BEAVER DAMS: THEIR SITE SELECTION, ESTABLISHMENT, AND IMPACT IN A NORTHERN ONTARIO WATERSHED

By

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ABSTRACT

The goal of this thesis was to gain a better understanding of the ecology of beaver dams in a boreal watershed. Three aspects of beaver dams were studied: i) the habitat factors affecting dam-site selection; ii) the preferential use of woody plants by beavers in dam construction; and iii) the effect of beaver herbivory on shoreline plant communities.

Within the Swanson River drainage area of the Chapleau Crown Game Preserve, physical and vegetation data were collected from 15 active, 15 abandoned, and 12 no dam sites. Using Discriminant analysis, upstream watershed area and stream cross-sectional area were identified as the most important habitat factors associated with beaver dams. The shoreline density (within 10 m) of woody plants with 1.5 - 4.4 cm diameter range was also found to be important.

When the Neu utilization-availability technique was applied to three newly formed beaver dams, it was found that beavers chose woody vegetation based on size rather than species when constructing dams. The preferred stem diameter range was 1.5 - 3.4 cm.

Beaver herbivory was mainly concentrated within 20 m of the impoundment edge of active dams. Beavers harvested alder, important for dam construction, more than trembling aspen, white birch, and willow, that are their food items. Woody plant density around the dam sites were low compared to the

adjacent control plots. The fluctuating water levels associated with the dam dynamics may be responsible for this low density.

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GENERAL INTRODUCTION

The beaver (*Castor* spp) is one of the largest members of the mammalian Order Rodentia, being surpassed only by the South American capybara (*Hydrochoerus spp*) (Novak 1976). At present, there are two species of beaver, *Castor fiber* L. found in Europe and *Castor canadensis* Kuhl found in North America. In this broad geographic distribution, these species affect a wide variety of habitats. Novak (1987) noted that the North American beaver occupied habitats in the arctic at one extreme and Mexico at the other. Irrespective of species and location, impounded water is the most important feature in the daily lives of beavers (Novak 1987). Beavers build dams to ensure the adequate supply of water for easy transport of food and construction materials and under ice storage of during winter.

For over 50 years, scientists have attempted to identify the physical and vegetation factors responsible for beaver dam-site selection. Their research showed that stream side physical features were more important than vegetation characteristics (Retzler et al. 1956, Rutherford 1964, Slough and Sadleir 1977, Howard and Larson 1985, McColm et al. 1990). A review of these studies showed that their vegetation analyses only measured species composition and did not account for size structure and spatial distribution. Beaver foraging studies have clearly documented that the collection of woody food items is based on stem size and their location with respect to the dam impoundment (Jenkins 1980, Pinkowski 1993, Beloski 1984, Fryxell and Doucet 1991, Fryxell 1992). Thus, in order to properly understand what factors influence beaver dam establishment, habitat analyses must include physical features of streams along with a more complete vegetation data.

The dam-building helps beavers to create impoundments along waterways where occurs shoreline supplies of hardwood trees, their chief food source as well as alder, the main construction material. These impoundments allow for expedient food transportation, construction of a lodge, and under-ice food storage for over-winter survival. Water as a mode of transport has the added advantage as it provides beaver good protection from potential predators such as timber wolves (*Canis lupus* L.) and black bears, (*Ursus americana* Pallus). In addition, beavers use a mixture of soil and water to plaster their lodge just before the onset of winter. This freezes solid providing an inpenetrable barrier to roaming predators such as the timber wolf. However, no studies have adequately documented the role of vegetation in the dam building process.

An increase in beaver populations in the last 50 years (Ingle-Sidorowicz 1982) has resulted in the creation of an increasing number of dammed impoundments across the landscape of northern Canada. The resulting proliferation of beaver dams has created a mosaic of temporally and spatially variable biophysical patches (Naiman et al. 1994). Despite the demonstrated increase in beaver dams and their adverse effects on the landscape, there has been little research conducted to determine the factors responsible for the dam site selection and to what extent the beaver dams affect woody plant communities along the impoundments.

The objectives of the present study were to:

i) identify the physical and vegetation factors associated with the beaver dam sites;

ii) determine if beavers show any preference in their selection of woody plants used in dam construction; and

iii) determine how beaver herbivory affect shoreline woody communities at the active and abandoned dam sites.

CHAPTER 1

1. Habitat factors influencing beaver dam-site selection in a northern Ontario watershed

1.1 Abstract

Beaver (*Castor canadensis* Kuhl) dam-site selection studies have traditionally relied on a narrow vegetation data base, i.e. plant composition. To properly understand how habitat factors influence dam establishment, 9 plant composition and size categories with their spatial distribution were compared with 4 physical features at 15 active dams, 15 abandoned dams, and 12 no dam sites. To estimate pre-dam vegetation densities, plots downstream and upstream from impoundments were averaged. Beavers relied on both physical (upstream watershed area and stream cross-sectional area) and vegetation (shoreline concentrations of woody plants with diameters 1.5 - 4.4 cm) factors in choosing dam sites. The model designed by McComb et al. (1990) was not effective in predicting dam sites in northern Ontario, therefore, managers are encouraged to test the model's regional accuracy in determining site locations.

1.2 Introduction

Impounded water is the most important ecological factor limiting beaver (*Castor canadensis* Kuhl) habitat use (Novak 1987). Despite the recognized importance of beaver dams, researchers have consistently identified physical features as being more significant habitat determinants than shoreline vegetation (Retzler et al. 1956, Rutherford 1964, Slough and Sadleir 1977, Howard and Larson 1985, McComb et al. 1990). Thus, in order to properly understand what factors influence beaver dam establishment, habitat analyses should include physical features combined with a more complete vegetation data set.

In this chapter, I test the following hypothesis: *the establishment of beaver dams on boreal stream sections is related to the species composition, stem size, and spatial distribution of streamside woody vegetation and certain measurable physical factors of the site.* The hypothesis was tested by comparing the species composition and size class distribution of pre-dam woody vegetation and physical habitat features of active and abandoned beaver dam sites with those randomly chosen stream sites without a dam (no dam sites).

1.3 Study Area Description

The study was conducted in the Swanson River drainage basin of the Chapleau Crown Game Preserve (48°05'N, 83°20'W; elevation range 348 - 510 m) of northern Ontario (Fig. 1.1).

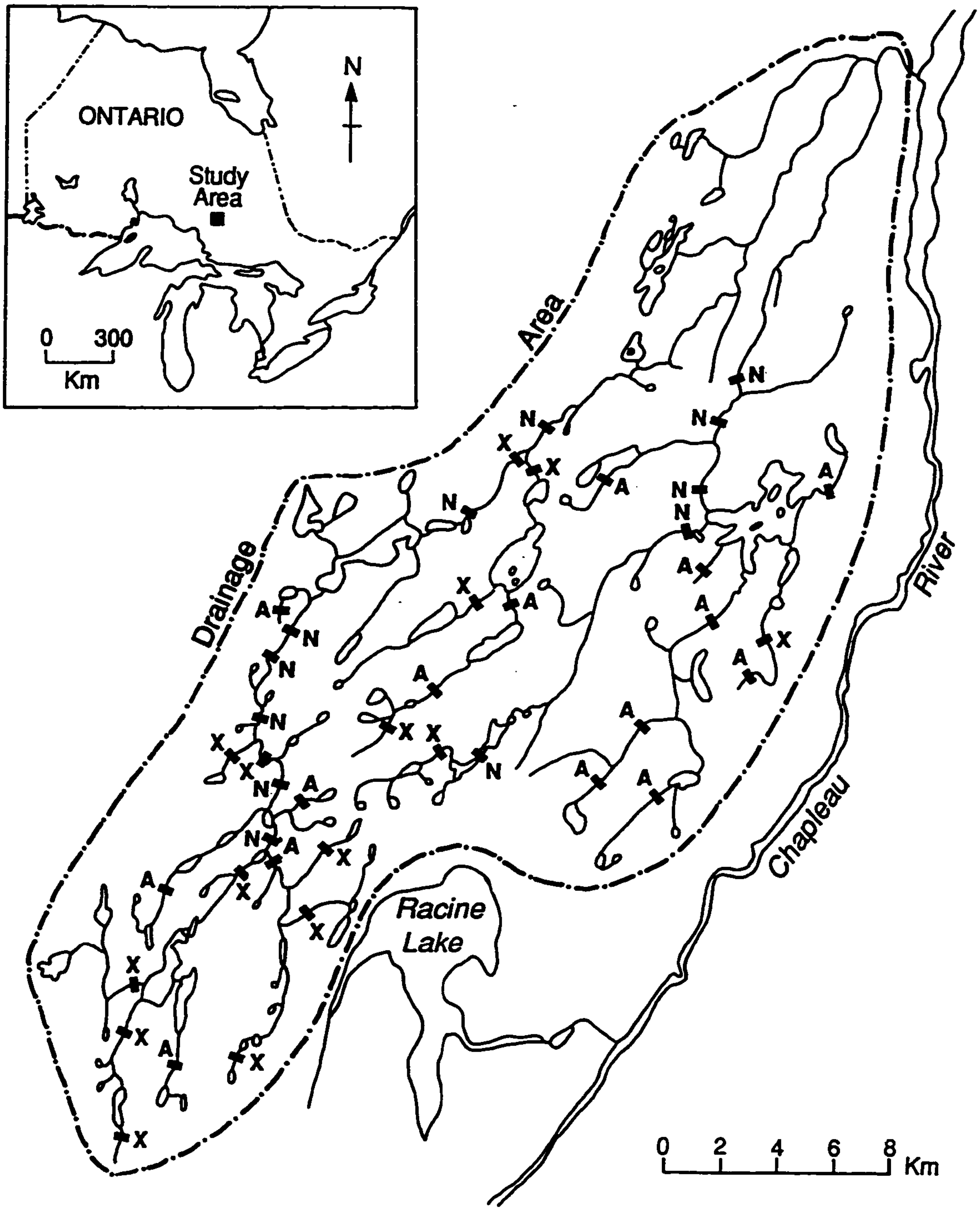

Figure 1.1 The Swanson River drainage basin study area (- -) with the location of 15 active (**A**), 15 abandoned (**X**), and 12 no dam sites (**N**). Location of the Chapleau Crown Game Preserve study site in Ontario is shown in the inset.

This drainage area was free from trapping and hunting and thus provided a natural boreal forest where beaver dams could be studied with minimum disturbance. The Swanson River watershed has 200 km of streams covering an area of 228 km^2. Riparian habitats were dominated by alder (*Alnus* spp.). The adjacent forests were dominated by jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* Mill.) interspersed with mixed stands of white spruce (*Picea glauca* Moench), balsam fir (*Abies balsamea* (L.) Mill.), white birch (*Betula papyrifera* Marsh.), and trembling aspen (*Populus tremuloides* (Michx.). Associated with these forest trees were understory trees and shrubs such as willow (*Salix* spp.), pin cherry (*Prunus pensylvanica* L.), mountain maple (*Acer spicatum* Lam.), red osier dogwood (*Cornus stolonifera* Michx.), showy mountain ash (*Sorbus americana* Marsh.), choke cherry (*Prunus virginiana* L.), black ash (*Fraxinus nigra* Marsh.), serviceberry (*Amelanchier* spp.), beaked hazel (*Corylus cornula* Marsh.), and river birch (*Betula glandulosa* Marsh.).

1.4 Methods

The stream system was sub-divided into 1-km stream sections (Howard 1982). Using an aerial count of food caches conducted with a Cessna 180 airplane (Bergerud and Miller 1977), a stereoscopic examination using 1980 and 1992 aerial photographs, 1:15830 and 1:8000, respectively, and on-site inspections, 40 stream sections were classified as active (at least 1 active dammed colony), 85 as abandoned (at least 1 abandoned dammed colony with no evidence of active dams), and 75 as no dam sites (no dam building activity evident). The aerial photo characteristics used to determine abandoned dam sites were: the state of deterioration of dams (i.e. a large sections of the dam missing), the presence of beaver meadows, the presence of dead vegetation, and the amount of impounded water. All site locations were recorded on a 1:50,000 topographic map. To sub-sample the 200 stream sites, 15 active, 15 abandoned, and 12 no dam sites were randomly selected and groundtruthed (Fig. 1.1). Since some of these sample sites were very remote and difficult to reach, part of the selection process involved an assessment of accessiblity. To ensure that the field work on all 42 sites would be completed by September, I selected sites in which data could be collected in one day. This strategy was advantageous as it allowed for some loss time due to inclement weather and any other unforseen situations.

