed (t = 0.61, 0.55) forests not significantly preferred (Figure 4b). Hence we could rank the habitats as D(POTR) >>> D > M > M(POTR) > F >>> C > H.

There was a significant effect of sex in the aspen-dominated mixed forest ( $F_{3,13} = 5.34$ , P = 0.038), where females showed a stronger preference for this habitat type than males. No significant pattern came out to put this trend in perspective with other habitats (Wilk's  $\lambda = 0.61$ ,  $F_{7,7} = 0.64$ , P= 0.72).

## 4<sup>th</sup> order of selection

*No den data set* – At the 4<sup>th</sup> order of selection, a significant pattern was detected (Wilk's  $\lambda = 0.31$ , F<sub>4,13</sub> = 7.28, P = 0.0026). Fruit trees were significantly preferred (t = 3.04, P = 0.0078), aspen (t = 1.88, P = 0.079) and cedar (t = 0.55, P = 0.59) were preferred –although not significantly –and all other deciduous (t = -2.30, P = 0.035) and conifer (t = -2.62, P = 0.019) species were significantly avoided (Figure 5). Since the overall pattern was significant, we can illustrate this significant pattern by ranking these species or group of species in the following manner: fruit trees >>> POTR > THOC >>> deciduous > conifer.

#### DISCUSSION

#### Den use

Where rock dens are present, porcupines use them more than any other type of den (Griesemer et al. 1998). Rock dens are present in great numbers in our study area,

and although we have not performed a systematic inventory, we can say with certainty that den availability is not a limiting factor in our study area. Given that each animal used the same den once or twice in 90% of cases, and that the quality of dens was good because 89% of the time porcupines were found in category 3 dens (highest quality), we can further affirm that our study area was offering all the protection opportunities needed.

Porcupines are known to use dens extensively as shelters during the winter (Roze 1987; Griesemer et al. 1996, 1998; Zimmerling and Croft 2001). In other seasons, den use is more sporadic and most of the summer is spent in trees (Marshall et al. 1962; Roze 1984, 1987; Griesemer et al. 1996, 1998). In our study area, there seemed to be a gradient of den use among the animals we followed: from individuals spending the vast majority of their time in trees for both feeding and resting, hence not using dens at all or relatively rarely, to others that primarily used dens to rest, using trees only to feed. Marshall et al. (1962) suggested that porcupines climb trees to escape mosquitoes, which could be the case here. Dens could be an alternative for the same purpose, explaining this gradient in den use strategies.

#### Habitat selection

Porcupine usage of habitat was selective at some, but not all scales, which brings us to compare the three levels of habitat selection and evaluate the hierarchy among these levels. We must note that the majority of standard deviations for mean proportion of use include 0, which indicates that habitat use by porcupines is extremely variable, making detection of selection patterns difficult.

At the  $2^{nd}$  order of selection, *i.e.* selection of a home range within the study area, porcupines established home ranges with a habitat composition that was not significantly different from the proportions available within the landscape. There was no effect of sex at this scale. Only human-used land (roads, trails and buildings) came out as being avoided in the no den data set. In essence, we can say that both male and female porcupines do not show a pattern of habitat selection at the  $2^{nd}$  order of selection, and that their use of habitat is in proportion to what is available in the whole study area. The study area as a whole therefore seems suitable for them in general, which makes detection of selection patterns difficult at the  $2^{nd}$  order (Aberg et al. 2000).

At the  $3^{rd}$  order of selection, which corresponds to selection of habitat within an individual's home range, selection patterns emerged. According to our results, porcupines preferably choose deciduous forest with aspen dominance and mixed forest. This is not very surprising knowing that aspen is the principal food source in their diet (73% of our observations of feeding animals were in aspen, n = 33). They seem to prefer getting to aspen where it is dominant, as opposed to where it is mixed with conifers, a habitat that is used in proportion to its availability. Unexpectedly, they prefer mixed forest to aspendominated mixed forest, which goes against our first impression that aspen-containing habitats should be selected. It is perhaps true for females, which preferred aspendominated mixed forest significantly more than males. But then why would males prefer mixed to aspen-dominated mixed forest? Perhaps mixed forest offers advantages that are worth the extra movements in and out of this habitat that females caring for young cannot afford (Arthur et al. 1996). Overall, mixed forest was used to a greater extent.

