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Beaver habitat along rivers and reservoirs in central Montana

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BEAVER HABITAT ALONG RIVERS AND RESERVOIRS IN CENTRAL MONTANA

By

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This study was initiated in 1982 as part of the mitigation studies for a proposed hydroelectric dam in central Montana, with the goal of determining the effects of run-of-the-river impoundments on beaver and developing potential mitigation strategies. The study areas were the Missouri River at Carter Ferry, Lake Elwell on the Marias River, and the Marias River below Lake Elwell.

At Carter Ferry, beaver use was associated with islands or backwaters, water depths at 1 m from shore of 1.5 dm or less, adjacent river channels of 70 m or less, non-cliff uplands, or the presence of woody vegetation. On the Marias River, beaver used islands or sites with shrubs. At Lake Elwell, beaver used sites with slopes of 19% or less, non-cliff uplands, or the presence of shrubs.

Lodges at Carter Ferry were associated with flat banks, soil substrates, or nearby shrubs. On the Marias River, beaver built lodges on non-cliff sites with soil substrates or greater than 10% underwater slope. At Lake Elwell, lodges were associated with bank aspects of 90 to 210 degrees, soil underwater substrates, or deep water near shore.

Seventy-two percent of the shrub cutting by beaver occurred in the fall. Within each size class, beaver cut shrubs as close to the water as available. Willow trees were cut more often than expected while other species, except cottonwood and chokecherry, were cut less often than expected. The cut trees were smaller than average and further from shore than expected.

Colony densities on the Missouri River varied from 0.03 to 0.31 per kilometer of shoreline. The Marias River below Lake Elwell varied from 0.10 to 0.23 colonies per kilometer. Lake Elwell averaged 0.18 colonies per shoreline kilometer while the Missouri River reservoirs ranged from no colonies to 0.17 per kilometer. Caches were located on islands more often than expected and steep mainland banks less often than expected.

Potential mitigation strategies include replanting vegetation on flat or terraced banks; controlling water fluctuations on the entire reservoir or small segments of reservoirs using sub-impoundments; controlling the timing and magnitude of downstream fluctuations; and protecting banks with erosion problems through structures or barrier islands.

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INTRODUCTION AND STUDY AREAS

INTRODUCTION

The beaver (Castor canadensis) is an important furbearing species along the Missouri River and its tributaries. The early quest for beaver pelts led to the exploration of many parts of North America, including Montana. One of the expressed purposes of the Lewis and Clark Expedition of 1804-06 was to secure the fur trade along the Missouri and Columbia rivers for the United States. Beaver remain economically important today. For example, the value of the 1980-81 Montana beaver harvest approached a million dollars.

In 1981 the Montana Power Company proposed construction of a run-of-the-river hydroelectric dam on the Missouri River at Carter Ferry, Montana. Before granting a license for construction, the Federal Energy Regulatory Commission requires the company to evaluate the project's impact on fish and wildlife and develop an effective mitigation plan. The following study was conducted to partially fulfill these requirements.

Although many species would be affected to varying degrees by the dam, only a few important or indicator species could be studied in depth. The beaver provided an excellent indicator species for studying the impact of dams, developing mitigation strategies, and assessing the success of such plans related to riparian zones. Beaver exist on most waterways capable of hydroelectric development. They quickly reinvade vacant habitat, or can be reintroduced at a minimal cost. Beaver are heavily dependent on the riparian zone for both food and shelter, including both physical and vegetative characteristics. They survive throughout most of the United States and Canada, and a closely related species, Castor fiber, occupies areas of Europe and Asia. If beaver can be successfully maintained on a reservoir, many other riparian-dependent species should also fare well.

Beaver have been studied extensively on streams, but until recently, they were virtually ignored on rivers and reservoirs. Although they are the same species, beaver living under different conditions exhibit quite different patterns of habitat use. On streams, beavers commonly build dams to control water levels and occupy a dome-shaped lodge in the resulting pond. Beavers on rivers and reservoirs cannot control water levels and are at the mercy of natural or human-influenced fluctuations. They must modify their behavior and habitat use to survive these fluctuations (Hammond 1943, Hill 1982).

Only within the last decade have studies been reported for beaver on rivers, lakes, and reservoirs. In 1977, Vanden Berge and Vohs, Jr. studied beaver populations on stabilized and unstabilized sections of the Missouri River in South Dakota. Swenson et al. (1983), Swenson and Knapp (1977) and Martin (1977) investigated beaver use along the Yellowstone and Tongue rivers in Montana. Collins (1979) studied the impact of water level fluctuations on regulated and unregulated waterways in Grand Teton National Park, Wyoming. Beginning in the 1930's, more extensive research was conducted on river-dwelling members of the closely related European beaver in the U.S.S.R. as part of an effort to reintroduce this economically important furbearer to its former range (Kirilloff 1957, Popoff 1957, Semyonoff 1957a, Semyonoff 1957b, and Zhdanoff 1957). Slough and Sadleir (1977) developed a land capability classification system for beaver on lakes that has some application to reservoir environments. Recently, beaver have been included in reservoir impact and mitigation studies in the Columbia River Basin (Tabor et al. 1980).

The effect of impoundments on beaver populations is just beginning to receive attention, and possible mitigation measures are largely unreported. Commonly, any impoundment is viewed as detrimental to beaver populations and active on-site mitigation is seldom pursued; yet, beavers are found on many reservoirs. Formal studies are necessary before the actual effects of impoundments can be assessed and effective mitigation plans formulated. Results of this and other studies will help in developing mitigation plans for the proposed Carter Ferry Dam and similar projects that may be initiated in the future.

This study involved several facets. To avoid confusion, I have presented the methods, results, and discussion for each as a separate chapter. Each chapter generally represents a paper once appropriate introductions and study area sections are added. Chapters 2 and 3 cover different types of habitat use by beaver, for feeding and denning. Chapter 4 deals with spatial and temporal food habits. Chapter 5 covers general population information. Chapter 6 includes a review of the literature on the effects of dams and some general ideas on mitigating for beaver in such areas.