Since the vegetation and original stream were flooded and altered by the presence of beaver, pre-dam conditions at active and abandoned sites of beaver dams were re-structured. Random selection was used to determine which side of the stream to sample at the upstream plots; the downstream plot was established on the opposite bank. A 40 m x 170 m plot was then established at each of these locations (Fig. 1.2). To determine the plot dimensions, the length and width of beaver harvesting activities was averaged at the 15 active dam sites. Three shoreline locations in each of the upstream and

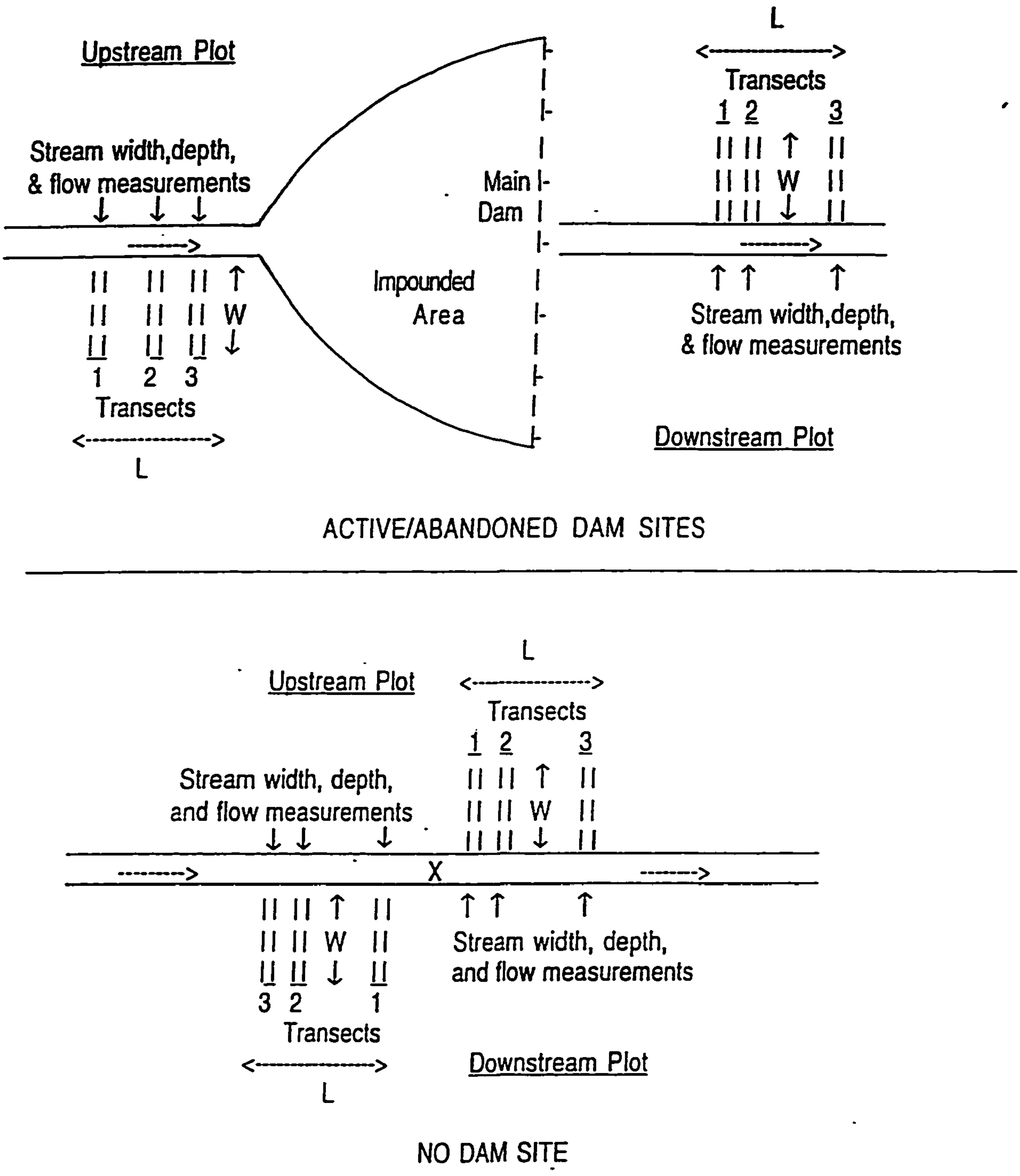

Figure 1.2 Sampling technique used to measure the vegetation and physical features at active, abandoned, and no dam sites in the Swanson River drainage basin of the Chapleau Crown Game Preserve. L, length of sample plot (170 m); W, width of sample plot (40 m); X, centre of no dam plot.

downstream plots were randomly selected. At these six shoreline locations, a 1 m x 40 m transect was established perpendicular to the stream's edge. Each transect was sub-divided into 40 1 m x 1 m sub-plots. Within each sub-plot, the diameter of all trees and shrubs was measured at 30 cm above the ground (Johnston and Naiman 1990). The upstream and downstream sampling plots were established at the 12 no dam sites by randomly selecting a point within each 1 km sampling unit. The selected point served to separate the upstream and downstream sampling plots. The sampling procedure used within each plot was similar to that of active and abandoned dams (Fig. 1.2).

Density of woody plant species was determined and placed into 4 categories: 1) alder, 2) shrubs (pin cherry, mountain maple, red-osier dogwood, mountain ash, choke cherry, service berry, beaked hazel, and river birch), 3) conifers, and 4) food species, notably trembling aspen, white birch, and willow (Bergerud and Miller 1977). Data on alder, shrubs, and conifers were collected because of their use as dam construction material. The plants were divided into 5 diameter classes: 0.5 - 1.4 cm, 1.5 - 2.4 cm, 2.5 - 3.4 cm, 3.5 - 4.4 cm, and ≥ 4.5 cm.

Four physical variables were measured at each active, abandoned, and no dam site. The upstream watershed area (UWA) was determined by delineation of watersheds on 1:50,000 topographic maps using a Tamaya Digital Planimeter, Planix 5,6 (Tamaya Technics Inc.). To determine cross-sectional area, 3 cross-sectional areas were established in the downstream and 3 in the upstream plots (Fig. 1.2); all the 6 measurements were then averaged. To determine a stream cross-sectional area, the mean stream depth was multiplied by the mean width of a stream profile (Dodge et al. 1984).

To identified geographic locations, a Geographic Information System (PC Arc/Info 3.4.2., Environmental Systems Research Institute) and the Ontario Base Map series was used. Sample sites were accurately positioned along the stream course using a Garmin Survey 2 Global Positioning System (Garmin Corp.) to establish the Universal Transverse Mercator coordinates of the site at the mid-point of each active and abandoned dam. To ensure maximum positioning accuracy, eight satellite readings per fix were used and Global Positioning System data were differentially corrected using a second Garmin Survey 2 unit as a base station with known coordinates.

Each Ontario Base Map was compiled with a number of different interchange files which represented various types of information. For each base map, drainage and elevation files were used. The Global Positioning System locations were used in a PC computer with ARC INFO. Stream locations and their corresponding Global Positioning System point coverage were overlaid to ensure maximum accuracy.

A Geographic Information System was used to establish stream elevations 150 m above and below the Global Positioning System points. To determine stream gradient, the vertical drop was divided by the horizontal distance for the downstream and upstream elevations and these two values were averaged. Stream gradient was expressed as % slope (Howard and Larson 1985).

Geographic Information Systems were also used to obtain topographic elevations 100 m in either direction of the Global Positioning System points. Using the same procedure outlined by Howard and Larson (1985) for stream gradient, the % slope for the shoreline topography was calculated for each shore and averaged.

Using stream gradient and cross-sectional area data derived from my study, the effectiveness of an Oregon model (McComb et al. 1990) to correctly identify beaver dam sites was tested under boreal conditions.

T tests were performed on the vegetation data collected at upstream and downstream plots to determine if there were significant differences between active, abandoned, and no dam sites. In the event of no significant difference, the above and below dam values were averaged.

To determine the significant differences among the variables associated with active, abandoned, and no dam sites, one-way analyses of variance (ANOVA) followed by Least Significant Difference (LSD) tests were performed (Data Desk 4.2, Data Description Inc.). A Discriminant Analysis (SYSTAT, SYSTAT Inc. 1992) was conducted using only those variables which showed a significant difference between either active or abandoned dams and no dam sites. The Wilks' lambda was used to determine if there was overall variation among active, abandoned, and no dam sites. The correlations between the original variables and the discriminant function were used to identify variables important in defining the axes ($r > 0.5$) (Merendino et al. 1993). To avoid the problem of multicollinearity (Howard and Larson 1985; Beire and Barrett 1987), a correlation matrix was used to eliminate highly correlated variables ($r > 0.8$) (Data Desk 4.2, Data Description Inc.).

1.5 Results

The species composition and size classes of the woody vegetation in downstream plots were not significantly different from the upstream plots at active, abandoned, or no dam sites (Table 1.1). Based on this, I averaged upstream and downstream vegetation values to arrive at an approximation of the pre-dam condition.

When active, abandoned, and no dam sites were compared using one-way ANOVA, the upstream watershed area, stream cross-sectional area, stream gradient, and woody stem diameter classes 1.5 - 2.4 cm, 2.5 - 3.4 cm, and 3.5 - 4.4 cm, were found to show significant differences (Table 1.2). These six significant variables were used in a Discriminant Analysis and a significant overall variation among active, abandoned, and no dam sites was found (Wilks' lambda = 0.333, $P = 0.0001$). The 2 discriminant functions (FUNCTION 1 and FUNCTION 2) described 93% and 7% of the variation between the

Table 1.1. Mean density (SE) of woody plants (no./120 m^2) downstream and upstream of active, abandoned, and no dam sites in the Chapleau Crown Game Preserve of northern Ontario, 1993.

	Active dam sites[a] (n = 10)			Abandoned dam sites (n = 15)			No-dam sites (n = 12)		
	Down-stream plot	Up-stream plot	P(*t*)	Down-stream plot	Up-stream plot	P(*t*)	Down-stream plot	Up-stream plot	P(*t*)
Plant classes									
Alder	128(32)	92(19)	0.35	87(29)	67(18)	0.55	111(21)	87(19)	0.40
Shrubs	19(6)	19(5)	0.99	26(8)	34(10)	0.52	30(11)	29(10)	0.97
Conifers	32(8)	51(13)	0.22	31(8)	34(7)	0.80	29(4)	44(8)	0.08
Food	18(4)	10(3)	0.11	5(2)	10(2)	0.09	9(2)	9(3)	0.95
Stem diameter classes									
0.5-1.4 cm	105(26)	90(22)	0.66	94(26)	93(20)	0.98	96(15)	85(17)	0.64
1.5-2.4 cm	42(11)	30(6)	0.39	22(6)	22(4)	0.93	39(7)	30(5)	0.30
2.5-3.4 cm	22(5)	16(4)	0.36	11(3)	9(2)	0.61	16(3)	16(3)	1.00
3.5-4.4 cm	9(2)	12(2)	0.46	7(2)	5(1)	0.51	7(1)	11(2)	0.09
≥4.5 cm	17(4)	21(4)	0.46	17(4)	15(3)	0.80	18(3)	26(4)	0.10

[a] Based on 10, as 5 of the 15 active sites did not have an upstream sampling plot.

Table 1.2. Mean values (SE) of habitat variables for active (Ac), abandoned (Ab), and no dam sites (Nd) in the Chapleau Crown Game Preserve of northern Ontario, 1993. Values connected by a line in the Least Significant Difference comparison (LSD) are not significantly different (P > 0.05).

