HABITAT FACTORS INFLUENCING BEAVER DAM ESTABLISHMENT IN A NORTHERN ONTARIO WATERSHED

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Abstract: Beaver (*Castor canadensis*) dam-site selection studies traditionally have relied on plant composition. To understand how habitat factors influence dam establishment, we compared 9 plant composition and size categories and their spatial distribution with 4 physical features at 15 active dams, 15 abandoned dams, and 12 no-dam sites. To establish pre-dam vegetation densities, plots downstream and upstream from impoundments were averaged. We found beaver 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, we recommend that managers test the model's regional accuracy in determining site locations.

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Key words: beaver, boreal, *Castor canadensis*, dam, foraging distance, Geographic Information System, GIS, Ontario, resource selection, stream cross-sectional area, tree diameter, vegetation, watershed.

Impounded water is the most important ecological factor limiting beaver habitat use (Novak 1987:288). Despite the recognized importance of beaver dams, researchers consistently have 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 understand properly what factors influence beaver dam establishment, habitat analyses should include physical features combined with a more complete vegetation dataset.

We hypothesized that 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 physical characteristics of the site.

We tested the hypothesis 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 randomly chosen stream sites without a dam (no-dam sites).

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STUDY AREA

We conducted the study 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). 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 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*) and black spruce (*Picea mariana*) interspersed with mixed stands of white spruce (*P. glauca*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*). Associated with these forest trees were understory trees and shrubs including willow (*Salix* spp.), pin cherry (*Prunus pensylvanica*), mountain maple (*Acer spicatum*), red-osier dogwood (*Cornus stolonifera*), showy mountain ash (*Sorbus americana*), choke cherry (*Prunus virgini-*

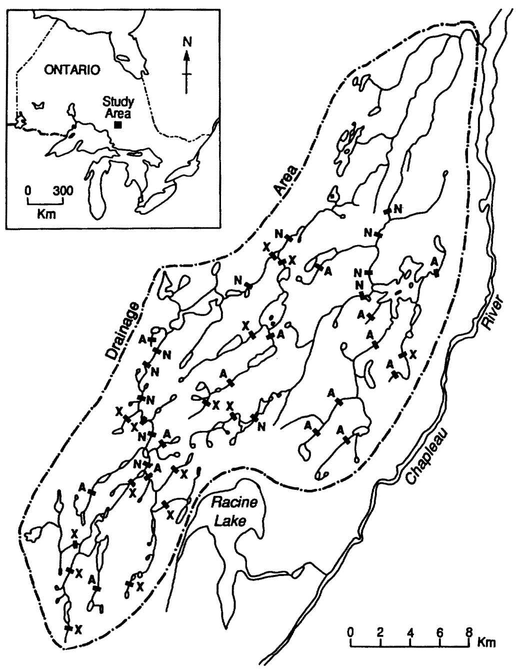

Fig. 1. The Swanson River drainage basin study area (– – –) with the location of 15 active (A), 15 abandoned (X), and 12 no-dam sites (N), 1993. Location of the Chapleau Crown Game Preserve study site in Ontario is shown in the inset.

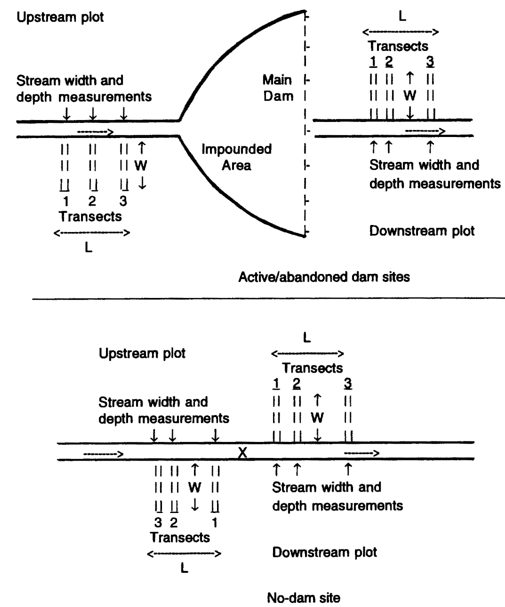

Fig. 2. Sampling technique used to measure the vegetation and physical features at active, abandoned, and no-dam sites in the Swanson River drainage basin of the Chapleau Crown Game Preserve of northern Ontario, 1993. L, length of sample plot (170 m); W, width of sample plot (40 m); X, centre of no-dam plot.

ana), black ash (*Fraxinus nigra*), serviceberry (*Amelanchier* spp.), beaked hazel (*Corylus cornula*), and river birch (*Betula glandulosa*).