OBJECTIVES

The overall objectives of this study were to determine the effects of run-of-the-river impoundments on beaver populations and develop possible mitigation strategies for the proposed Carter Ferry Dam. These have been divided into 3 sub-objectives:

1. document patterns of habitat use by beaver on impounded and unimpounded river segments;
2. determine and compare population densities of beaver on impounded and unimpounded river segments; and
3. develop a "profile" of occupied beaver habitat for use for predicting the effect of proposed reservoirs on beaver populations.

STUDY AREAS

Three primary study areas were chosen in central Montana, the proposed Carter Ferry Dam site, Lake Elwell (Tiber Dam), and the Marias River below Tiber Dam (Figure 1.1).

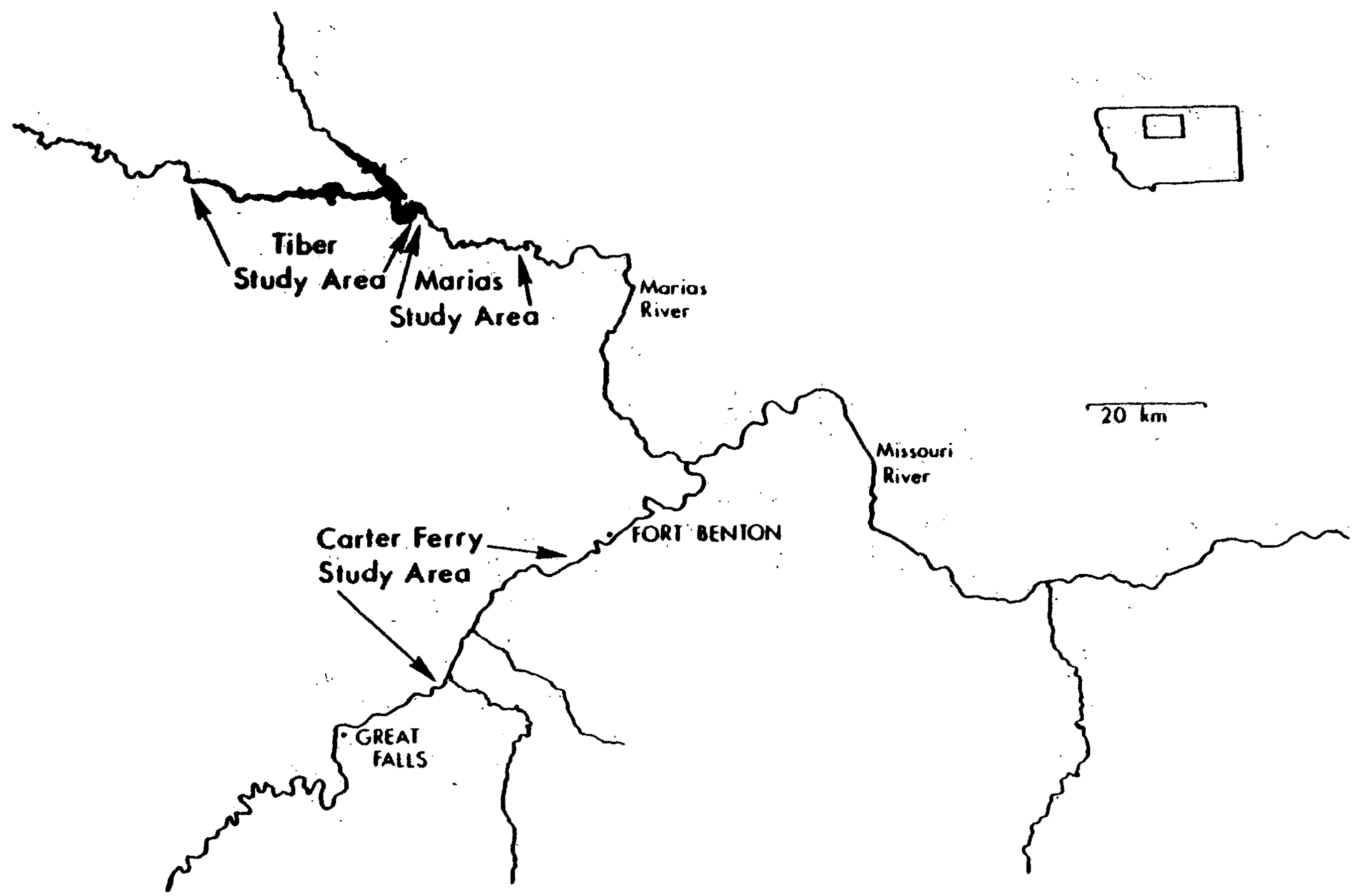


Figure 1.1. Principle study areas in central Montana.

Primary Study Areas

Carter Ferry - The proposed Carter Ferry Dam site lies on the Missouri River northeast of Great Falls, Montana, and would be the sixth in a series of run-of-the-river dams extending downstream from Great Falls. The River is further influenced by 2 additional run-of-the-river dams and a retention dam upstream near Helena, Montana, as well as over 15 smaller dams upstream. The study area extends from the upper reach of the expected maximum pool to a point 10 km below the proposed dam site, approximately 35 km of river.

Currently, the Missouri River flows within a relatively straight bed about 100 m below the surrounding plains. Much of this elevational change occurs within 1 km of the river, although the plains are deeply dissected by a series of extensive coulees. Most of the coulees are dry except for short periods following rains. A few contain permanent, though often stagnant, water from upslope springs. Two permanent streams, Highwood and Belt creeks, flow into the River within the study area.

Woody riparian vegetation is confined almost exclusively to the margins of the few islands and river benches. Only 3 major islands lie within the inundation area, and benches are seldom greater than 1.0 km wide and 3 km long. The riparian vegetation rarely extends more than 50 m inland and is virtually nonexistent in many areas. The woody riparian vegetation consists mainly of willow (Salix sp.) and rose (Rosa sp.) shrubs with an occasional strip of cottonwood (Populus sp.), box elder (Acer negundo), peachleaf willow (S. amygdaloides), and chokecherry (Prunus virginiana) trees. The remaining bench land is in cultivation or arid sage/grass range.