Variables	Ac	Ab	Nd	Trans[a]	LSD
Physical Features					
Watershed area(ha)	521.1(154.8)	948.8(402.9)	6247.3(741.4)	$\log_{10}$	Ac Ab Nd[b]
Cross-sectional area(m^2)	1.0(0.3)	1.3(0.3)	14.2(4.2)	$\log_{10}$	Ac Ab Nd[c]
Gradient(%)	1.1(0.3)	0.6(0.1)	0.5(0.2)	sq rt	Ac Ab Nd
Shoreline slope(%)	6.4(0.8)	5.6(1.9)	4.6(1.9)	$\log_{10}$	Ac Ab Nd
Stem diameter classes[d]					
0.5 - 1.4 cm	97.4(11.3)	90.3(12.7)	95.9(23.0)	$\log_{10}$	Ac Ab Nd
1.5 - 2.4 cm	36.4(5.1)	34.8(3.6)	23.5(3.9)	$\log_{10}$	Ac Ab Nd
2.5 - 3.4 cm	17.3(2.5)	16.9(1.9)	10.8(2.0)	none	Ac Ab Nd
3.5 - 4.4 cm	11.1(1.4)	9.7(1.1)	6.8(1.4)	none	Ac Ab Nd
≥ 4.5 cm	24.7(3.4)	22.7(2.6)	17.1(3.6)	$\log_{10}$	Ac Ab Nd
Plant categories[d]					
Alder	91.3(13.2)	115.4(18.1)	76.8(21.8)	$\log_{10}$	Ac Ab Nd
Shrubs	34.9(9.9)	34.4(9.9)	33.4(7.6)	$\log_{10}$	Ac Ab Nd
Conifers	46.9(11.1)	49.9(8.5)	33.2(6.7)	$\log_{10}$	Ac Ab Nd
Food[e]	13.0(2.0)	11.7(2.1)	7.6(1.1)	none	Ac Ab Nd

[a] Transformations using normal probability plots.
[b] Ac-Nd: $P < 0.0000001$; Ab-Nd: $P < 0.00001$.
[c] Ac-Nd: $P < 0.0001$; Ab-Nd: $P < 0.0001$.
[d] Pre-dam assessment of plant densities [no. stems/120 m^2] achieved by averaging plots downstream and upstream from the impoundment.
[e] Trembling aspen present within the foraging range of 46% of active and 33% of no dam sites.

Table 1.3. Correlations between the original variables and the discriminant functions indicating the importance of each variate to the separation of active, abandoned, and no-dam sites. Variables important in defining the axes are underlined.

	Correlations between original variables and the discriminant functions	
Variables	Function 1	Function 2
Physical Features		
Watershed area (ha)	- 0.921	0.019
Cross-sectional area (m^2)	- 0.593	0.355
Gradient (%)	0.198	0.704
Stem diameter classes		
1.5 - 2.4 cm	0.271	- 0.073
2.5 - 3.4 cm	0.279	- 0.120
3.5 - 4.4 cm	0.281	0.177
Eigenvalues	1.663	0.127
% variation explained	93	7
Probability	0.0001	0.498

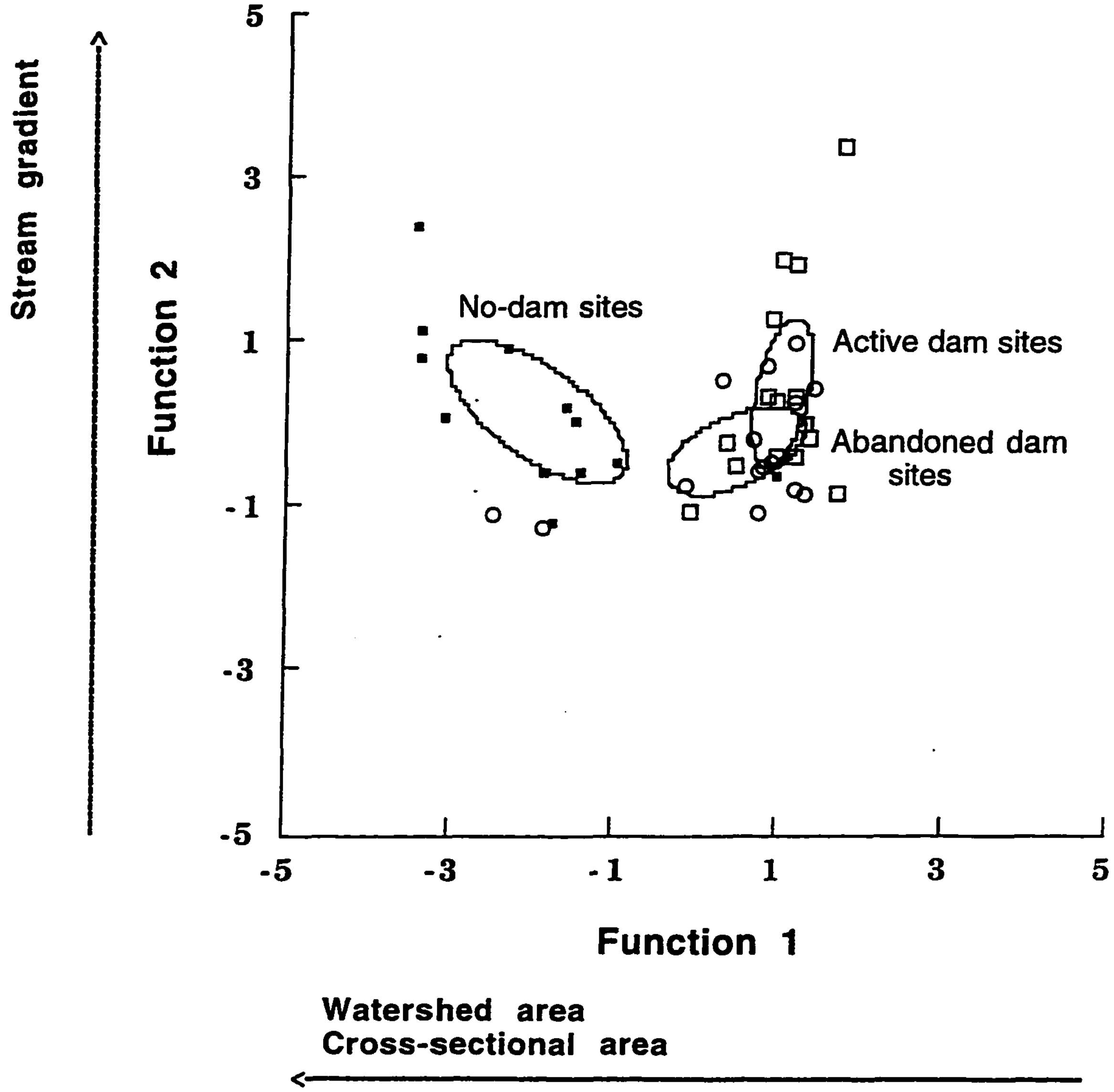

Figure 1.3. Ninety-five percent confidence ellipses based on a Discriminant Analysis of 3 vegetation and 3 physical features at active (❑), abandoned (o), and no dam sites (■) in the Chapleau Crown Game Preserve of northern Ontario. Variables important in defining discriminant functions 1 and 2 are shown adjacent to arrows.

sites, respectively (Table 1.3). FUNCTION 1 delineated 2 groups: no dams; and active and abandoned dams. The upstream watershed area contributed most to the separation, while cross-sectional area was secondarily important (Fig. 1.3). FUNCTION 2 failed to delineate between any groups or group combinations (Fig. 1.3).

An analysis of spatial distribution of woody vegetation showed that active dams had significantly greater densities of woody stems 1.5 - 2.4 cm, 2.5 - 3.4 cm, and 3.5 - 4.4 cm, adjacent to water (within 10 m) than the no dam sites. Similar results were found for woody stems 0.5 - 1.4 cm (Table 1.4). In addition, food species density within 10 m of abandoned dams was significantly higher than no dam sites (Table 1.4).

When my data were tested with the McComb Model, 27% of active dams and 58% of no dam sites fit the model (Fig. 1.4).

1.6 Discussion

Contrary to most habitat selection research, this study showed that beavers chose to build dams at stream sections with high shoreline densities of woody vegetation with stem diameters 1.5 - 4.4 cm (Tables 1.2 and 1.4) (Howard and Larson 1985, Beire and Barrett 1987, McComb et al. 1990). The close proximity of these stems to water is advantageous as it ensured the speedy establishment of a dam, thus ensuring optimal foraging conditions while minimizing the risk of predation by timber wolves (*Canis lupus* L.) (Potvin

Table 1.4. Mean density (SE) of plant categories and stem diameter classes (no./120 m^2) showing spatial distribution within 40 m of the stream's edge at active[a] (Ac), abandoned[a] (Ab), and no-dam sites (Nd). Values connected by a line in the Least Square Difference comparison (LSD) are not significantly different ($\underline{P} > 0.05$).

Variables[b]	Distance (m)	Ac	Ab	Nd	LSD
Plant categories					
Alder	0-9.9	40.8(5.6)	59.1(11.0)	20.4(4.7)	Ac Ab Nd
	10-19.9	21.9(4.5)	27.4(4.4)	17.4(5.4)	Ac Ab Nd
	20-29.9	18.3(3.8	18.0(3.7)	18.6(6.3)	Ac Ab Nd
	30-40	10.3(2.3)	12.5(3.4)	20.3(3.4)	Ac Ab Nd
Shrubs	0-9.9	10.4(3.5)	11.2(2.7)	10.8(3.9)	Ac Ab Nd
	10-19.9	9.9(3.2)	6.4(2.3)	11.4(3.2)	Ac Ab Nd
	20-29.9	6.7(2.8)	8.1(3.2)	8.1(2.2)	Ac Ab Nd
	30-40	7.9(2.9)	7.7(3.4)	3.1(1.1)	Ac Ab Nd
Conifers	0-9.9	9.2(2.7)	19.3(5.7)	6.7(2.4)	Ab Ac Nd
	10-19.9	12.3(3.3)	9.6(1.7)	8.1(1.9)	Ac Ab Nd
	20-29.9	13.7(3.6)	10.1(1.7)	9.7(1.5)	Ac Ab Nd
	30-40	10.9(1.3)	11.6(2.9)	8.8(1.6)	Ac Ab Nd
Food	0-9.9	2.7(0.6)	4.9(1.5)	1.0(0.5)	Ab Ac Nd
	10-19.9	2.8(0.7)	2.4(0.8)	1.8(0.6)	Ac Ab Nd
	20-29.9	3.3(1.0)	1.9(0.4)	2.4(0.5)	Ac Ab Nd
	30-40	4.1(0.9)	2.3(0.5)	2.3(0.5)	Ac Ab Nd
Stem diameter classes					
0.5 - 1.4 cm	0-9.9	33.0(4.3)	31.5(4.7)	22.7(4.7)	Ac Ab Nd
	10-19.9	24.9(3.8)	22.7(3.0)	25.2(5.8)	Ac Ab Nd
	20-29.9	22.6(3.5	19.8(3.9)	26.1(7.7)	Ac Ab Nd
	30-40	16.9(3.2)	16.3(3.9)	21.9(8.6)	Ac Ab Nd
1.5 - 2.4 cm	0-9.9	13.1(2.2)	12.1(1.8)	6.9(1.8)	Ac Ab Nd
	10-19.9	10.1(2.1)	10.1(1.3)	5.0(1.0)	Ac Ab Nd
	20-29.9	7.4(1.2)	6.8(1.3)	6.0(1.0)	Ac Ab Nd
	30-40	5.7(1.0)	4.9(1.1)	5.6(1.1)	Ac Ab Nd

Table 1.4 (Continued)

2.5 - 3.4 cm	0-9.9	5.9(1.0)	5.7(1.2)	3.2(0.9)	Ac Ab Nd
	10-19.9	4.1(0.5)	4.5(0.6)	2.5(0.7)	Ac Ab Nd
	20-29.9	3.9(1.0)	3.5(2.4)	2.4(0.5)	Ac Ab Nd
	30-40	3.4(0.9)	3.1(0.5)	2.8(0.4)	Ac Ab Nd
3.5 - 4.4 cm	0-9.9	4.3(0.8)	2.8(0.6)	2.4(0.9)	Ac Ab Nd
	10-19.9	2.7(0.6)	2.5(0.4)	1.3(0.3)	Ac Ab Nd
	20-29.9	2.1(0.4)	2.2(0.3)	1.4(0.3)	Ac Ab Nd
	30-40	3.4(0.9)	3.1(0.5)	2.8(0.4)	Ac Ab Nd
≥4.5 cm	0-9.9	7.0(1.7)	4.5(0.8)	3.5 (1.2)	Ac Ab Nd
	10-19.9	4.7(1.0)	5.4(0.8)	4.8 (1.2)	Ac Ab Nd
	20-29.9	6.6(0.9)	6.0(0.7)	3.8 (0.8)	Ac Ab Nd
	30-40	6.3(1.0)	6.8 (0.8)	4.9 (0.9)	Ac Ab Nd

[a] See footnote [d] in Table 2.