METHODS

We subdivided the stream system into 1-km stream sections (Howard 1982:13). Using an aerial count of food caches conducted with a Cessna 180 airplane (Bergerud and Miller 1977: 1481), a stereoscopic examination using 1980 and 1992 aerial photographs, 1:15,840 and 1: 8,000 and on-site inspections, we classified 40 stream sections 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). All site locations were recorded on a 1:50,000 topographic map. To subsample the 200 stream sites, we randomly selected 15 active, 15 abandoned, and 12 no-dam sites (Fig. 1). Since some of these sample sites were remote and difficult to reach, part of the selection process involved an assessment of accessibility. To ensure that the fieldwork on all 42 sites would be completed by September, we selected sites in which data could be collected in one day. This strategy was advantageous as it allowed for down time due to inclement weather and other unforeseen situations.

Since the vegetation and original stream were flooded and altered by the presence of beaver, it was necessary to reconstruct pre-dam conditions at active and abandoned sites of beaver dams. We located a point above and below the main dam where the stream returned to its original width. We randomly chose which side of the stream to sample at the upstream plot; the downstream plot was established on the opposite bank. A 40- × 170-m plot was established at each location (Fig. 2). To determine the plot dimensions, we averaged the length and width of beaver harvesting activities at the 15 active dam sites. Three shoreline locations in each of the upstream and downstream plots were randomly selected. At these 6 shoreline locations, a 1- × 40-m transect was established perpendicular to the stream's edge. Each transect was subdivided into 40 1- × 1-m subplots. Within each subplot, we measured the diameter of all trees and shrubs at 30 cm above the ground (Johnston and Naiman 1990:1037).

We established the upstream and downstream sampling plots 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. 2).

Density of woody plants was determined and species placed into 4 categories: alder, shrubs (pin cherry, mountain maple, red-osier dogwood, showy mountain ash, choke cherry, serviceberry, beaked hazel, and river birch), conifers, and food species, notably trembling aspen, white birch, and willow (Bergerud and Miller 1977:1492). We combined these 3 food species, because individually their densities were too low at streamside to facilitate analysis. Data on alder, shrubs, and conifers were collected because of their use as dam construction material (Barnes and Mallik 1996). 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 site. The upstream watershed area was determined by delineation of watersheds on 1:50,000 topographic maps with a Tamaya Digital Planimeter, Planix 5,6 (Tamaya Technics Inc.). To determine cross-sectional area, we established 3 cross-sectional areas in the downstream and 3 in the upstream plots (Fig. 2); all the 6 measurements then were averaged. To determine a stream cross-sectional area, we multiplied the mean stream depth by the mean width of a stream profile (Dodge et al. 1984:127).

To identify geographic locations, we used a GIS and the Ontario Base Map (OBM) series. Sample sites were positioned accurately along the stream course with a Garmin Sury 2 GPS to establish the Universal Transverse Mercator coordinates of the site at the midpoint of each active and abandoned dam. The GPS unit was positioned at mid-stream for each no-dam site. To ensure maximum positioning accuracy, 8 satellite readings per fix were used and GPS data were corrected differentially with a second Garmin Sury 2 unit as a basestation with known coordinates. Each OBM was compiled with a number of different interchange files that represented various types of information. For each base map, drainage and elevation files were used. The GPS locations were identified in an ARC INFO GIS. Stream location and corresponding GPS point coverage were overlaid to ensure maximum accuracy.

A GIS was used to establish stream elevations 150 m above and below the GPS points. To determine stream gradient, we divided the vertical drop by the horizontal distance for the downstream and upstream elevations and averaged these 2 values. Stream gradient was expressed as percent slope (Howard and Larson 1985:21).

We also used GIS to obtain topographic elevations 100 m in either direction of the GPS points. Using the same procedure outlined by Howard and Larson (1985:21) for stream gradient, the percent slope for the shoreline topography was calculated for each shore and averaged.

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

We performed Student's t tests on the vegetation data collected at upstream and downstream plots to evaluate differences among active, abandoned, and no-dam sites. In the event of no statistically significant difference, we averaged the above and below dam values.