The proposed Carter Ferry Dam would impound a reservoir approximately 23 km long and 38 m deep at the dam. The normal reservoir operating level would be 857 m with a maximum of 858.6 m. The Carter Ferry Dam would be run-of-the-river; therefore, water level fluctuations would be minimal and water retention-time short. The completed reservoir would have a surface area of approximately 1417 ha. In addition to 23 km of the Missouri River, it would inundate 4.25 km of Highwood Creek and 2.25 km of Belt Creek. The inundation area includes most of the river benches, all islands, and many coulee bottoms. With the exception of the upper portion of Highwood Creek, Carter Ferry Dam would flood essentially all riparian habitat within the study area.

Tiber Dam and Lake Elwell - Lake Elwell, the reservoir behind Tiber Dam, approximately 100 km north of Great Falls, was chosen as the second study area. Current conditions on the reservoir are comparable to the projected conditions at the Carter Ferry Dam site. Prior to impoundment, the Marias River meandered within the confines of a narrow bottomland, usually less than 1 km wide, surrounded by higher plains with extensive coulee systems. Tiber Dam, built in 1955, produced a long and deep reservoir, 60 m deep at the dam, with a highly convoluted shoreline approximately 295 km long. Much of the reservoir is flanked by highly eroded mud and cobble cliffs. Riparian shrub and tree development is slight and confined to the few remaining flats. Recent water level increases have flooded and killed what little woody vegetation had developed.

Tiber Dam is primarily a flood control structure, though a small portion of the water is diverted for irrigation and domestic water supplies. Water levels fluctuate depending on inflow and projected flooding. If severe flooding is projected, the reservoir is partially drained to accommodate the flood waters. Generally, the reservoir level reaches a peak during late spring or early summer, then drops progressively until early the next spring. Flooding in 1964 damaged the floodgates and forced managers to manage water levels to insure the dam's safety, dropping levels more than normal to allow for potential flooding. Prior to 1964, water levels fluctuated from 2.1 to 5.3 m with an average of 3.3 m annually. Between 1964 and 1984, annual fluctuations ranged from 1.4 to 10.3 m with an average of 5.7 m.

Marias River - The Marias River from Tiber Dam to a point 22 km below the Dam was chosen as the third study area. The Marias River below the Dam meanders through a well developed bottomland flanked by high plains. The deep coulees which dissect the surrounding plains seldom contain flowing water. Extensive flood plains as much as 1 km wide border the River, yet the river itself is fairly narrow (25 m to 100 m wide).

Riparian shrub and tree development is extensive on the broad flood plains and cottonwood groves are common. The woody riparian vegetation is similar in species composition to the Carter Ferry study site. Some benches are in cultivation but the primary land use is cattle grazing.

Flows within the Marias River are controlled primarily by the outflows from Tiber Dam. These flows have varied from a minimum of 0.2 to over 10,100 cfs with an average of 853 cfs. During the 1964 flood, Tiber Dam released more than 5000 cfs for 22 days while above the dam, levels reaches 241,000 cfs but remained greater than 5000 cfs for only 11 days.

Additional Study Areas

Eight reservoirs and 2 sections of river were chosen for an extended series of cache counts.

Reservoirs - Hauser and Holter dams are run-of-the-river hydroelectric facilities on the Missouri River near Helena, Montana. Total shoreline distance is 100 km for Holter Lake and 76 km for Hauser Lake. A substantial portion of both reservoirs lies within steep-walled rocky canyons. Shorelines in the non-canyon sections are often rocky or composed of tall soil cutbanks. Remains of the Eldorado Strip Mine occupy some shoreline on Hauser Lake. Even on the remaining, favorable shoreline, riparian shrub development is sparse. Water level fluctuation is minimal on Hauser Lake. The average annual fluctuation through 1986 was only 1.67 m and occurred primarily in March. Holter Lake has a normal drawdown of approximately 2 m. This drawdown, primarily for ice control, occurs in October.

Canyon Ferry Dam is a multi-purpose facility, including hydroelectric generation and irrigation, directly upstream of Hauser

Lake. The current federal facility flooded a previous Montana Power Company dam. Canyon Ferry Reservoir is large, with 164 km of shoreline. Riparian shrub development is localized and confined to the backwaters and upper reaches of the pool.

The pool level peaks in June, then drops several meters by the next March, with the most rapid drawdown occurring in September. The timing and extent of the drawdown is controlled by energy and irrigation needs. Maximum fluctuation is quite variable. In 1967, the water level drop exceeded 10 m. A series of 5 run-of-the-river hydroelectric dams occupy the Missouri River directly above the Carter Ferry study area. These dams range in age from Black Eagle, built in 1890, to Cochrane, built in 1958. The reservoirs are confined to relatively narrow channels in what was once a canyon. Total shoreline distance varies from a high of 17 km on Morony Reservoir to 6 km on Ryan Reservoir, with all 5 reservoirs totaling 49 km. Because the banks are steep and rocky, riparian shrub development is sparse and confined to backwaters and islands at the upper reach of the pools. Normal annual water level fluctuations are minimal, as expected for run-of-the-river dams. However, substantial fluctuations may occur irregularly in response to emergencies or necessary repairs. In 1983, Morony Reservoir experienced a drop of 4.4 m, Rainbow Reservoir 3.5 m, Ryan Reservoir 2.0 m, and Cochrane Reservoir 1.6 m. These drawdowns occurred primarily during the late summer and fall.

Rivers - Cache counts were continued on the Missouri River from the Carter Ferry study area 181 km downstream to Dauphine Rapids.

The nature of the River varies greatly along this stretch, from the straight, fast-flowing White Cliffs section to the meandering broad bottoms of the Marias River delta. The River from Fort Benton, 25 km below Carter Ferry, to the Robinson Bridge, almost 240 km downstream, is a federally designated Wild and Scenic River. For the first 83 km, to Pilot Rock, the River flows almost exclusively through private lands and is designated Recreational. Below Pilot Rock, an increasing proportion of the shoreline is under Bureau of Land Management jurisdiction and the River is designated Wild.