[b] Square root transformation using normal probability plots

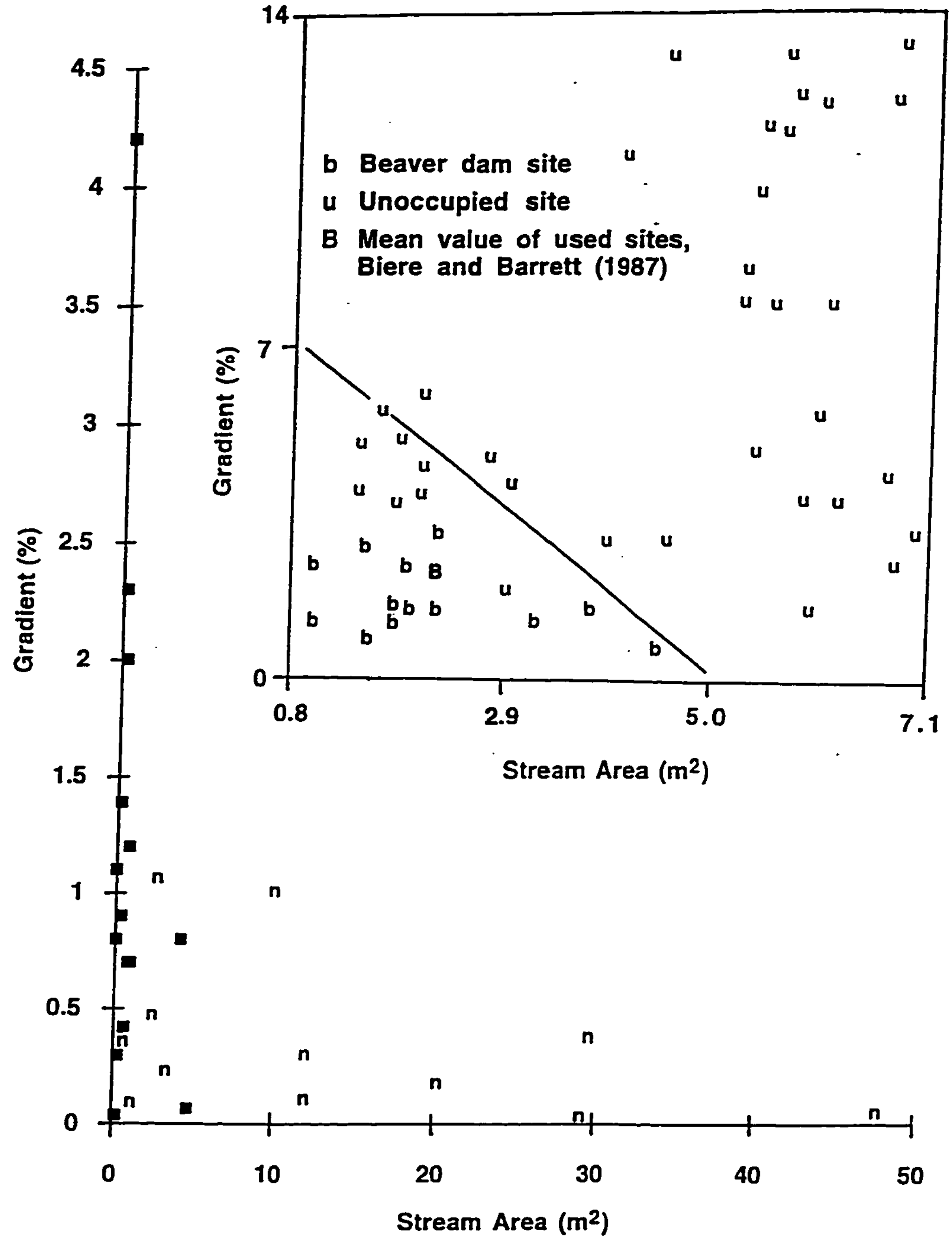

Figure 1.4. The relationship between stream gradient and cross-sectional area at active (■) and no dam sites (n) within the Chapleau Crown Game Preserve study area. For comparison with the graphical model presented in McComb et al. (1990), see inset, reproduced with permission from the Great Basin Naturalist.

et al. 1992).

Although the availability of food, especially trembling aspen, has traditionally been considered an important determinant of habitat suitability for beavers, recent studies have shown that food may not be a strong influencing factor when choosing stream sites to dam (Howard and Larson 1985, Novak 1987, McComb et al. 1990). I found no evidence of beavers choosing dam sites based on the presence of their main food item, trembling aspen. When trembling aspen densities were considered separately, it was found that plants were present within the foraging range (40 m) of 46% of active and 33% of no dam sites (Table 1.2). Based on the low densities of the important food plants available at streamside, it seemed unlikely that beavers would use the presence of food plants as a cue for building dams in northern streams. Because beaver dams have been recorded to reach lengths of up to 652 m (Novak 1987), this overland flooding would allow beavers to forage on more food plants (Table 1.4). I, therefore, postulate that the presence of food trees was not strong a habitat determinant for dam establishment.

In the present study, the most significant habitat determinant for the location of beaver dams was a reduced upstream watershed area. Despite this demonstrated importance, many studies in the past did not include it as a variable (Retzler et al. 1956, Slough and Sadleir 1977, Allen 1983, Beire and Barrett 1987). Of the studies which included upstream watershed area in their analyses, Howard and Larson (1985) found it important in identifying beaver dam sites, while McComb et al. (1990) did not. A plausible reason for this difference may be the differing spatial distribution of dams used. In the McComb et al. (1990) study, 71% of all the active dams were located within 8% of their studied stream system. Such a restrictive distributional pattern may have biassed their watershed values. In my study area (Fig. 1.1) and that of Howard (1982), active dam sites were distributed across a larger segment of the upstream watershed area, approximately 75% and 90%, respectively.

Many researchers have recognized stream gradient and cross-sectional area as important determinants for beaver dam location (Retzler et al. 1956, Slough and Sadleir 1977, Howard and Larson 1985, Beire and Barrett 1987, McComb et al. 1990). Beavers rely on the sound of running water caused by landscape gradient to trigger dam building behaviour (Novak 1987). The cross-sectional area has two main implications; (1) if the stream has a sufficient width and depth, this will facilitate autumn food gathering and under ice food storage and locomotion; and (2) in small CSA streams, the reduced depth and width makes dam building much easier.

Over the past 10 years, beaver researchers have claimed that vegetative management was a useless endeavor (Beire and Barrett, 1987). This directive was based on research which showed that physical factors were largely responsible for dam site selection. In contrast, boreal beaver chose dam sites based on the streamside vegetation structure. Since both Howard and Larson (1985) and Beire and Barrett (1987) recommended against wide-scale extrapolation of beaver research findings, I suggest that regional management decisions concerning beaver should be made only when streamside vegetation has been assessed to reflect its structural and distributional nature.

In conclusion, I contend that beavers select dam sites based on physical (reduced upstream watershed area and reduced cross-sectional area) and increased shoreline densities of vegetation (woody plants with diameters 1.5 - 4.4 cm) features.

1.7 Management Implications

McComb et al. (1990) formalized the relationship between stream gradient, stream cross-sectional area, and dam site location in the form of a graphical model and showed that it successfully identified of dam sites in eastern Oregon. The logic underlying their model is that beavers living in a high gradient watershed dam stream sections with a reduced gradient. The flat boreal terrain of northern Ontario is problematic to their model, as both the used and unused stream sections are low gradient and as a consequence stream cross-sectional areas are larger. Since the model was not successful in northern boreal landscapes, I recommend that managers test the model's regional accuracy in determining dam site locations.

CHAPTER 2

2. Use of woody plants in construction of beaver dams in northern Ontario.

2.1 Abstract

Newly formed beaver dams were studied in the Chapleau Crown Game Preserve of northern Ontario to determine if beavers (*Castor canadensis* Kuhl) showed any preference in their choice of woody plants in building the dams. Application of the Neu utilization-availability technique showed that beavers exhibited a high preference for alder (*Alnus* spp., plant species not commonly used as food) stems with diameters 1.5 - 3.4 cm and lesser preference for food-tree stems with diameters ≥ 4.5 cm. I maintain that beavers used large food-tree stems for dam construction only because they become more accessible after dam construction. Since the alder stems available close to the water's edge accounted for most stems of preferred size, 1.5 - 3.4 cm, I postulated that selection of woody stems by beavers for construction purposes was based on size rather than on species.

2.2 Introduction

Optimal foraging theory suggests that animals can increase their fitness by maximizing the net rate of intake of some essential resources per unit time (Pyke et. al. 1977, Krebs 1978). Several authors have presented the special case of the central-place forager (Andersson 1978, Orians and Pearson 1979, Schoener 1979). They postulated that when the prey items are small compared with the predator, central-place foragers should select progressively larger food items with increasing distance from the central place. Beavers (*Castor canadensis* Kuhl) are an exception because they feed on such large trees in relation to their body size, so they have been the focus of many foraging studies (Jenkins 1980, Pinkowski 1983, Belvosky 1984, McGinley and Whitham 1985, Fryxell 1992, Fryxell and Doucet 1991). Although these studies have contributed greatly to our understanding of beaver foraging behaviour, they dealt primary with foraging for food.

Beavers are known for their extensive dam construction activity. Impounded water is crucial for their survival (Retzer et al. 1956, Nixon and Ely 1969), as it provides protection from predators. Impounded water also provides an efficient means to access and transport food items (Novak 1987). To accomplish this engineering activity, beavers need a ready supply of shoreline shrubs and trees (Novak 1976). To date, little research has been done to understand the cutting behaviour of beavers in obtaining items for constructing dams.

A review of the literature on beaver dams showed that emphasis has largely been placed on effects monitoring and control of beaver dams. The studies that focused on beaver dams were based on evaluations of construction materials used in the dam, not on resource availability (Shaw 1948, Nash 1951, Hodgdon and Hunt 1953, MacDonald 1956, Pullen 1975, Pinkowski 1983). Thomas and Taylor (1990) stated that studies evaluating resource use but not availability have resulted in inferences about use but not preference. Over the years, wildlife researchers have presented many definitions for "preference". Despite these inconsistencies, it is generally agreed that the best way to study resource preference is to employ techniques for comparing use and availability (Johnson 1980, Alldredge and Ratti 1986 and 1992, Thomas and Taylor 1990, Schooley 1994).

The Neu utilization-availability comparison (Neu et al. 1974) was applied to test whether beavers showed a preference for particular woody plant species in constructing dams or for specific sizes of materials.

2.3 Study Area

The study was conducted in the Swanson River drainage basin of the Chapleau Crown Game Preserve (48°05'N, 83°20'W) of northern Ontario (Fig. 2.1). This drainage area was free from trapping and hunting and thus provided a natural boreal forest setting where beaver dams could be studied with minimum disturbance. The Swanson River has a 200-km network of streams covering an area of 228 km^2. Riparian habitats were dominated by alder (*Alnus* spp). The forests were dominated by jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* Mill.) interspersed with mixed stands of white spruce (*Picea glauca* Moench), balsam fir (*Abies balsamea* (L.) Mill.), white birch (*Betula papyrifera* Marsh.), and trembling aspen (*Populus tremuloides* Michx.). Associated with these forest trees were numerous understory trees and shrubs such as willow (*Salix* spp.), pin cherry (*Prunus pensylvanica* L.), mountain maple (*Acer spicatum* Lam.), dogwood (*Cornus stonoifera* Michx.), mountain ash (*Sorbus americana* Marsh.), choke cherry (*Prunus virginiana* L.), black ash (*Fraxinus nigra* Marsh.), serviceberry (*Amelanchier* spp.), hazel (*Corylus cornula* Marsh.), and river birch (*Betula glandulosa* Marsh.).