To evaluate differences among variables associated with active, abandoned, and no-dam sites, we performed 1-way analyses of variance followed by Least Significant Difference tests (Velleman 1992). We conducted a discriminant analysis (Wilkinson et al. 1992) using only those variables that showed a significant difference between either active or abandoned dams and no-dam sites. Wilks' lambda was used to determine if there was overall variation among active, abandoned, and no-dam sites. 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. 1993:202). To avoid the problem of multicollinearity (Howard and Larson 1985, Beire and Barrett 1987), we used a correlation matrix to eliminate highly correlated variables ($r > 0.8$).

RESULTS

Species composition and size classes of woody vegetation in downstream plots were not significantly different from the upstream plots at active, abandoned, or no-dam sites (Table 1). Consequently, we 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 1-way ANOVA, we found that 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–

Table 1. Mean density (SE) of woody plants (no./120 m²) 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)		
	Downstream plot	Upstream plot	$P(t)$	Downstream plot	Upstream plot	$P(t)$	Downstream plot	Upstream 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 diam 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, because 5 of the 15 active sites did not have an upstream sampling plot.

4.4 cm, showed significant differences (Table 2). We used these 6 significant variables in a discriminant analysis and found significant overall variation among active, abandoned, and no-dam sites (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 sites (Table 3). Function 1 delineated 2 groups: no-dams, and active and abandoned dams. The upstream watershed area contributed most to the separation, while the stream cross-sectional area was secondarily important (Fig. 3). Function 2 failed to delineate between any groups or group combinations (Fig. 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 0.5–1.0 cm (Table 4).

When our data were tested with the McComb Model, only 27% of active dam sites and 58% of no-dam sites fit the model (Fig. 4).

DISCUSSION

Contrary to most habitat selection studies, we confirmed that beavers chose to build dams at stream sections with high shoreline densities of woody vegetation with diameters 1.5–2.4 cm, 2.5–3.4 cm, and 3.5–4.4 cm (Tables 2 and 4; Howard and Larson 1985:24, Beire and Barrett 1987:798, McComb et al. 1990:279). In an earlier use-availability study, we found that beavers preferred these stem sizes for dam construction (Barnes and Mallik 1996). Proximity of these stems to water was advantageous because it ensured the speedy establishment of a dam and optimal foraging conditions while minimizing the risk of predation by timber wolves (*Canis lupus*; Potvin et al. 1992:180).

Although the availability of food, especially trembling aspen, traditionally has 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 1985:24, Novak 1987:295, McComb et al. 1990:280). We found no evidence of beavers choosing dam sites based on the presence of food items. When trembling aspen densities were considered separately, we found aspen present within the foraging range of 46% of active and 33% of no-dam sites. Based on the low densities of food 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 1987:297), the subsequent overland flooding would be sufficient to bring higher densities of food plants into foraging range (Table 4). We, therefore, postulate that the presence of food trees was not a habitat factor that determined dam establishment.

In our northern boreal watershed, we found that the most significant habitat determinant for the location of beaver dams was the upstream watershed area. Despite this importance, many studies in the past did not include it as a variable (Retzler et al. 1956:5, Slough and Sadleir 1977:1328, Allen 1983:8, Beire and Barrett 1987:795). Of the studies which included the upstream wa-

Table 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) significantly are not different ($P > 0.05$).

Variables	Ac	Ab	Nd	Trans[a]	LSD
Physical features					
Watershed area (ha)	521.1(154.8)	948.8(402.9)	6,247.3(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 diam 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 with 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) by averaging plots downstream and upstream from the dam.
[e] Trembling aspen present within the foraging range of 46% of active and 33% of no-dam sites.

tershed area in their analyses, Howard and Larson (1985:19) found it important in identifying beaver dam sites, while McComb et al.(1990:273) did not. A plausible reason for this difference may be the differing spatial distribution of dams used. In the McComb et al.(1990:274) study, 71% of all the active dams were located within 8% of their stream system. Such a restricted pattern of distribution may have biassed their watershed values. In our study area (Fig. 1) and that of Howard (1982:20), active dam sites were distributed across a larger segment of the watershed, about 75% and 90%.

Table 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.