From 1860 to 1890, steamboats carried goods and passengers from St. Louis to Fort Benton. In 1878 alone, 60 steamboats made the trip. Such travel had a great influence on the riparian environment. The steamboats were fueled by wood and woodcutters were busy along the River supplying the need. An average boat burned 25 to 30 cords of wood daily and cottonwoods were soon scarce. The loss of trees undoubtedly affected beaver populations and the residual effects may be with us today. In 1887, the railroad reached Fort Benton and sealed the fate of the steamboats. Some cottonwood groves have recovered, but managers are now concerned by the lack of recent regeneration within these groves.

Riparian vegetation along the Missouri River is similar in species composition to the Carter Ferry study area. In addition, some areas show significant amounts of red-osier dogwood (Cornus stolonifera) and currants (Ribes sp.). The fast-flowing canyon sections of the River contain little woody riparian vegetation while the broader meandering sections above Coal Banks Landing contain dense cottonwood and willow growth. Suitable river bottoms in accessible areas are devoted to hay and small grain production. Remaining lands are primarily utilized for grazing.

Cache counts were also conducted on the Marias River below the study area to its confluence with the Missouri River, a total of 109 km. Conditions along the Marias River are similar to the primary study area upstream. Most of the river between Circle Bridge (39 km below the Tiber Dam) and Loma (128 km below the dam) is in private ownership and inaccessible except by boat.

BEAVER HABITAT USE

METHODS

Developing mitigation strategies for any species requires an understanding of the species' habitat requirements. Little has been published concerning beaver habitat on large rivers and reservoirs. Therefore, the primary thrust of this study was to investigate habitat use on such areas. To determine beaver habitat affinities on large rivers and reservoirs, I measured a wide variety of environmental factors that might affect the beaver's choice of habitat and compared sites with beaver activity to those without. Beaver activity was defined by the presence of beaver sign such as cuttings, tracks, scent mounds, dams, and lodges.

At the Carter Ferry study area, the Missouri River shoreline was divided into 100 m segments, and each segment was classified as cliff, bench, or island. Fifty-eight sites were chosen at random (10% of the total available segments) from the 3 categories listed above, according to their representation on the study area (ie. because 10% of the shoreline was classified island, 6 sites were chosen from the island segments). On Lake Elwell and the Marias River, sites were chosen completely at random. Forty-five sites were chosen along the Marias River, representing 10% of the available. Time constraints prevented such a sampling intensity of Lake Elwell's 295 km of shoreline. Instead, 75 sites were chosen, 2.5% of the total available. At each site, measurements were taken of bank, river, upland, and vegetative characteristics. The type and presence or absence of beaver sign was noted.

Bank slope and height were measured 2 m inland and 1 m into the water from the shore. Both areas were classified as to configuration (convex, flat, or concave) and substrate (mud, mud with some cobbles, mud and cobbles, cobbles, talus, or rock). Shoreline aspect was recorded. Height and configuration (cliff, bench, coulee, or island) of adjacent uplands were determined from USGS topographic maps. River width was taken from 1:7200 scale maps provided by Montana Power Company. Water depth was recorded at 0.5 m intervals, perpendicular to the shore, for 5 m or until the depth exceeded 1 m.

The presence or absence of woody riparian vegetation was mapped on 1:7200 scale maps. The length of continuous riparian vegetation upstream and downstream of the site center was estimated from these maps. Shrub density, crown cover, and height by species were recorded using point transects. At Carter Ferry and Lake Elwell, transect lines were established, perpendicular to the bank, at the site center, 25 m and 50 m upstream and downstream. On the Marias River, 2 transect lines were established, 10 m above and below the site center. Transects extended 50 m inland. A pole was held perpendicular to the ground at 1 m intervals along the transect. The number of stems touching the pole was recorded and species noted. Shrub density was defined as the average number of stems per 100 points. The crown cover and shrub height was also recorded at each point on the transect. The site crown cover was defined as the percent crown cover. Shrub heights were averaged.

While running the shrub transects, the presence or absence of tree crown cover was also recorded. Tree crown cover for each site was defined as the percent cover. In addition, the diameter at 0.5 m above the ground was measured for all trees within 50 m of the site center at Carter Ferry and Tiber Reservoir, and within 10 m of the site center on the Marias River. Only trees greater than 10 cm in diameter were considered, with the exception of chokecherries which were initially recorded down to 2 cm. The species and degree of beaver cutting were recorded for each tree.

Habitat measurements were compared between the random sites based on the presence or absence of beaver sign. Categorical variables were compared using the Chi-square test (SPSSx 1983). Continuous variables were tested using the Kolmogrov-Smirnoff two-sample test of distributional differences (SPSSx 1983). Significance within each category was determined using the Bonferoni Z statistic through a computer program developed by Matchett (1984). Continuous variables were assigned to categories chosen to reflect biological significance or observed break points in the data. Values were tested using the Bonferoni Z statistic in an attempt to maximize the differences or similarity between used and unused sites within each category. Because the data were used to develop the categories for continuous variables, significance levels cannot be accurately determined. The significance levels presented for the categorized form of the continuous variables shown in the tables are only approximations and are marked as such.

RESULTS

All random sites were classified as used or unused based on the presence of beaver sign. Sign included old or new cutting, trails, tracks, lodges and dens, dams, and scent mounds. Sites with and without beaver activity were compared to determine differences between used and unused sites. Significant variables differed between the study areas so each area is presented separately.

Carter Ferry

Used and unused sites differed significantly in bank location ($p < 0.001$), bank configuration ($p < 0.005$), river width ($p < 0.005$), upland height ($p < 0.005$), upland configuration ($p < 0.001$), length of continuous riparian shrubs ($p < 0.001$), and all measures of riparian shrubs and trees. All other environmental parameters showed no significant difference (Table 2.1).

Significant variables fell into 3 categories, differences in the physical character of the site, characteristics of the area adjacent to the site, and measurements of woody riparian vegetation both adjacent to and on the site. All variables were compared separately. Due to limitations within the data, no attempt was made to test multivariate effects.

A significantly greater proportion of the sites along the main river bank were unused while all island and backwater sites contained some beaver sign. Sites with concave banks were often used by beaver. There was no significant difference between the degree of use for sites with flat or convex banks.