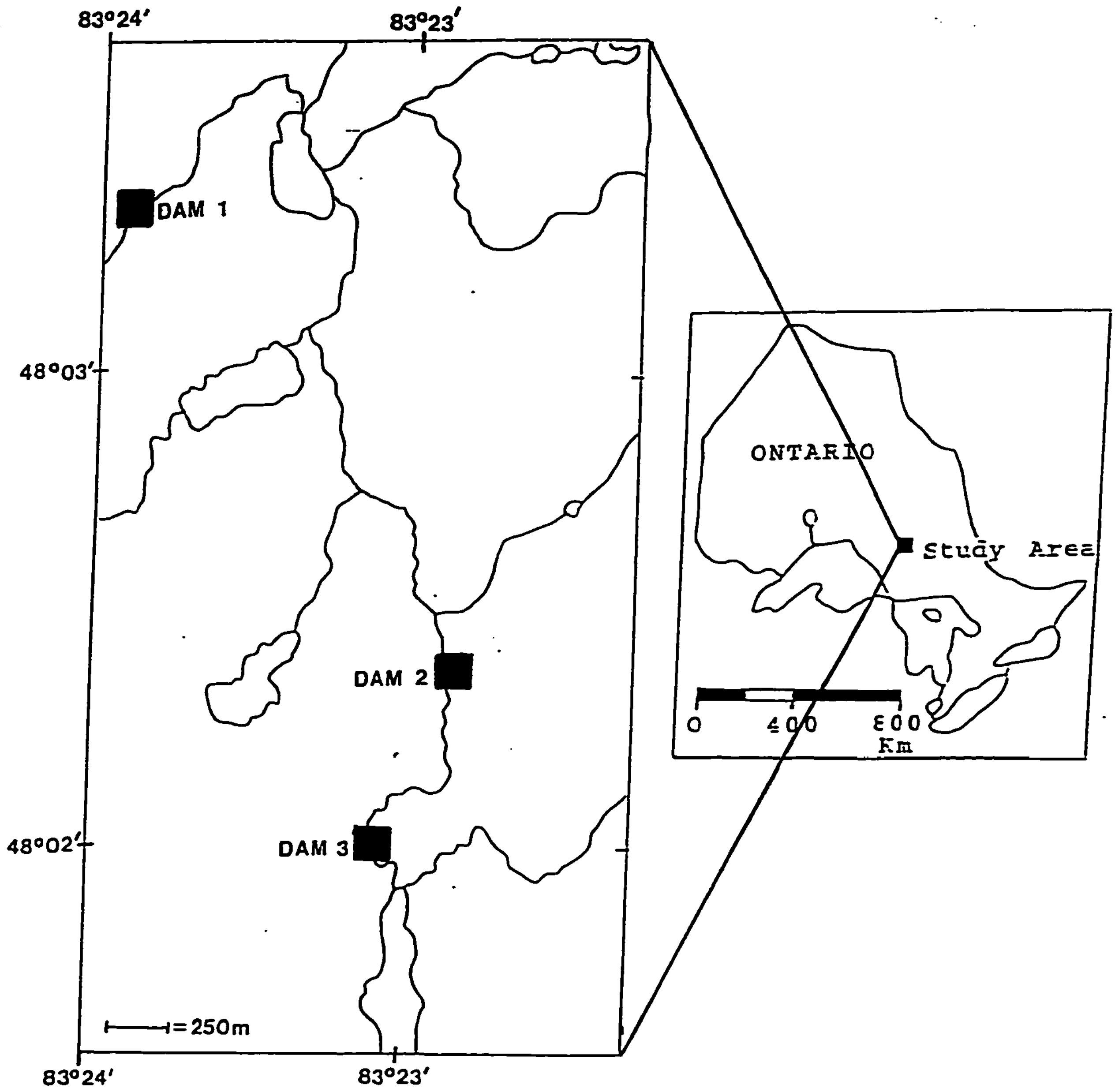

Figure 2.1 The location of newly formed beaver Dams 1, 2, and 3 within the Swanson River drainage basin of the Chapleau Crown Game Preserve in northern Ontario.

2.4 Methods

In June of 1993, a ground reconnaissance was conducted to locate newly formed dams in the study area, i.e. the dams constructed during the previous fall. Newly formed dams were chosen because beavers would have multiple options for obtaining woody plants, one of which would be to harvest woody plants from the sides of the stream. The use of streamside vegetation would not be an option at older dam sites because these materials would have been flooded and (or) browsed.

Of the 25 active colonies located during our survey, three newly formed dams were selected for this study (Fig. 2.1). Dam 1 had a length of 24 m and was situated on a 2 m wide second-order stream. The stream-order classification was based on Strahler (1957). Dam 2 was established on a 30 m wide third-order stream and had a length of 59 m. Dam 3 had a length of 8 m and was situated on a 5 m wide third-order stream.

A 0.25 m wide transect was established on the face of each dam and all woody materials visible along the dam face were identified and measured. Using calipers, the diameter of each stem base was determined, where the cut portion interfaced with the bark. The plant diameters were divided into five classes: < 1.5 cm, 1.5 - 2.4 cm, 2.5 - 3.4 cm, 3.5 - 4.4 cm, and ≥ 4.5 cm.

Each alder stem was examined for evidence of feeding. I decided against a detailed examination of all stems, because this would have meant dismantling the dams in high spring water conditions. There was no way of ensuring that stems would not be washed away or broken. As a compromise, alder stems were visually examined without their removal from the dam. Evidence of feeding, notably gnawing of bark and branch removal, was noted.

The pre-dam vegetation composition was re-constructed by studying vegetation above and below the main beaver dam, where the stream returned to its original width. Plots, 40 m wide and 170 m long, were established upstream and downstream. The plot dimensions were derived from analysis of the woody plant harvesting pattern around 15 active dammed colonies (unpublished data). Within each plot, three 1 m x 40 m transects, that extended perpendicularly from the stream's edge to inland, were randomly selected. The diameter of all shrubs and trees was measured at a height of 30 cm above ground. The 30 cm height was established by measuring 20 beaver-cut stumps. This value was consistent with that reported by Johnston and Naiman (1990). Average values of the upstream and downstream plots were used to simulate the impoundment pre-dam shoreline vegetation. *T* tests were used to determine whether the upstream and downstream vegetation compositions were significantly different.

The Neu method of utilization-availability comparison (Neu et al. 1974; Byers et al. 1984) was chosen to test the hypothesis that beavers have a preference for particular woody species or a specific size class of stems irrespective of species in the construction of dams. The utilization-availability method involves the use of Bonferroni confidence intervals. Using this technique, one can be at least 100 (1 - α)% confident that the intervals contain their respective true proportions, p_{actual}:

$$\hat{p}_{act} - Z_{\alpha/2k}\sqrt{\hat{p}_{act}(1-\hat{p}_{act})/n} \leq p_{act} \leq \hat{p}_{act} + Z_{\alpha/2k}\sqrt{\hat{p}_{act}(1-\hat{p}_{act})/n}$$

where $\hat{p}_{act.}$ is the predicted value of $p_{act.}$, α is the level of significance, k is the number of categories tested, $Z_{\alpha/2k}$ is the upper standard normal table value corresponding to a probability tail area of $\alpha/2k$, and n is the the number of stems used.

For each of the actual utilization proportions, $p_{act.}$, a Bonferroni confidence interval was constructed. When the expected proportion of usage, $p_{exp.}$, fell within the interval, I concluded that the expected and actual utilizations were not significantly different, i.e. the selection was by chance. If the Bonferroni confidence interval was greater than the expected usage, then the vegetation type was being utilized more than its availability, i.e. it was preferred. If the Bonferroni confidence interval was less than the expected usage, then the vegetation type was being utilized less than its availability, i.e. it was avoided (Byers et al. 1984).

To ensure a convincing case for determining the beaver's selection process, the joint effects of species and diameter on selection were analyzed. In addition, the spatial distribution of the plant categories adjacent to the water's edge was recorded. These data were used to determine the forage-distance relationships as they applied to the collection of construction material.

2.5 Results

Our results showed that the density of stems of the downstream and upstream vegetation were not significantly different (Table 2.1). This provided the justification for averaging the data of the upstream and downstream plots.

Alder stems were used for construction only. Our analysis of the stems used in dam construction found that all alder stems were placed in the dam intact, with no sign of feeding activity.

Beavers showed a preference for stems 1.5 - 2.4 cm diameter class when cutting alder, other shrubs, and conifers (Table 2.2). In addition, they showed a preference for alder stems of 2.5 - 3.4 cm diameter and food stems of $\geq$ 4.5 cm diameter and avoided alder, shrub, and food stems with diameters 0.5 - 1.4 cm. Beavers utilized alder over the other plant categories when cutting stems $<$ 4.5 cm diameter. For stems of $\geq$ 4.5 cm diameter, beavers search out food trees (Table 2.2). Generally, shrub and conifer stems were selected against.

The highest concentration of 1.5 - 3.4 cm diameter alder stems was found within 10 m of the shore (Fig. 2.2). No other plant group had as many stems of preferred size class in

Table 2.1. Mean density of woody stems (number/120 m^2) in downstream and upstream plots of the three beaver dams.

Woody plant categories	Downstream plots	Upstream plots	t-test
Alder	134 (30[a])	165 (61)	p = 0.7
Shrubs	79 (22)	89 (45)	p = 0.9
Conifers	59 (21)	48 (21)	p = 0.7
Food[b]	27 (14)	19 (10)	p = 0.7

[a] Standard error of mean

[b] Food is considered to be trembling aspen, white birch, and willow.

Table 2.2 Utilization-availability analysis of woody stems used in the construction of newly-formed dams in the Chapleau Crown Game Preserve, Chapleau, Ontario.

Woody plant class	Diameter class (cm)	Total stems available[a]	Actual no. of stems used[b]	Expected proportion used (Pexp.)	Actual proportion used (Pact.)	Bonferroni confidence of Pact.[c]
Alder	0.5-1.4	93(29.1)	65(30.5)[c]	0.62	0.19	-0.09 ≤ Pact. ≤ 0.29[d]
	1.5-2.4	39(8.6)	172(93.7)	0.26	0.49	0.36 ≤ Pact. ≤ 0.62[e]
	2.5-3.4	11(3.8)	79(47.9)	0.07	0.22	0.11 ≤ Pact. ≤ 0.33[e]
	3.5-4.4	4(2.1)	32(10.4)	0.03	0.09	0.02 ≤ Pact. ≤ 0.16[f]
	≥4.5	2(0.5)	2(0.6)	0.02	0.01	-0.02 ≤ Pact. ≤ 0.04[f]
Shrubs	0.5-1.4	75(17.8)	5(0.9)	0.86	0.29	0.22 ≤ Pact. ≤ 0.36[d]
	1.5-2.4	6(4.5)	9(3.2)	0.08	0.53	0.45 ≤ Pact. ≤ 0.61[e]
	2.5-3.4	2(0.5)	1(0.3)	0.04	0.06	0.02 ≤ Pact. ≤ 0.10[f]
	3.5-4.4	0(0)	1(0.3)	0.0	0.06	0.02 ≤ Pact. ≤ 0.10[g]
	≥4.5	1(0.4)	1(0.3)	0.02	0.06	0.02 ≤ Pact. ≤ 0.10[f]
Conifers	0.5-1.4	6(2.7)	1(0.3)	0.13	0.20	0.06 ≤ Pact. ≤ 0.25[f]
	1.5-2.4	6(2.1)	2(0.6)	0.11	0.32	0.21 ≤ Pact. ≤ 0.45[e]
	2.5-3.4	3(1.2)	1(0.3)	0.06	0.16	0.06 ≤ Pact. ≤ 0.25[f]
	3.5-4.4	5(1.8)	1(0.3)	0.09	0.16	0.06 ≤ Pact. ≤ 0.25[f]
	≥4.5	33(2.3)	1(0.3)	0.60	0.16	0.06 ≤ Pact. ≤ 0.25[d]
Food[h]	0.5-1.4	10(3.6)	7(5.3)	0.44	0.08	0.01 ≤ Pact. ≤ 0.15[d]
	1.5-2.4	4(1.4)	16(10.9)	0.20	0.17	0.07 ≤ Pact. ≤0.27[f]
	2.5-3.4	2(0.7)	16(11.3)	0.08	0.17	0.07 ≤ Pact. ≤ 0.27[f]
	3.5-4.4	1(0.3)	11(6.1)	0.04	0.11	0.03 ≤ Pact. ≤ 0.19[f]
	≥4.5	6(4)	44(24.3)	0.24	0.47	0.34 ≤ Pact. ≤ 0.60[e]
Alder	all	149(42.3)	350(181.2)	0.49	0.75	0.64 ≤ Pact. ≤ 0.86[e]
Shrubs	all	84(21.8)	17(3.0)	0.27	0.04	-0.01 ≤ Pact. ≤ 0.10[d]
Conifers	all	53(4.7)	6(0.8)	0.17	0.01	-0.01 ≤ Pact. ≤ 0.04[d]
Food	all	23(7.7)	94(56.7)	0.07	0.20	0.10 ≤ Pact. ≤ 0.30[e]
	Total	309	467			

[a] Mean density of woody stems (no./120 m^2) available at three dams. Values in parentheses represent standard errors.
[b] Mean density of woody stems used in three dams. Values in parentheses represent standard errors.
[c] If Pexp value is within the Bonferroni Interval, the hypothesis of proportional use, i.e. H_o : Pexp. = Pact.
[d] Avoided plant stems (i.e., Pact. < Pexp.).
[e] Preferred plant stems (i.e., Pact. > Pexp.)
[f] Plant stems selected by chance (i.e., Pexp. within Bonferroni interval).
[g] Pact. value not used, as we recorded no stems available.
[h] Food is considered to be trembling aspen, white birch, and willow.