Variables	Correlations between original variables and the discriminant functions: Function 1	Function 2
Physical features		
Watershed area (ha)	<u>−0.921</u>	0.019
Cross-sectional area (m^2)	<u>−0.593</u>	0.355
Gradient (%)	0.198	<u>0.704</u>
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

Many researchers have recognized stream gradient and cross-sectional area as important determinants for beaver dam location (Retzler et al. 1956:18, Slough and Sadleir 1977:1329, Howard and Larson 1985:23, Beire and Barrett 1987:797, McComb et al. 1990:279). Beavers rely on the sound of running water caused by landscape gra-

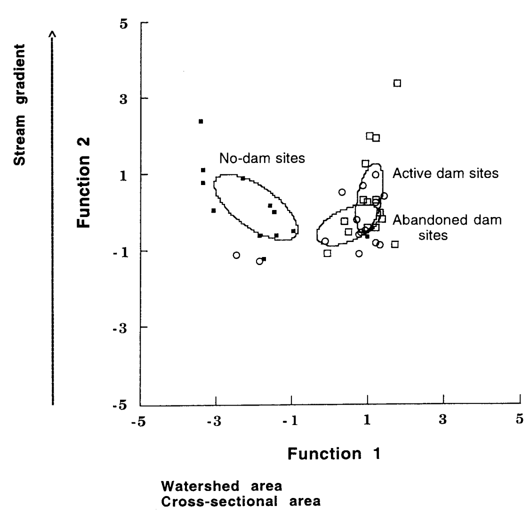

Fig. 3. Ninety-five percent confidence ellipses based on a discriminant analysis of 9 vegetation and 4 physical features at active (□), abandoned (○), and no-dam sites (■) in the Chapleau Crown Game Preserve of northern Ontario, 1993. Variables important in defining discriminant functions 1 and 2 are shown adjacent to arrows.

Table 4. Mean density (SE) of plant categories and stem diameter classes (no./120 m²) 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 ($P > 0.05$).

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 diam classes					
0.5–1.5 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
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.

dient to trigger dam building behavior (Novak 1987:297). The stream cross-sectional area has 2 main implications: (1) if the stream has a sufficient width and depth, then autumn food gathering and under ice food storage and locomotion will be facilitated; and (2) in streams with small cross-sectional areas, the reduced depth and width makes dam building much easier.

Over the past 10 years, beaver researchers have claimed that vegetation management was useless (Beire and Barrett 1987:798). This directive was based on research that showed physical factors largely were responsible for dam site selection. In contrast, we found that boreal beaver chose dam sites based on the streamside vegetation structure. Because both Howard and Larson (1985:24) and Beire and Barrett (1987:798) recommended against wide-scale extrapolation of beaver research findings, we suggest that regional management decisions concerning beaver habitats should be made only when streamside vegetation has been assessed.

MANAGEMENT IMPLICATIONS

McComb's graphical model showed that stream gradient and stream cross-section could be used to identify dam sites in eastern Oregon (McComb et al. 1990:279). Despite the logic underlying their model, we found that beaver dams were not predicted accurately with their

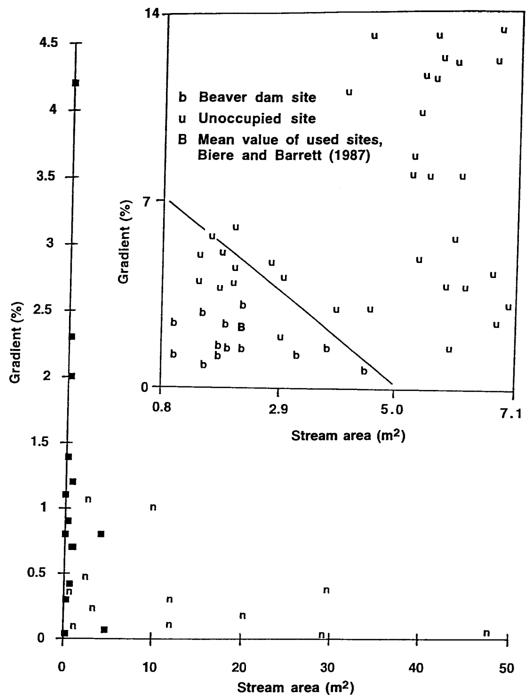

Fig. 4. The relation between stream gradient and cross-sectional area at active (■) and no-dam sites (n) in Chapleau Crown Game Preserve of northern Ontario, 1993. For comparison with the graphical model presented in McComb et al. 1990, see inset, reproduced with permission from the *Great Basin Naturalist.*

model in northern Ontario. We recommend that managers test the model's regional accuracy in determining dam site locations.

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