Table 2.1. Differences between characteristics of used and unused sites on the Carter Ferry study area, including test type and significance level. KS = Kolmogrov-Smirnoff two-sample test Chi = Chi-square test

Variable	Test	df	Value	Significance
Bank				
Slope	KS		1.004	0.266
Aspect	KS		1.035	0.235
Location	Chi	1	16.96	0.000
Configuration	Chi	2	11.19	0.004
Substrate	Chi	3	4.650	0.200
Water/Underwater				
Slope	KS		0.906	0.385
Depth at 1 m	KS		1.250	0.088
Depth at 2 m	KS		1.281	0.075
Configuration	Chi	2	0.989	0.610
Substrate	Chi	3	1.583	0.663
River Width	KS		1.429	0.034
Upland				
Height	KS		1.763	0.004
Configuration	Chi	2	30.95	0.000
Woody Vegetation				
Continuous - Upstream Length	KS		2.526	0.000
Continuous - Downstream Length	KS		2.444	0.000
Continuous - Total Length	KS		2.788	0.000
Shrubs - Combined Species				
Height	KS		3.625	0.000
Density	KS		3.429	0.000
Crown Cover	KS		3.527	0.000
Shrubs - Willow Species				
Height	KS		3.159	0.000
Density	KS		3.524	0.000
Crown Cover	KS		3.656	0.000
Trees - Combined Species				
Number	KS		1.969	0.001
Diameter	KS		1.969	0.001
Crown Cover	KS		2.246	0.000
Trees - Cottonwood/Willow				
Number	KS		1.133	0.154
Diameter	KS		1.133	0.154
Crown Cover	KS		0.870	0.436

Sites with adjacent river widths of 70 m or less, uplands between 790 and 850 m in elevation, or island or bench configurations were more apt to be used by beaver. Sites with river widths over 125 m, uplands greater than 900 m in elevation, or island or bench configurations were commonly unused. Intermediate sites with river widths between 70 and 125 m or uplands with elevations between 850 and 900 m were equally likely to be used or unused.

The presence of islands or backwaters, low elevation uplands, and relatively narrow river channels are likely correlated. Narrow channels are created by the presence of islands or the remains of old islands. All islands and backwaters on the study area were created by deposition, not carved from the surrounding uplands, resulting in uniformly low areas.

The presence or absence of woody riparian vegetation, particularly of the family Salicaceae, was a good indicator of beaver use. This is not surprising, as the primary beaver sign was cuttings and stumps. Even sites with relatively small amounts of trees or shrubs usually contained evidence of beaver use. Willow shrub densities of as little as 1 stems per 100 points or crown covers of 1% were sufficient to distinguish used from unused sites. Sites with any trees usually showed signs of use. Because the trees measured are species of the riparian zone and are confined to sites with greater-than-average subirrigation, a relationship undoubtedly exists between the significant topographic and vegetation variables. For details of the values, see Table 2.2.

Table 2.2. Bonferoni Z tests of significance within categories for beaver use of habitat on the Carter Ferry study area. Values in parentheses are approximate, see text for explanation.

Variable	Bonferoni Z Value	Significance Level *
Bank Location		
Mainland	4.61	---
Island/Backwater	4.61	+++
Bank Configuration		
Concave	1.96	NS
Flat	1.00	NS
Convex	3.16	++
River Width		
0 - 70 m	(3.43)	++
71 - 125 m	(0.40)	NS
> 125 m	(2.86)	-
Upland Height		
790 - 850 m	(3.54)	++
851 - 900 m	(0.60)	NS
> 900 m	(5.37)	---
Upland Configuration		
Cliff	5.65	---
Bench/Island	5.65	+++
Length of Continuous Riparian Shrubs		
0 - 100 m	(5.71)	---
> 100 m	(5.71)	+++
Mean Shrub Height - Combined Species		
0 - 4 dm	(12.71)	---
> 4 dm	(12.71)	+++
Mean Shrub Height - Willow Species		
0 - 1 dm	(11.64)	---
> 1 dm	(11.64)	+++
Shrub Density - Combined Species		
0 - 2 stems/100 points	(10.41)	---
> 2 stems/100 points	(10.41)	+++
Shrub Density - Willow Species		
0 stems/100 points	(10.41)	---
> 0 stems/100 points	(10.41)	NS

Table 2.2. Continued

Variable	Bonferoni Z Value	Significance Level
Shrub Crown Cover - Combined Species		
0 - 2 %	(10.99)	---
> 2 %	(10.99)	+++
Shrub Crown Cover - Willow Species		
0 - 1 %	(9.80)	---
> 1 %	(9.80)	+++
Number of Trees - Combined Species		
0	(4.46)	---
> 0	(4.46)	+++
Mean Tree Diameter - Combined Species		
0 cm	(4.46)	---
> 0 cm	(4.46)	+++
Tree Crown Cover - Combined Species		
0 -1 %	(3.32)	--
> 1 - 11 %	(4.12)	++
> 11 %	(0.18)	NS

* Significance levels.

+ = use greater than availability
- = use less than availability

+++ or --- $p < 0.001$
++ or -- $p < 0.01$
+ or - $p < 0.05$

Marias River

On the Marias River, active and inactive sites differed in bank location ($p < 0.05$), length of continuous riparian shrubs ($p < 0.05$), shrub density for combined species ($p < 0.005$), and shrub crown cover for willow ($p < 0.001$) and combined species ($p < 0.001$). All other variables exhibited no significant difference (Table 2.3).

Only 1 physical site characteristic was significant, that of bank location. All unused sites were located on the mainland while 30% of the active sites were located on islands and backwaters.

Few measurements of woody riparian shrubs were significant and no tree variables displayed any significance. Sites with greater than 100 m of continuous riparian shrubs immediately adjacent to the site were commonly used by beaver. Again, only small densities of shrubs, as little as 3 stems per 100 points, were sufficient to increase chance of beaver use. However, this held only when all shrub species were combined for the analysis. No significant difference was found when density for willow species alone were considered. Sites with even low values for both combined species and willow crown cover were more apt to contain evidence of beaver use. For details of the values, see Table 2.4.