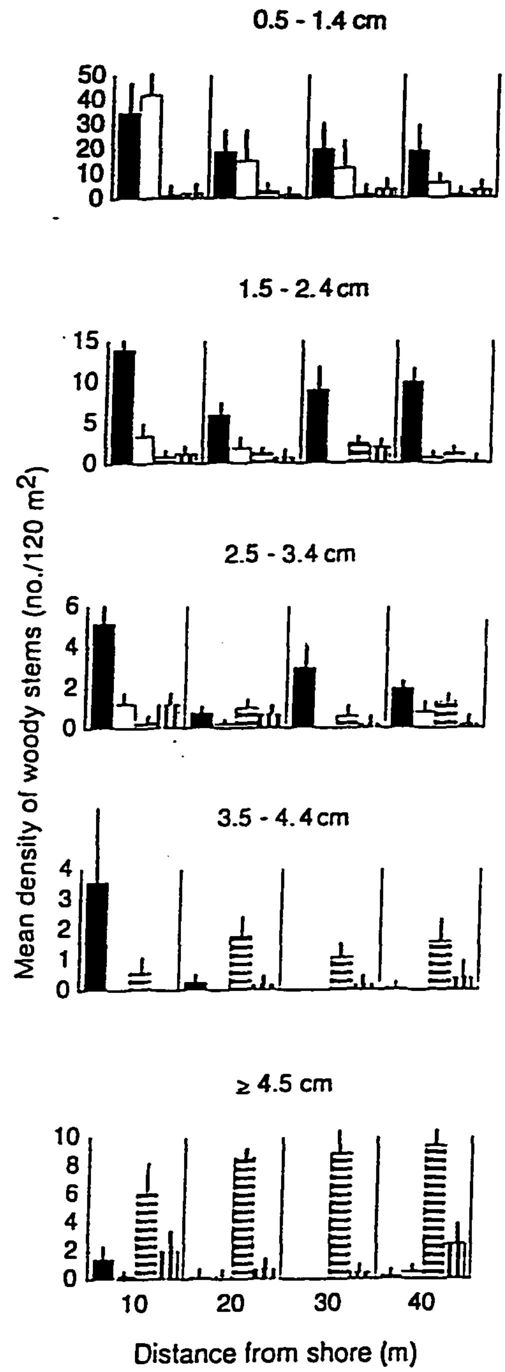

Figure 2.2 Composition and diameter classes of woody plants within 40 m of the shorelines of Dams 1, 2, and 3, representing alder ■, shrubs □, conifers ▤, and food trees ▥. The bars on each column represents standard error of the mean.

close proximity to the shoreline. The densities of food plants were low within 40 m of shore, determined to be the average foraging distance for beaver within my study area (see Chapter 3), therefore, beavers had to travel beyond this foraging distance to obtain food items for use in dam construction.

2.6 Discussion

The present study found that boreal beavers showed a preference for alder stems of diameter class 1.5 - 3.4 cm. Although previous studies demonstrated that plant species not commonly used as food, such as alder, were utilized to a great extent in the establishment of dams (Hodgdon and Hunt 1953; Slough and Sadlier 1977; Slough 1978; Novak 1987), none have shown the nature of the preference by using utilization-availability comparisons.

In his work on eastern woodrats, McGinley (1984) noted that they collected large twigs to ensure the house was strong enough, whereas small twigs were used to ensure that it was adequately waterproofed. I postulate that beavers show a similar collection bias. From my observations of dam construction, I concur with Macnamara (1931) and Johnson (1932) who showed that beavers construct dams by positioning whole, intact stems so that the leafy branches are oriented upstream. In our study, for the most part beavers used intact alder stems with diameters of less than 4.5 cm when constructing dams. J.M. Fryxell (personal communication) found that beavers were able to haul intact aspen up to a diameter of 4.2 cm. In his opinion, no appreciable energy was utilized by beaver hauling these large alder stems to water. Based on this, I felt that the beavers were probably selecting smaller sized stems for the practical reason that energy and time were invested for in-water rather than out-of-water effort. I suspect that the larger alder stems would probably be more difficult to handle in the fast-flowing water associated with dam locations. Further, the smaller (less than 1.5 cm) stems probably made the dam less porous, as they could be easily woven amongst the larger stems.

Beavers showed a secondary preference for food stems greater than or equal to 4.5 cm diameter when constructing new dams (Table 2.2). Spatial analysis of woody plants showed that the larger food stems occurred outside the foraging range of beaver (Fig. 2.2). In his beaver-foraging study, Pinkowski (1983) found that larger trees used for food as well as construction were likely to be cut at a greater distance than larger trees of the species used primarily for construction. He claimed that trees used for both food and construction would yield more benefits per unit cost than the species used only for construction purposes. Based on the results of the present study, an alternative explanation is offered. I believe that it is the smaller stems which are advantageous in dam building, and that larger food stems may be selected primarily on a net energy gain basis. Since the utilization and availability data were collected in the spring following dam establishment, I contend that these food trees were harvested largely in the previous fall and stored in food caches for over-winter consumption. The impounded waters of the beaver dam then served to reduce the distance to food plants. I speculate that the flowing spring waters would push the utilized food stems towards the dam. I feel beavers, being very opportunistic (Pullen, Jr. 1975), would make use of these stems to maintain dam integrity. All food items had been fully debarked before use in dam construction, indicating that their primary purpose was nutrition. This may explain why beaver in our study area would haul these large food stems over such long distances.

From our analysis, beavers used alder for construction purposes only. From an evolutionary standpoint, the use of specific plants solely for construction purposes would seem to be a good strategy, as it ensures that other food items were not depleted unnecessarily (Pinkowski 1983). However, based on our research, I feel that there is a more basic, utilitarian reason for the extensive use of alder. In boreal areas, the timber wolf (*Canis lupus* L.) is very effective at preying upon beaver on land (Pimlott et al. 1969; Kolenosky 1972; Frenzel 1974; Voigt et al. 1976; Theberge et al. 1978; Bergerud et al. 1983) and has been shown to reduce beaver populations (Potvin et al. 1992). As a result, beavers must establish a dam as quickly as possible to guarantee a safe home place. I feel that whole alder plants provide beavers with a source of ideally sized building material to harvest and use in close proximity to water. In our study, no other plant group contributed nearly as many stems of a suitable diameter class. For beavers, this situation is ideal as it minimizes the time they need to be on land, thus minimizing predation.

Based on our utilization-availability study of new dams, I postulate that beavers require shoreline concentrations of woody plants with a diameter range of 1.5 - 3.4 cm to effectively dam boreal streams. Further field work is planned to establish cause-and-effect relationships to further validate our findings.

CHAPTER 3

3. Effects of beaver herbivory on stream side vegetation in a northern Ontario watershed

3.1 Abstract

To date, there has been no adequate study to determine the effects of beaver (*Castor canadensis*) herbivory on streamside plant communities and the re-vegetation of abandoned dam sites. Beavers use riparian plants as food, notably trembling aspen (*Populus tremuloides*), willow (*Salix* sp.), and white birch (*Betula papyrifera*) and for dam construction mainly alder (*Alnus* sp.) and other deciduous shrubs, such as pin cherry (*Prunus pensylvanica*), mountain maple (*Acer spicatum*), dogwood (*Cornus stonoifera*), mountain ash (*Sorbus americana*), choke cherry (*Prunus virginiana*), black ash (*Fraxinus nigra*), serviceberry (*Amelanchier* spp.), hazel (*Corylus cornula*), and river birch (*Betula glandulosa*). Based on the life-form and their utility to beaver the riparian plants around beaver impoundments were classified into 5 categories: alder (dam construction), trembling aspen (primary food), white birch and willow (secondary foods), shrubs (dam construction), and conifers (dam construction) including mainly jack pine (*Pinus banksiana*), black spruce (*Picea mariana*) white spruce (*Picea glauca*), balsam fir (*Abies balsamea*). Influence of beaver activity on these plants were studied at 15 active, 7 recently abandoned and 8

old abandoned dam sites. Most of the cutting (73%) of woody stems at active dam sites was concentrated within 20 m from the impoundment edge. The most often cut species was alder (52%) followed by trembling aspen (16%) and birch and willow together (14%). With the exception of trembling aspen and shrubs such as mountain maple and hazel, woody plant groups showed no significant difference in density due to beaver activity. The fluctuating water level induced by cyclic dam establishment and abandonment of beaver dams is suggested as a possible reason for low plant densities adjacent to abandoned dam edges.

3.2 Introduction

Johnston and Naiman (1990) stated that of all the North American herbivores, beavers have the greatest potential to affect plant communities. They provided three reasons why beaver herbivory has such an impact: 1) beavers cut down trees and shrubs, thus affecting the canopy and sub-canopy light levels of forests; 2) beavers restrict their cutting activity to narrow, riparian habitats, thus concentrating the impact along shorelines; and 3) beavers harvest trees far in excess of the amount actually ingested.

Despite this recognized importance, most research has concentrated on food acquisition (Chabreck 1958, Hall 1960, Hall 1960, Brenner 1962, Nixon and Ely 1969, Northcott 1971, Jenkins 1979 and 1980, Belovsky 1984, McGinley and Whitham 1985, Fryxell 1992). Research dealing with the effects of herbivory on plant communities has largely been restricted to a few active colonies where cutting was on going (Dibble and Barnes 1988; Johnston and Naiman 1990). Furthermore, little emphasis has been placed on documenting the re-vegetation process after the cutting activity was stopped and sites were abandoned.

The objectives of the present study were: 1) to determine the effect of beaver herbivory on shoreline woody plants at active dam sites; and 2) to assess the recovery of shoreline plant communities at abandoned beaver dam sites.

3.3 Study Area

The study was conducted in the Chapleau Crown Game Preserve (48°05'N, 83°20'W; elevation range 348 - 510 m above sea-level) of northern Ontario (Fig. 3.1). The preserve was established in 1925 and encompasses a 700,000 ha of northern boreal forest. Since no hunting and trapping of mammals was permitted within this area, it provided a natural boreal forest setting where beavers could be studied with minimum disturbance.

Within the Chapleau Crown Game Preserve, the Swanson River drainage basin was selected as the study area. The Swanson River has a 200 km network of streams covering an area of 228 km^2. Riparian habitats were dominated by alder (*Alnus* spp). The forests were dominated by jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) interspersed with mixed stands of white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*). Associated with these forest trees were numerous understory trees and shrubs such as willow (*Salix* spp.), pin cherry (*Prunus pensylvanica*), mountain maple (*Acer spicatum*), dogwood (*Cornus stonoifera*), mountain ash (*Sorbus americana*), choke cherry (*Prunus virginiana*), black ash (*Fraxinus nigra*), serviceberry (*Amelanchier* spp.), hazel (*Corylus cornula*), and river birch (*Betula glandulosa*).