Porcupines avoided pure conifer forests, fields and human-used land. Pure conifer forests are not very attractive in summer because they lack food. Conifer forest avoidance was consistent with the avoidance of conifer trees other than cedar at the 4<sup>th</sup> scale. Note that conifer forest and conifer trees are, at all levels, the most available resources.

We did not take behaviour into account at the 4<sup>th</sup> order to differentiate between trees that were used for feeding or resting because in 21% of observations in trees the behaviour of the porcupine was disturbed. Instead of removing these observations from the data set and then use behaviour in our analyses, which could perhaps yield biased conclusions, we preferred to use tree observations irrespective of behaviour. We suggest that future studies should find means to circumvent this problem. Porcupines are cryptic animals that are difficult to find in a forest, and can detect humans and stay immobile long before they are found.

Some porcupines, but not all, use fields at night during summer for feeding purposes. This restriction in usage of fields is probably why they appear avoided or least preferred. Trails and roads are seldom used, and mostly as "highways" in night travelling as we witnessed regularly during our patrols. Of course the chance of tracking an individual down using telemetry at the exact moment where it is walking on a trail is extremely low (and never happened during our study), which is why this habitat is one of the least preferred ones. These three least preferred habitats were similarly classified in the results obtained from the no den data set and from the complete data set, showing that they are a fundamental characteristic of the porcupine habitat selection in this type of ecosystem.

The 4<sup>th</sup> order of selection showed that fruit trees were very important to porcupines, especially to males. We used the ripening of mountain-ash fruits to determine the end of the "porcupine summer", to focus on the summer diet. Hence this result was unexpected. Perhaps some animals were anticipating the ripening of mountain-ash fruits in late August and eating the leaves while visiting the trees, explaining this result.

The no den data set confirmed also that aspen alone was relatively important for porcupines, especially for females, even though it is so widespread in our study area. As a consequence of this nearly monospecies diet, all other species of deciduous trees are ranked lower in porcupine preference. Eastern white cedar being the favoured resting tree species of porcupines, it makes sense that other conifers were used less than they were available.

Most research on porcupine habitat use considered solely the tree level (4<sup>th</sup> order of selection) (*e.g.* Marshall et al. 1962; Gill and Cordes 1972; Harder 1980; Roze 1987; Snyder and Linhart 1997; Griesemer et al. 1998; Zimmerling and Croft 2001), but comparison of our results with these is difficult since most concern winter use, and the tree species available in those studies during winter are not present in our study area.

However, there is one exception. Griesemer et al. (1998) looked at porcupine summer preferences, including some tree species present in our area. In their study, porcupines used a broader range of tree species for feeding, of which only aspen, white birch (*Betula papyrifera*), larch (*Larix laricina*) and white pine (*Pinus stobus*) are present in our study area. Their results also showed that preferred trees in summer were oaks (*Quercus* spp.). In addition, aspen and white birch were used almost exclusively in July and August, but aspen was also used in May and significantly more in one of their two study areas. However, these two species represent a marginal portion of the diet of porcupines in their study (Griesemer et al. 1998). This study also concluded that porcupines selected trees of larger diameter than a random sample of the population. Conversely, our results show a marked preference for aspen, and avoidance of other deciduous species, including white birch. We did not investigate tree size selection as it seems clear from the literature that porcupines prefer larger trees (*e.g.* Griesemer et al. 1998; Zimmerling and Croft 2001).