Lake Elwell

On Lake Elwell, used and unused sites differed in bank slope ($p < 0.005$), upland height ($p < 0.001$), upland configuration ($p < 0.005$), length of continuous riparian shrubs ($p < 0.001$), and all

Table 2.3. Differences between characteristics of used and unused sites on the Marias River study area, including test type and significance level. KS = Kolmogrov-Smirnoff two-sample test, Chi = Chi-square two-sample test.

Variable	Test	df	Value	Significance
Bank				
Slope	KS		0.868	0.439
Aspect	KS		0.724	0.671
Location	Chi	1	4.114	0.043
Configuration	Chi	2	1.749	0.417
Substrate	Chi	1	2.157	0.142
Water/Underwater				
Slope	KS		1.001	0.258
Depth at 1 m	KS		0.957	0.319
Depth at 2 m	KS		1.100	0.178
Configuration	Chi	2	2.860	0.239
Substrate	Chi	1	0.780	0.377
River Width	KS		0.383	0.999
Upland				
Height	KS		0.403	0.997
Configuration	Chi	1	1.142	0.285
Woody Vegetation				
Continuous - Upstream Length	KS		1.599	0.012
Continuous - Downstream Length	KS		1.524	0.019
Continuous - Total Length	KS		1.449	0.030
Shrubs - Combined Species				
Height	KS		1.244	0.091
Density	KS		1.449	0.030
Crown Cover	KS		1.449	0.030
Shrubs - Willow Species				
Height	KS		1.244	0.091
Density	KS		1.244	0.091
Crown Cover	KS		1.708	0.000
Trees - Combined Species				
Number	KS		1.168	0.130
Diameter	KS		1.244	0.091
Crown Cover	KS		1.168	0.130
Trees - Cottonwood/Willow				
Number	KS		1.168	0.130
Diameter	KS		1.244	0.091
Crown Cover	KS		1.052	0.218

Table 2.4. Bonferoni Z tests of significance within categories for beaver use of habitat on the Marias River study area. Values in parentheses are approximate, see text for explanation.

Variable	Bonferoni Z Value	Significance Level *
Bank Location		
Mainland	3.35	--
Island/Backwater	3.35	++
Length of Continuous Riparian Shrubs		
0 - 100 m	(2.93)	--
> 100 m	(2.93)	++
Shrub Density - Combined Species		
0 - 3 stems/100 points	(4.27)	---
> 3 stems/100 points	(4.27)	+++
Shrub Crown Cover - Combined Species		
0 - 2 %	(4.65)	---
> 2 %	(4.65)	+++
Shrub Crown Cover - Willow Species		
0 - 1 %	(5.68)	---
> 1 %	(5.68)	+++

* Significance levels.

+ = use greater than availability
- = use less than availability
  - +++ or --- $p < 0.001$
  - ++ or -- $p < 0.01$
  - + or - $p < 0.05$

measures of shrubs. All other variables showed no significant differences (Table 2.5). Again, 3 categories of significant variables exist, on site physical characteristics, adjacent areas, and woody riparian vegetation.

Beaver used sites with bank slopes of 19% or less more often than expected. Sites with banks of greater than 19% slope were often unused. A greater proportion of sites with adjacent uplands between 885 and 925 m in elevation or bench-like configurations were used by beaver than sites with uplands over 925 m or with cliff-like configurations.

The simple presence or absence of shrubs was significant to determine beaver use. Due to the nature of the reservoir, few areas contain any shrubs. Only 1 site with shrubs showed no sign of beaver use. Most sites without shrubs showed no evidence of beaver use. No significance was found between used and unused sites for all tree variables. In the case of trees, the extremely small sample size for sites with trees probably prevented any significant differences in use from being discovered. For details of the values, see Table 2.6.

DISCUSSION

Two basic problems occur with the methods presented and should be dealt with before proceeding. Because the variables did not meet the assumptions of parametric statistics, nonparametric forms were employed. This, in turn, forced me to utilize univariate techniques.

Table 2.5. Differences between characteristics of used and unused sites on the Lake Elwell study area, including test type and significance level. KS = Kolmogrov-Smirnoff two-sample test, Chi = Chi-square two-sample test.

Variable	Test	df	Value	Significance
Bank				
Slope	KS		1.819	0.003
Aspect	KS		0.810	0.528
Location	Chi	1	0.000	1.000
Configuration	Chi	2	4.919	0.086
Substrate	Chi	1	0.710	0.790
Water/Underwater				
Slope	KS		1.123	0.161
Depth at 1 m	KS		0.611	0.849
Depth at 2 m	KS		0.881	0.419
Configuration	Chi	2	1.919	0.383
Substrate	Chi	1	0.012	0.913
Width	KS		1.009	0.260
Upland				
Height	KS		2.089	0.000
Configuration	Chi	1	12.63	0.004
Woody Vegetation				
Continuous - Upstream Length	KS		1.748	0.004
Continuous - Downstream Length	KS		2.018	0.001
Continuous - Total Length	KS		2.018	0.001
Shrubs - Willow Species				
Height	KS		2.146	0.000
Density	KS		2.146	0.000
Crown Cover	KS		2.146	0.000
Trees - Combined Species				
Number	KS		0.938	0.342
Diameter	KS		0.938	0.342
Crown Cover	KS		0.625	0.829

Table 2.6. Bonferoni Z tests of significance within categories for beaver use of habitat on the Lake Elwell study area. Values in parentheses are approximate, see text for explanation.

Variable	Bonferoni Z Value	Significance Level *
Bank Slope		
0 - 19 %	(3.84)	+++
> 19 %	(3.84)	---
Upland Height		
885 - 925 m	(13.79)	+++
> 925 m	(13.79)	---
Upland Configuration		
Cliff	11.89	---
Bench	11.89	+++
Length of Continuous Riparian Shrubs		
0 - 100 m	3.90	---
> 100 m	3.90	+++
Shrubs		
0	5.47	---
> 0	5.47	+++

* Significance levels.