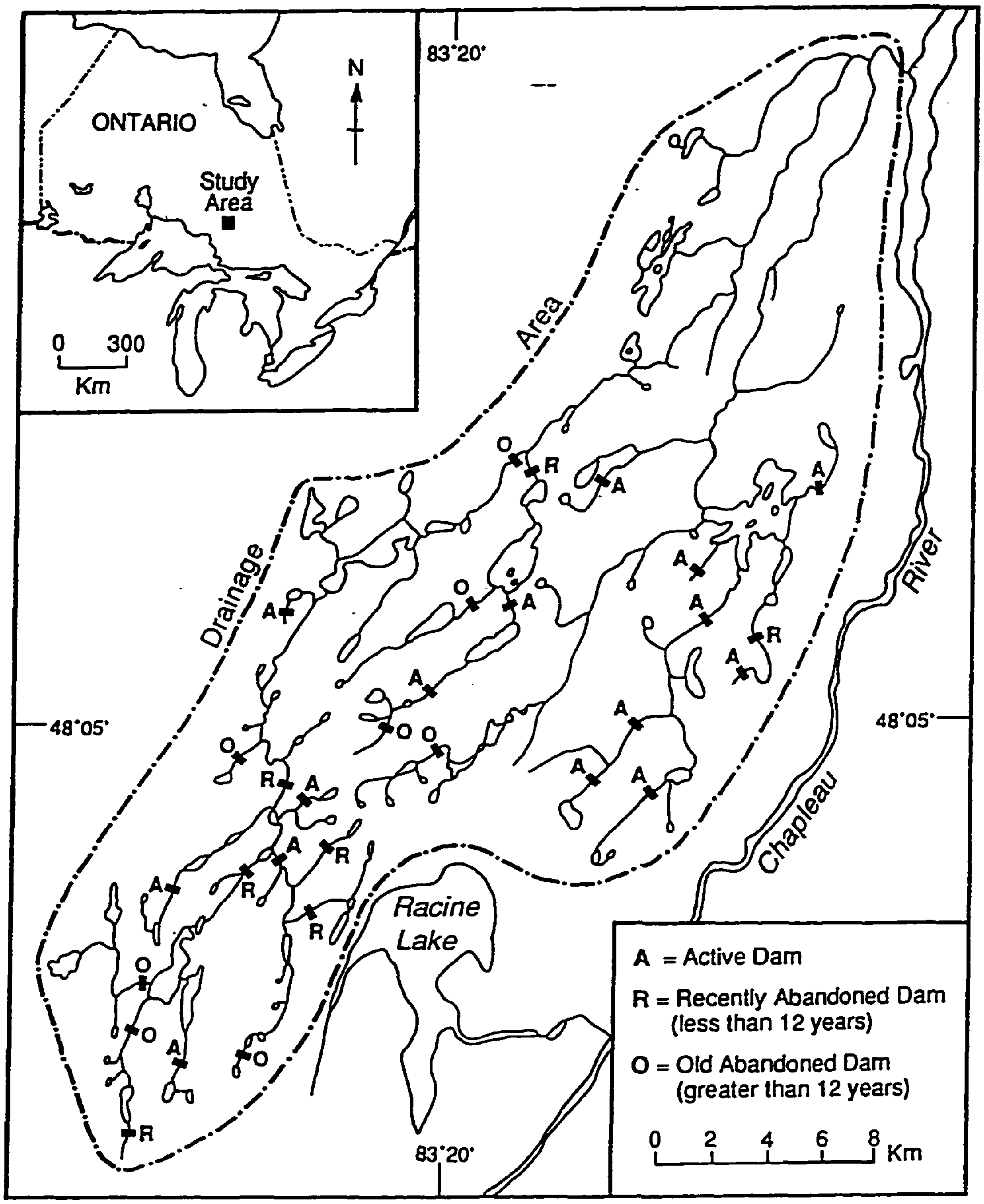

Figure 3.1. The Swanson River drainage basin study area with the location of active, recently abandoned and old abandoned beaver impoundments, 1993. Location of the Chapleau Crown Game Preserve study site in Ontario is shown in the inset.

3.4 Methods

Within the Swanson River drainage system, 40 active and 85 abandoned beaver impoundments were located using a Cessna 180 airplane in the fall (Bergerud and Miller 1977) and a stereoscopic examination of 1980 (R:F-1:15840) and 1992 aerial photographs (R:F-1:8000). From these 125 sites, 15 active, 7 recently abandoned (> 12 years) and 8 old abandoned (< 12 years) impoundments were randomly selected (Fig. 3.1). Active beaver impoundments were identified by recognizing the presence of food caches. Time since abandonment was assessed using aerial photographs. Several criteria were used to locate the abandoned dam sites, for example, condition of dams, presence of beaver meadows (Wilde et al. 1950), presence of dead vegetation, and the amount of impounded water.

Control plots were established downstream of both active and abandoned impoundments, where the stream returned to its original width. To ensure appropriate positioning inland, the distance from mid-stream to the end of the dam was measured. This ensured the sampling of a similar forest sector as that of the impoundment plots, but further away from the water's edge (Fig. 3.2).

At each of the active, recently and old abandoned dam sites, the shoreline of the impoundment to be analyzed was chosen at random. Along the chosen shoreline, a sample plot was established with a width and length of 40m and 170m, respectively (Fig. 3.2). Within each sampling plot, 3

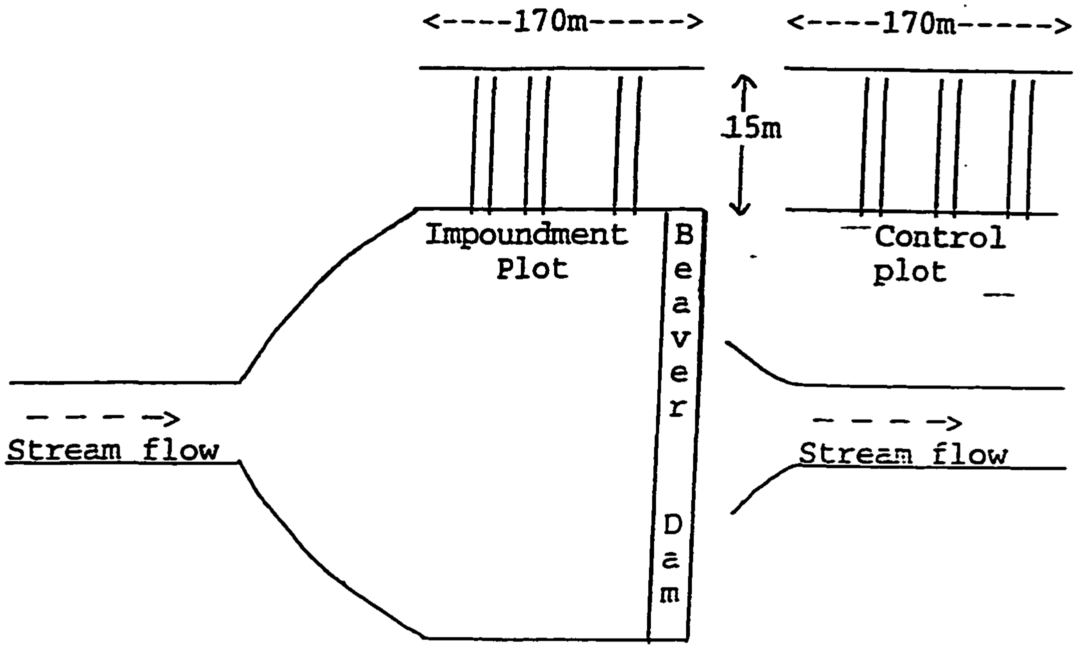

Figure 3.2. Sampling technique for studying the impact of beaver herbivory on shrubs and trees at active beaver impoundments, recently abandoned impoundments (< 12 years), old abandoned impoundments (> 12 years), and forest control plots in the Swanson River basin of the Chapleau Crown Game Preserve, northern Ontario, 1993.

shoreline locations were randomly selected and 3 - 1 m x 40 m belt transects were established perpendicular to the impoundment's edge. Each transect was divided into 40 - 1 m x 1 m sub-plots (Fig. 3.2). At the 15 active sites, all the beaver-cut stumps and uncut stems with diameters ≥ 0.5 cm were recorded from a total of 1,800 - 1 m x 1 m sub-plots. Because of the low number of cut stems encountered in each transect, the total stem numbers (combining all the plots) were used to determine the beaver herbivory. At recent and old abandoned dam sites, only standing uncut stems with diameters ≥ 0.5 cm were recorded, since the decayed state of cut stumps made species identification unreliable.

Species richness of shoreline woody vegetation was determined by a direct count of the number of species within the sampling plots (Ludwig and Reynolds 1983).

Importance values (sum of the relative density, relative frequency, and relative dominance) were used to calculatespecies diversity and evenness (Odum 1971, Krebs 1978). Although most ecologists have used the Shannon's Index, (i.e. $-[\Sigma(n_i/n)/\ln(n_i/n)]$, where n_i = *i*th of S species in the sample and n = total number of individuals in the sample) to determine species diversity, this estimator is biased, as the total number of species found within a community will most likely be greater than the number of species observed in any sample (Ludwig and Reynolds 1983). To overcome this bias, Hill's diversity number 1: $N1 = e^{-[\text{Shannon's Index}]}$ (Hill 1973, DeJong 1975) was used to measure species diversity.

There have been several indices developed to measure species evenness. In each case, if all species in a sample are equally abundant, then the evenness index should have a maximum value. Conversely, lower values means a divergence away from evenness. Based on Ludwig and Reynolds (1983), I used Evenness Index 5: E5 = N2-1/N1-1, where N1 = Hill's diversity number 1 and N2 = Hill's diversity number 2: N2 = 1/Simpson's index, where Simpson's index = $\sum(n_i(n_i-1)/(n(n-1)]$, n_i = ith of S species in the sample and n = total number of individuals in the sample). E5 values approach zero when species become dominant and one when evenness is maximum (Alatalo 1981).

3.5 Results

In a total of 1,800 1 x 1 m sub-plots sampled at 15 active dam sites, 79 cut stumps (all species included) were recorded, 58 of which were cut within 20 m of the water's edge (Fig. 3.3). In addition, 1,733 uncut stems were recorded.

The majority of the cut stems (52%) were alder. No alder stump was noted at distances greater than 20 m from the impoundment's edge. Similiarly when harvesting trembling aspen, beavers concentrated their herbivory close to impoundment edges; 44% of available stems were cut within 10 m of shore and 35% within 20 m, while only 13% of trembling aspen trees were cut at greater distances (Fig. 3.3).

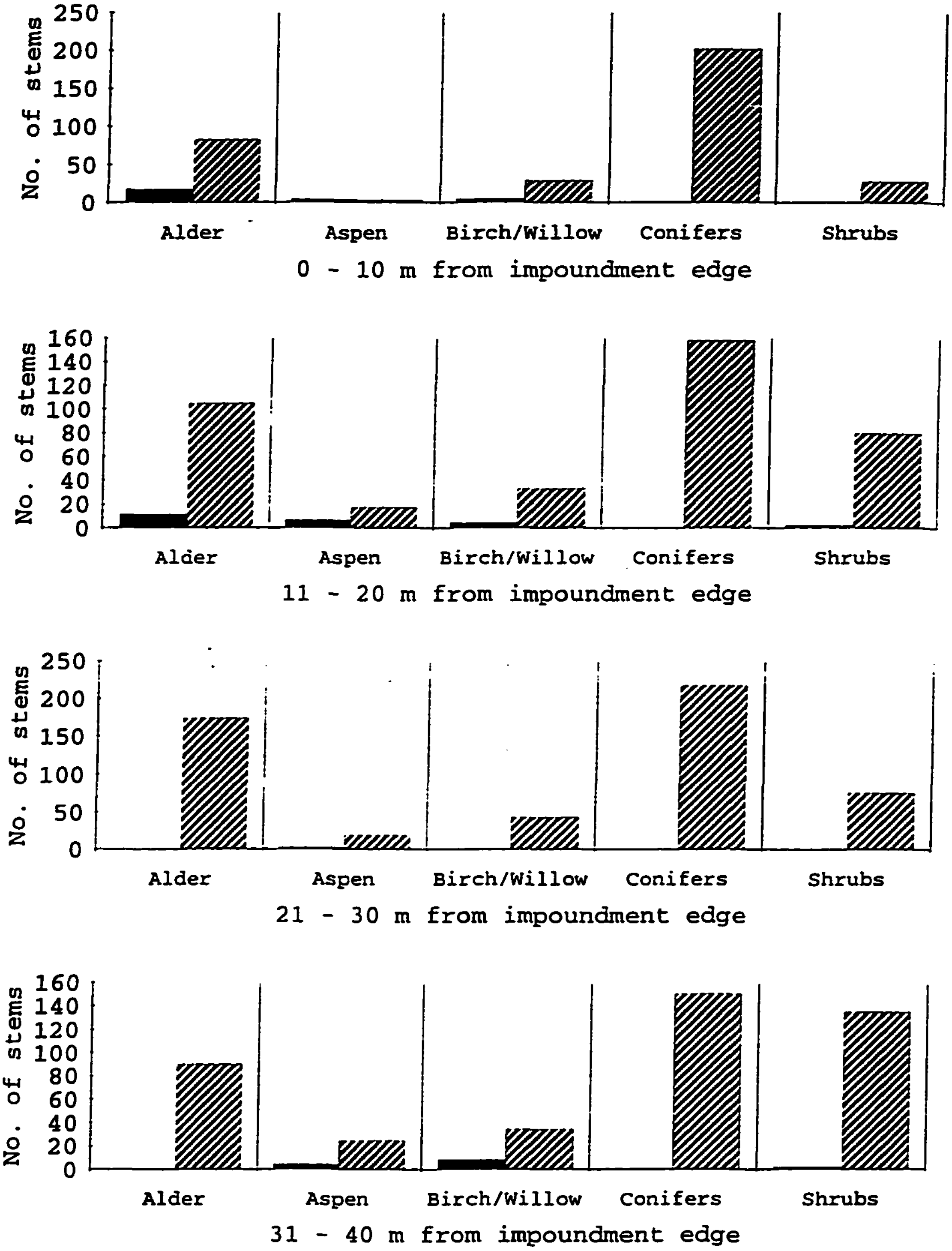

Figure 3.3. Number of beaver cut (■) and uncut (▨) woody plant species at 10 m intervals from the water's edge of 15 active beaver dams in the Chapleau Crown Game Preserve, northern Ontario, 1993.