#### Hierarchy in habitat selection

The no den data set allows us to compare and contrast results obtained at all three scales. Porcupines consistently avoid human-used land at the 2<sup>nd</sup> and 3<sup>rd</sup> orders. But this is the only common point between results at the 2<sup>nd</sup> and 3<sup>rd</sup> order. Between the 3<sup>rd</sup> and 4<sup>th</sup> orders, the preference for aspen and avoidance of conifer forest were consistent. The three categories of deciduous species we used at the 4<sup>th</sup> order allowed us to understand porcupine preferences better than we could have at the 3<sup>rd</sup> order. Consequently we could detect the strong selection of fruit-producing trees, the preference for aspen and the avoidance of all other deciduous species. These preferences differ from previous reports of porcupine habitat selection studies because the available tree species were different. In these studies, a great deal of attention was given to tree species selection (Griesemer et al. 1998; Zimmerling and Croft 2001), with little effort on how it translates at lower orders of selection (home range or landscape scale) as we did here.

Apparently, porcupines can accommodate to the various tree species found in their extensive geographic distribution. Trembling aspen, for example, is their primary food here but porcupines were also found to use this species in Massachusetts, but it was not the principal species used (Roze 1989; Griesemer et al. 1998). Because of this strong plasticity in choice of food, we suggest that porcupines are opportunistic, adapting their diet to what is present in the area they use. Habitat selection can still operate at high orders of selection once this "choice" is made.

Our results concur with many studies of porcupine habitat selection and arboricolous folivores in general, which show that porcupines do not feed on tree species at random (Gill and Cordes 1972; Roze 1984; Sullivan et al. 1986; Snyder and Linhart 1997; Griesemer et al. 1998; Zimmerling and Croft 2001). There is a great level of variation in the feeding ecology of arboreal folivores (Lawler et al. 1998). The chemical composition, nutritional quality and plant secondary metabolites of foliage are brought forward as potential explanations to observed foraging behaviour in arboricolous folivores (Roze 1989; Snyder and Linhart 1997; Lawler et al. 1998; McIlwee et al. 2001). As these underlying explanations of foraging decisions are probably similar for the porcupine and many arboricolous folivorous species, our approach might benefit to other researcher working with similar study models.

#### Importance of hierarchal, multi-scale approach

Our results confirm the need to adopt a multi-scale approach in habitat selection studies because of the discrepancies between scales (Schaefer and Messier 1995; Chamberlain et al. 2002; McLoughlin et al. 2002), which show that conclusions at one scale may not apply to all scales (Wiens 1989). Rettie and McLoughlin (1999) proposed that decisions at coarser scales should reveal environmental features that are more important to fitness than decisions at finer scales. In our porcupine population, significant patterns of habitat selection emerged from the 3<sup>rd</sup> and 4<sup>th</sup> orders, but not from the 2<sup>nd</sup> order. The absence of selection patterns at the 2<sup>nd</sup> order could mean that 1) porcupines are not faced with significant limiting factors at this scale, 2) our study area is already more suitable than the surroundings and some selection occurred at an even coarser scale, or 3) densities are so high that subordinate individuals are forced to use sub-optimal habitats.

Our study area is dominated by aspen, which is more abundant than any other tree species. Even at larger scales, aspen-dominated forests (mixed and deciduous together) occupy a greater proportion of the landscapes or home ranges than any other type of forest. This species is the principal food source of porcupines in the type of ecosystem our study area is in. Similarly, rock dens of high quality are present in abundance. Finally, since the density of porcupines is exceptional within our study area, higher than in the region, we can conclude that all the above reasons contribute to the absence of selection patterns at the second order.

On the other hand, the accuracy of our data (direct observations) allows a finer understanding of habitat selection. The hierarchy in porcupine habitat selection we observed could also reflect the hierarchy of factors limiting its survival, hence suggesting that they operate at the 3<sup>rd</sup> and 4<sup>th</sup> orders rather than at the 2<sup>nd</sup> order. More research effort is needed to verify this.

Some elements of the porcupine preferences (preference for fruit trees, importance of aspen) would not have been apparent without making direct observations that allowed

analysis at the 4<sup>th</sup> order. In that respect, we believe that direct observations should be preferred over triangulation when dealing with animals that are not wide-ranging. Although the number of observations made decreases because direct observations are more time-consuming, the quality of the data largely compensates for the reduced sample size and reduces the risk of habitat misclassification (Kenow et al. 2001).