+ = use greater than availability
- = use less than availability

+++ or --- $p < 0.001$
++ or -- $p < 0.01$
+ or - $p < 0.05$

If we choose $p < 0.05$ as our acceptable significance level, we would expect 5% of the variables tested to register a significant difference where none exists. Therefore, we might expect 1 or 2 of the 32 variables tested in this study to test falsely positive. To reduce the chance of such an occurrence, I have reported, but generally distrust, any variable with $p < 0.05$. Many of the variables are intuitively correlated, such as water depth and underwater slope. If only 1 of the correlated variables exhibited significance, particularly at the $p < 0.05$ level, I discounted the test.

A second problem lies in the bias created by the variable visibility and longevity of beaver sign. Some sign, such as cutting activity, are readily visible and last for several years. Other sign, such as tracks, require a certain type of substrate and are very ephemeral. Without the use of radiotelemetry, or another technique unaffected by conditions, such bias cannot be completely removed. Beaver tend to use the shoreline primarily for denning, resting, and feeding. Denning activity will be dealt with in detail in the following chapter. Resting sites, if different from feeding and denning, will generally be missed by sign surveys. Therefore, the following results should be viewed as primarily tests of feeding activity.

Although beaver habitat affinities on the 3 study areas differed in details, they all appear to relate to woody food availability and the bank or water characteristics that promote the growth of preferred species. The importance of woody food remains a common thread in most studies of beaver habitat, regardless of the water type (Northcott 1964, Henry 1967, Williams 1968, Slough and Sadleir 1977, Boyce 1981, Allen 1983, Howard and Larson 1985, Bissell and Bown 1987). The differences in habitat use noted during this study are probably related to differences in the requirements for growth of woody species in the 3 areas.

Characteristics leading to adequate and stable food supplies for beaver are well documented on streams and small wetlands. Few in-depth studies have been completed on rivers, reservoirs, and large lakes, despite the fact that major differences exist in growing conditions.

On large rivers, such as the Missouri and Marias, willows and cottonwoods thrive on low elevation, low relief areas, particularly if the banks are protected from floods, erosion, ice scour, or extensive grazing. Beaver exhibited a statistically significant affinity for sites with such physical characteristics on the Carter Ferry study area. Yet on the Marias, only vegetation measurements correlated with beaver use. The apparent differences in use on the two areas is probably due to differences in the average condition on each area.

The Missouri River is a large, deep river with many steep, cliff-like banks. Intensive agriculture and human use of the low, subirrigated areas has reduced riparian shrubs and trees to a small fraction of their former abundance. In many places, a few meters of shrubs edged by a single line of trees is all that remains of once extensive bottomland forests. As a result, beaver concentrate their activity on the few remaining areas that support willows and cottonwoods, the low, subirrigated areas along the margins of the river floodplains. Because such areas are uncommon, the apparent selection by beaver stands out.

The Marias is a small, shallow, and meandering river. Although it flows through a broad canyon, the bottomland is flanked by steep and erosive bluffs that have effectively prevented human use of many areas. Where access is available, the floodplains are intensively farmed and resemble the Carter Ferry area. The lack of access and relatively small size of the arable land have saved many of the cottonwood groves. Only a small section of the Marias River is bordered directly by cliffs. As a result, beaver and their food supply are not confined to small portions of the river bank. If differences in the use of sites due to physical characteristics existed, they were too subtle to be detected by this study design.

Large lakes and reservoirs present additional problems to beaver. Willows and cottonwoods are again concentrated in areas of low elevation, low relief, and subirrigation. However, extensive fluctuations of many reservoirs may lower underground water tables or flood vegetation, further reducing the area suitable for riparian shrub growth. Many authors consider extensive fluctuations of water levels extremely destructive to beaver (Northcott 1964, Henry 1967, Slough and Sadleir 1977, Allen 1983, Bissell and Bown 1987).

On large bodies of water, wind and wave erosion may further reduce the areas suitable for riparian shrubs and trees. Without protected areas, such as bays or inlets sheltered from prevailing winds, lakes and reservoirs may be totally unsuitable for any sustained use by beaver (Slough and Sadleir 1977, Allen 1983).

Although Lake Elwell contains many protected areas, few have the low relief and subirrigation needed to promote willows and cottonwoods. In the case of reservoirs, the age and history of a facility may also have bearing on the extent of riparian shrub development.

Lake Elwell is a young facility where few riparian trees have had time to develop. Those that exist are heavily exploited by beaver. Because much of the shoreline is steep, shrub and tree development is limited to the few low-elevation areas that exist. Strong and persistent winds create huge waves, leading to extensive erosion of any exposed areas. Erosion, coupled with fluctuations in water levels, further reduce suitable shrub areas. Given the severely restricted habitat for willow and cottonwood growth, beaver activity is predictably confined to those areas.

BEAVER DENNING ACTIVITY

METHODS

Habitat variables were measured on all active and inactive lodges located on all 3 study areas. Measurements taken were identical to those for the random sites described in Chapter 2. At each lodge, the lodge type, length, width, height, and water depth at the offshore edge of the lodge were also recorded. Lodge and random sites were compared using the Chi-square, Kolmogrov-Smirnoff, and Bonferoni tests as described in Chapter 2.

RESULTS

Lodge sites were compared to random sites to determine differences between the placement of lodges and the availability of environmental parameters throughout the study areas. Each study area is presented separately because substantial differences existed between areas.

Carter Ferry

Significant differences were found between the lodge and random sites for bank configuration ($p < 0.001$), bank substrate ($p < 0.001$), underwater configuration ($p < 0.01$), underwater substrate ($p < 0.005$), upland configuration ($p < 0.001$), length of continuous woody riparian vegetation ($p < 0.001$), and all measurements of woody vegetation quality and quantity. All other variables showed no significant difference (Table 3.1).

Significant variables on the Carter Ferry study area fell into 3 categories, physical site characteristics, characteristics of areas adjacent to the site, and measurements of woody vegetation. All variables were tested separately because statistical limitations prevented multivariate comparisons.

Beaver built lodges or dens more often than expected on sites with soil banks, soil underwater substrates, or flat bank configurations. Sites with rocky banks, any rock in the underwater substrate, convex banks, or concave underwater configurations were seldom used. There was no significant difference in the use and availability of sites with concave banks, bank substrates containing only a few rocks, or flat or convex underwater configurations.