Beavers cut white birch and willow stems throughout the 40 m sample area. Thus, 15% of available stems were cut within 20 m and 11% stems cut between 20 and 40 m from the water's edge (Fig. 3.3). Cutting of conifers and other hardwood shrub species was minimal (Fig. 3.3).

At abandoned dam sites, the density of shoreline woody species within 20 m of the water's edge was not significantly different from the vegetation found between 21 - 40 m (*t*-tests, $\alpha = 0.05$, Table 3.1 and 3.2). In addition, no woody plant category was significantly affected over time within 40 m of the shore (Table 3.1 and 3.2). None of the shoreline woody vegetation at active and abandoned dam sites were significantly different from the forest control sites (Tables 3.2 and 3.2). Shoreline densities of trembling aspen and shrubs did show a reduction with an extended abandonment period of more than 12 years (Table 3.1 and 3.2). Mountain maple and hazel are two hardwood shrubs that reflected this trend most dramatically (Tables 3.1 and 3.2). The other 3 plant groups did not show any distributional difference.

Species richness, diversity, and evenness index values for woody plants were generally lower at distances less than 20 m from the water's edge (Table 3.3). When active and abandoned dam sites were compared, it was noted that the index values were generally higher at active dam sites than the abandoned dam sites (Table 3.3).

Table 3.1. The density [no. of stems/ha] (SE) of woody species found within 20 m of the shoreline of active (AC), recently abandoned (RAB) < 12 years ago, and old abandoned (OAB) impoundments, > 12 years ago, and downstream control forest plots (CN) in the Chapleau Crown Game Preserve, 1993. Values connected by a line in the least square difference comparisons are not significantly different (P > 0.05).

Woody Plants[a]	Active Density	Recently Abandoned Density	Old Abandoned Density	Control Plots Density	Least Square Differences
Alnus[b] spp	2427(766)	4103(1400)	5991(2823)	4114(818)	AC RAB OAB CN
Populus tremuloides[c]	211(65)	24(23)	0(0)	295(118)	AC RAB OAB CN
Salix/Betula papyrifera[b]	768(196)	334(237)	1106(574)	657(141)	AC RAB OAB CN
Salix spp	468(128)	72(70)	459(371)	228(67)	
Betula papyrifera	300(108)	262(230)	647(453)	429(138)	
Conifers[b]	4425(927)	3483(968)	3360(455)	3824(600)	AC RAB OAB CN
Pinus banksiana	368(148)	239(132)	814(312)	507(92)	
Pinus resinosa	50(50)	0(0)	0(0)	0(0)	
Picea mariana	1447(297)	2624(937)	1607(543)	1525(234)	
Picea glauca	345(145)	48(30)	42(42)	273(104)	
Abies balsamea	2160(669)	501(392)	605(318)	946(300)	
Larix laricina	11(11)	71(70)	0(0)	61(31)	
Thuja occidentalis	44(29)	0(0)	292(215)	512(391)	
Shrubs[b]	1158(382)	1670(1238)	521(221)	2717(971)	AC RAB OAB CN
Cornus stolonifera	134(91)	239(88)	188(147)	551(207)	
Acer spicatum	234(131)	763(747)	0(0)	590(314)	
Amelanchier spp	200(84)	95(60)	188(125)	139(36)	
Corylus cornuta	301(222)	501(185)	0(0)	902(524)	
Sorbus americana	189(70)	24(23)	62(30)	195(61)	
Prunus pensylvanica	100(88)	48(46)	62(63)	200(116)	
Prunus virginiana	0(0)	0(0)	21(21)	84(72)	
Acer rubrum	0(0)	0(0)	0(0)	6(5)	
Betula glandulosa	0(0)	0(0)	0(0)	39(29)	
Fraxinus nigra	0(0)	0(0)	0(0)	11(10)	

[a] Only woody plants with diameters ≥ 0.5 cm were used in the analyses.
[b] Logarithmic transformations using normal probability plots.
[c] Kruskal-Wallis was used in place of ANOVA as data could not be normalized using normal probability plots.

Table 3.2. The density [no. of stems/ha] (SE) of woody species found between 20 and 40m of the shoreline of active (AC), recently abandoned (RAB) < 12 years ago, and old abandoned (OAB) impoundments, > 12 years (ago), and downstream control forest plots (CN) in the Chapleau Crown Game Preserve, 1993. Values connected by a line in the least square difference comparisons are not significantly different ($P > 0.05$).

Woody Plants[a]	Active Density	Recently Abandoned Density	Old Abandoned Density	Control Plots Density	Least Square Differences
Alnus[b] spp	3073(984)	6799(4255)	2902(1819)	3151(801)	AC RAB OAB CN
Populus tremuloides[c]	479(188)	191(125)	42(42)	362(179)	AC RAB OAB CN
Salix/Betula papyrifera[b]	824(196)	1193(325)	918(432)	868(180)	AC RAB OAB CN
Salix spp	278(115)	453(246)	605(407)	384(146)	
Betula papyrifera	546(201)	740(363)	313(136)	484(143)	
Conifers[b]	3874(836)	4222(1101)	4279(656)	3613(436)	AC RAB OAB CN
Pinus banksiana	456(184)	453(158)	772(285)	702(197)	
Pinus resinosa	0(0)	0(0)	0(0)	0(0)	
Picea mariana	1136(224)	2362(624)	1524(375)	1553(246)	
Picea glauca	111(41)	119(68)	104(63)	184(71)	
Abies balsamea	2115(910)	1288(785)	1190(410)	946(268)	
Larix laricina	11(11)	0(0)	21(21)	67(32)	
Thuja occidentalis	45(34)	0(0)	668(650)	161(93)	
Shrubs[b]	3508(899)	2934(2209)	1167(668)	2305(655)	AC RAB OAB CN
Cornus stolonifera	201(129)	239(184)	114(58)	184(108)	
Acer spicatum	657(335)	1074(1051)	84(63)	601(276)	
Amelanchier spp	312(154)	358(196)	176(79)	317(127)	
Corylus cornuta	1191(525)	1169(1118)	626(632)	763(340)	
Sorbus americana	278(121)	48(30)	104(51)	189(82)	
Prunus pensylvanica	89(45)	48(46)	21(21)	195(101)	
Prunus virginiana	0(0)	0(0)	42(42)	6(5)	
Acer rubrum	0(0)	0(0)	0(0)	0(0)	
Betula glandulosa	0(0)	0(0)	0(0)	50(49)	
Fraxinus nigra	0(0)	0(0)	0(0)	0(0)	

[a] Only woody plants with diameters > 0.5 cm were used in the analyses.
[b] Logarithmic transformations using normal probability plots.
[c] Kruskal-Wallis was used in place of ANOVA as data could not be normalized.

Table 3.3. Richness, diversity, and evenness indices determined active beaver impoundments, impoundments recently abandoned within < 12 years, and old abandoned impoundments > 12 years, in the Chapleau Crown Game Preserve, 1993.

Ecological indices	Active impoundments		Recently abandoned impoundments		Old abandoned impoundments	
	0-20m	21-40m	0-20m	21-40m	0-20m	21-40m
Species Richness	6.1	7.1	5.5	7.3	5.3	6.0
Hill's Diversity Number 2	7.9	9.6	5.4	7.2	5.6	8.0
Evenness Index 5	0.7	0.9	0.6	0.8	0.8	0.8

3.6 Discussion

In the Chapleau Crown Game Preserve, beavers concentrated their foraging for food and construction materials to within 20 m of the impoundment edge. Johnston and Naiman (1990) found that Minnesota beavers also preferred to cut within 20m of the water's edge. These findings suggest a narrow foraging range for beaver, although they have the ability to haul woody stems 200m overland (Novak 1987). Given the high wolf (*Canis lupus*) populations in Ontario and Minnesota (Carbyn 1987), it is possible that beavers adjusted their foraging pattern to minimize predation by timber wolves (Pimlott et al. 1969; Kolenosky 1972; Frenzel 1974; Voigt et al. 1976; Theberge et al. 1978; Bergerud et al. 1983, Potvin et al. 1992). Recent studies support the idea that animals have the ability to assess and behaviourally influence their risk of being preyed upon (Lima and Dill 1990).

Alder plants were harvested more than any other plant group including food trees. Since impounded water is the most important factor affecting habitat use by beaver (Novak 1987), this pre-occupation with alder could have been in response to dam maintenance. Barnes and Mallik (1996) showed that alder was the woody species of choice when building a dam because of their ideal stem size and proximal location to water.

Johnston and Naiman (1990) studied the effects of beaver herbivory at active impoundments and found that beavers opened the forest canopy by the removal of large trees. They claimed that the resulting combination of increased light penetration, decreased competition for soil water and nutrient, and increased reproductive rates of plants by suckering and seed germination, caused a dramatic increase in sub-canopy trees and shrubs. Their results are in contrast to the present study which showed no significant difference in the density of woody plants between the dam sites and control plots. Given the high variability and the low number of replicates used in my analysis, there may well be differences but my tests were probably not powerful enough to detect them.

Part of the explanation, however, may be that Johnston and Naiman (1990) conducted their stduy at active dam sites where ground water levels were high but stable. Wilde et al. (1950) found that when beaver dams were abandoned and no longer supported impounded water, the rapid decrease in ground water levels created drought-induced injury causing a general decrease in forest plants, such as aspen. In addition, they attributed low plant growth potential of conifers to partial "drowning" of root systems and decreasing soil aeration which hampered mycorrhizal root development. Fluctuating water levels may well have had adverse effects on the plant species growing adjacent to beaver impoundment sites.

GENERAL DISCUSSION

Beaver dams in northern Ontario were studied by focusing on three aspects: 1) habitat factors influencing dam-site selection, 2) use of woody plants in construction of beaver dams, and 3) impact of beaver herbivory and the revegetation of abandoned dam sites.

The present study showed that both physical characteristics of streams such as upstream watershed area and stream cross-sectional area and vegetation features such as availability of woody plants with diameters 1.5 - 4.4 cm are important determinants of dam site location. This finding differs from the previous studies that claimed dam-site selection was triggered by physical features only (Retzler et al. 1956, Rutherford 1964, Slough and Sadleir 1977, Howard and Larson 1985, McComb et al. 1990).

Prehaps the reason for alder as an important habitat determinant for beaver dam site location was because of its role in dam construction. Alder contributed most of the stems of preferred diameter range (1.5 - 3.4 cm) used by beavers in dam building (Barnes and Mallik 1996). Since beavers are able to transport whole alder stems overland with no appreciable energy cost (J. Fryxell, pers. comm.), they were able to construct dams with high efficiency. Across the northern landscape, the unbiquity of streamside alder stems provides beaver with a ready source of preferred building material ensuring the efficient establishment of water impoundments.

Over the years several authors have commented on the role of predation on beaver foraging behaviour (Jenkins 1980; Dalton 1984). In the present study, I noted that beavers restricted their foraging range to 20m from the water's edge. Since timber wolf commonly prey on beavers in the study area (Carbyn 1987; Macdonnell 1993), I suggest that this reduced foraging range may be in response to the risk of predation. Over the years, researchers have speculated about how predation can affect beaver foraging behaviour (Jenkins 1980, Belvosky 1984, Dalton 1984). Recently, Basey and Jenkins (1995) showed experimentally that beaver were "trading off maximization of profitability against minimization of predation" by coyotes (*Lupus latrans*). I suspect that high shoreline concentrations of ideally sized construction plants enables the speedy establishment of a dam. In addition to facilitating the collection of food and construction material, I believe that the beaver dam impoundment serves as a haven from predators. Johnston and Naiman (1990) working in northern Minnesota, an area noted for its high wolf populations also documented that reduced their foraging range to 20 m from water.

To date, little work has been devoted to studying the revegetation of abandoned beaver dams. Research conducted at active dam sites showed that beaver herbivory opened the canopy thus increasing plant growth (Johnston and Naiman (1990). When I documented the plant growth at recent and old abandoned dam sites, I noted that woody vegetation did not show any significant increase in density. Fluctuating water levels associated with the establishment and abandonment of dams have been shown to influence woody plant growth within aspen communities (Wilde et al. 1950). This may be a possible reason for the lower species diversity of woody plants observed in the present study.

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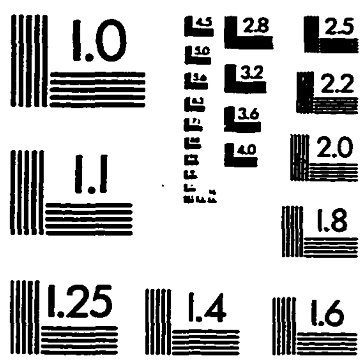
IMAGE EVALUATION TEST TARGET (QA-3)



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