We found that porcupines are generalists at the 2<sup>nd</sup> order, and that 3<sup>rd</sup> and 4<sup>th</sup> orders better describe the needs of these herbivores. A next step in similar research could be to integrate habitat juxtaposition and interspersion (Garshelis 2000) in a mosaic approach, using a buffer around each telemetry location as a measure of habitat use.

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## TABLES

Table 1. Vegetation classification scheme used to create a habitat map for  $2^{nd}$  and  $3^{rd}$ orders of selection in North American porcupine, in Parc National du Bic, Québec, Canada.

Criteria 1	Criteria 2	Vegetation type	Code
Trembling aspen	Conifers <20%	Deciduous forest (POTR <sup>b</sup> dominance)	D(POTR)
$\geq 50\%^{a}$	Conifers >20%	Mixed forest (POTR dominance)	M(POTR)
T	Deciduous <20%	Conifer forest	С
Trembling	Conifers <20%	Deciduous forest	D
aspen <50%	Deciduous >20% Conifers >20%	Mixed forest	М
No trees	Fields	Fields	F
no nees	Roads, trails, buildings	Human	Н

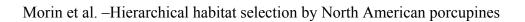
<sup>a</sup> Percentage of the total basal area in each polygon <sup>b</sup> Abbreviation for Populus tremuloides, Trembling aspen

Table 2. Distribution of observations made with respect to the location of the porcupine in the habitat (ground or less than 1m from the ground, tree, den or unknown) and its behaviour (feeding, resting, travelling, disturbed or unknown). "Disturbed" indicates that the behaviour of the porcupine had probably been affected by the observer's presence, and could thus not be recorded without bias. Porcupines localized in dens were assumed to be resting.

	Feeding	Resting	Travelling	Disturbed	Unknown
Ground	4	3	6	32	1
Trees	33	140	7	51	14
Den	0	135	0	0	0
Unknown	0	0	0	0	5

## FIGURES

Figure 1. Location of our study area in Parc National du Bic, Québec, Canada (68°46W, 48°21N) and vegetation map created for our study of habitat selection. Habitat types: C = conifer forest, D = deciduous forest, D(POTR) = trembling aspendominated deciduous forest, F = fields, H = human-used land, M = mixed forest, M(POTR) = trembling aspen-dominated mixed forest. Grid gives UTM coordinates (zone 19N).



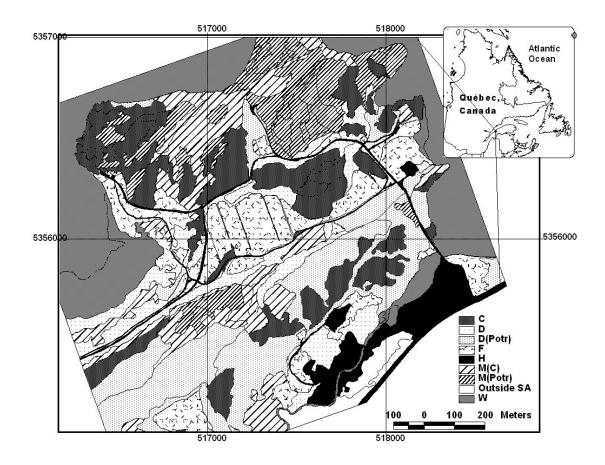


Figure 2. Proportion of observations on the ground, in trees and in dens for porcupines of each sex (F = females, M = males) followed in Parc National du Bic, Québec, Canada. The number of observations is shown above each bar. Observations in dens, trees and on the ground are in black, white and grey, respectively.

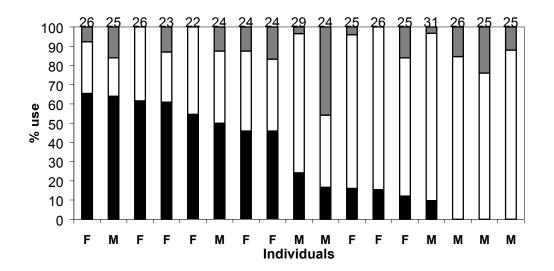


Figure 3. Mean proportion of habitat types (C = conifer forest, D = deciduous forest, D(POTR) = trembling aspen-dominated deciduous forest, F = fields, H = human-used land, M = mixed forest, M(POTR) = trembling aspen-dominated mixed forest) in the study area (availability) against their proportion in porcupine home ranges (use) for a) the complete data set and b) the no den data set. Error bars correspond to one standard deviation in use. There is no standard deviation for available habitat at this scale since as it is constant for all animals. An asterisk indicates a significant preference or avoidance (P < 0.05). Bars indicate availability and diamonds indicate use.

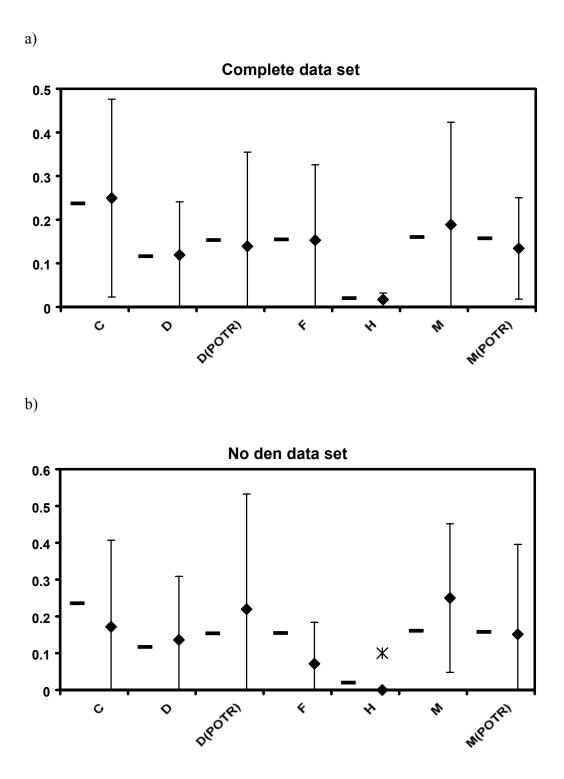


Figure 4. Mean proportion of habitat types (C = conifer forest, D = deciduous forest, D(POTR) = trembling aspen-dominated deciduous forest, F = fields, H = humanused land, M = mixed forest, M(POTR) = trembling aspen-dominated mixed forest) in porcupine home ranges (availability) against their proportion in used habitat patches (use) for a) the complete data set and b) the no den data set. Error bars correspond to one standard deviation in use. An asterisk indicates a significant preference or avoidance (P < 0.05). Bars indicate availability and diamonds indicate use. Refer to Table 1 for habitat codes.



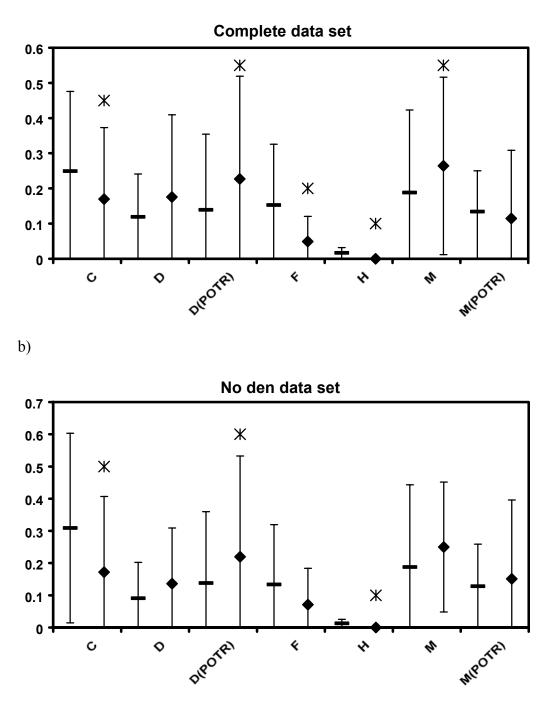
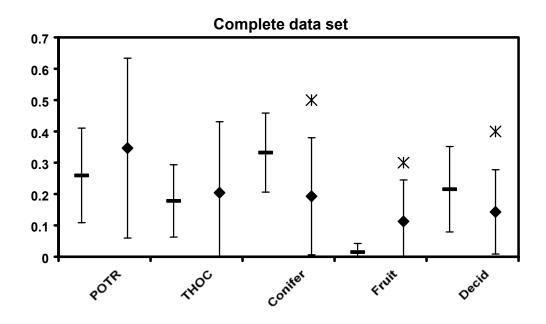


Figure 5. Mean proportion of tree species (POTR = trembling aspen, THOC = eastern white cedar, Conifer = all conifers except THOC, Fruit = fruit-producing deciduous trees, Decid = all deciduous species except POTR and fruit trees) in used habitat patches (availability) against their proportion of use by porcupines (use) for the no den data set. Error bars correspond to one standard deviation in use. An asterisk indicates a significant preference or avoidance (P < 0.05). Bars indicate availability and diamonds indicate use.



#### **GENERAL CONCLUSIONS**

The objectives of this masters project were to 1) improve existing chemical immobilization procedures for the North American porcupine 2) test whether porcupines exhibit different patterns of habitat selection at three spatial scales during summer, 3) investigate the potential divergence in habitat selection between sexes as well as patterns of den use. As a whole, this thesis contributes to expand our limited knowledge of porcupine ecology.

Our analysis of chemical immobilization techniques showed that injecting the ketamine-xylazine mixture in the tail reduced occurrence of multiple injections. The range of dosage we tested had no effect on the measured parameters, and hence it can be reduced to 50% of what is suggested in the literature (*i.e.* 5 mg ketamine/kg + 2 mg xylazine/kg).

Porcupines showed selectivity, but not at all scales. Being generalists in selecting their home ranges within the landscape, porcupines were more selective at the home range and feeding site scales, where male and female porcupines showed differences in habitat selection. At the stand level, porcupines prefer using trembling aspen-dominated deciduous forest and somewhat less mixed forest, from what is available in their home range. Fields, human-used land and conifer forest were least preferred habitat types, although a few animals use fields substantially at night. Because this tendency is restricted to a few animals, it does not appear in overall results. At the tree level, my results suggest that porcupines prefer trembling aspen and fruit trees, while conifers and other deciduous species are least preferred. Placing my results into perspective with previously published tree selection data (Roze 1989; Griesemer et al. 1998; Zimmerling and Croft 2001), I can conclude that porcupines are opportunistic, adapting their food source to what is available throughout their wide geographical range.

To fully understand porcupine habitat use and selection, the approach used here is essential; performing direct observations instead of triangulating the animals' positions allowed us to record behaviour and location within the habitat. Hence we were able to observe the relatively high den use and reorganize our data sets accordingly. Although it is not possible to use such an approach with all species, it should always be favoured where possible, as the quality and precision of the data recorded largely compensates for the decrease in number of observations for each animal. More specifically, our approach and results may apply to other arboricolous-folivorous species (Lawler et al. 1998; McIlwee et al. 2001), which foraging decisions are based on common factors with the North American porcupine (Roze 1989; Snyder and Linhart 1997).

Throughout the fieldwork, it became increasingly obvious that each porcupine has its own "habits", which introduced a lot of inter-individual variation in the data. Some common patterns could still be detected from our data, but to fully understand porcupine habitat use, the ecological reasons behind the different "strategies" they use, it would be useful to increase the number of individuals followed, and perhaps expand this analysis to all seasons to help us understand limitations that groups of individuals are faced with. For example, preliminary observations suggest that males may invest a lot of time and energy into competing for mates in the fall, and pregnant females may have different habitat selection strategies in summer because of the extra energetic cost from the foetus. Our methods improved dramatically from the beginning of this project, thus it will be more feasible to reach these goals, since less time and energy will be needed to fine-tune field methods and equipment.

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## **APPENDIX 1**

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Department:	Natural Resource			Fa	
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