Beaver built very few lodges on sites with cliffs adjacent to the shore. There was no significant difference between the use and availability of sites with adjacent islands or bench-like uplands.

Most lodges were built on sites with some woody riparian vegetation within 100 m of the lodge. Lodges were seldom found on sites with less than 500 m of continuous riparian shrubs adjacent to the lodge, willow shrub densities below 6 stems per 100 points, or willow crown covers of less than 3%. Beaver tended to build lodges on sites with some trees present while avoiding sites without trees. For details of the values, see Table 3.2.

Table 3.1. Differences between characteristics of random sites and lodges on the Carter Ferry study area, including test type and significance level. KS = Kolmogrov-Smirnoff two-sample test Chi = Chi-square test.

Variable	Test	df	Value	Significance
Bank				
Slope	KS		0.972	0.302
Aspect	KS		0.853	0.460
Location	Chi	1	6.200	0.085
Configuration	Chi	2	6.050	0.001
Substrate	Chi	3	21.34	0.001
Water/Underwater				
Slope	KS		0.697	0.716
Depth at 1 m	KS		0.381	0.999
Depth at 2 m	KS		0.535	0.937
Configuration	Chi	2	10.08	0.006
Substrate	Chi	3	5.425	0.002
River Width	KS		0.732	0.658
Upland				
Height	KS		0.930	0.353
Configuration	Chi	2	10.24	0.006
Woody Vegetation				
Continuous - Upstream Length	KS		1.887	0.002
Continuous - Downstream Length	KS		1.780	0.004
Continuous - Total Length	KS		1.927	0.001
Shrubs - Combined Species				
Height	KS		1.646	0.009
Density	KS		2.117	0.000
Crown Cover	KS		1.794	0.003
Shrubs - Willow Species				
Height	KS		1.674	0.007
Density	KS		1.477	0.025
Crown Cover	KS		1.854	0.002
Trees - Combined Species				
Number	KS		1.679	0.007
Diameter	KS		1.484	0.024
Crown Cover	KS		1.498	0.022
Trees - Cottonwood/Willow				
Number	KS		1.807	0.003
Diameter	KS		1.915	0.001
Crown Cover	KS		1.512	0.021

Table 3.2. Bonferoni Z tests of significance within categories for random sites versus lodges on the Carter Ferry study area. Values in parentheses are approximate, see text for explanation.

Variable	Bonferoni Z Value	Significance Level *
Bank Configuration		
Concave	0.88	NS
Flat	4.08	+++
Convex	2.77	-
Bank Substrate		
Soil	4.77	+++
Soil with Few Cobbles	0.76	NS
Rock or Cobbles	4.43	---
Underwater Configuration		
Concave	3.70	---
Flat	0.74	NS
Convex	1.83	NS
Underwater Substrate		
Soil	3.46	++
Rock	3.46	--
Upland Configuration		
Cliff	3.60	---
Bench	0.86	NS
Island	2.10	NS
Length of Continuous Riparian Shrubs		
0 - 500 m	(3.09)	--
500 - 1000 m	(3.15)	++
> 1000 m	(0.05)	NS
Mean Shrub Height - Combined Species		
< 5 dm	(2.85)	-
5 - 10 dm	(0.10)	NS
> 10 dm	(3.20)	+
Mean Shrub Height - Willow Species		
< 5 dm	(2.74)	-
5 - 10 dm	(0.31)	NS
> 10 dm	(2.91)	+
Shrub Density - Combined Species		
0 - 10 stems/100 points	(4.37)	---
> 10 stems/100 points	(4.37)	+++

Table 3.2. Continued

Variable	Bonferoni Z Value	Significance Level
Shrub Density - Willow Species		
< 1 stem/100 points	(3.09)	--
1 - 6 stems/100 points	(0.14)	NS
> 6 stems/100 points	(2.79)	+
Shrub Crown Cover - Combined Species		
< 4 %	(3.78)	---
4 - 13 %	(0.14)	NS
> 13 %	(3.67)	+++
Shrub Crown Cover - Willow Species		
0 - 3 %	(3.96)	---
> 3 %	(3.96)	+++
Number of Trees - Combined Species		
0	(3.64)	---
1 - 20	(3.16)	++
> 20	(0.45)	NS
Number of Trees - Cottonwood/Willow		
0	(3.83)	---
1 - 20	(4.02)	+++
> 20	(0.27)	NS
Mean Tree Diameter - Combined Species		
0 - 10 cm	(2.93)	--
> 10 cm	(2.93)	++
Mean Tree Diameter - Cottonwood/Willow		
0	(3.83)	---
> 0	(3.83)	+++
Tree Crown Cover - Combined Species		
0 %	(2.74)	--
> 0 %	(2.74)	++
Tree Crown Cover - Cottonwood/Willow		
0 %	(3.21)	--
> 0 %	(3.21)	++

* Significance levels.
+ = use greater than availability
- = use less than availability

+++ or --- $p < 0.001$
++ or -- $p < 0.01$
+ or - $p < 0.05$

Marias River

Significant differences existed on the Marias River between the lodge and random sites for bank aspect ($p < 0.05$), bank configuration ($p < 0.05$), underwater slope ($p < 0.001$), water depth at 1 m ($p < 0.005$) and 2 m ($p < 0.01$) from shore, underwater substrate ($p < 0.001$), and some measurements of shrub density and crown cover. All other variables showed no significant differences (Table 3.3).

Significant variables on the Marias River fell into 2 general categories, physical site characteristics and some measurements of riparian shrubs. Beaver built lodges on sites with bank aspects between 60 and 180 degrees more often than expected, 180 and 300 degrees less often than expected, and 300 and 60 degrees in approximately the same proportion as available.

Sites with flat banks contained fewer lodges than expected. There was no significant difference between use and availability of convex or concave banks. Lodges were found more often than expected on sites with soil substrates below the waterline and less often than expected on sites with rocky substrates. Sites with underwater slopes greater than 10%, water depths at 1 m greater than 1 dm, and water depths at 2 m from shore greater than 2 dm were used more often than expected. Sites with shallower water were used less often than expected.

Only measurements of the density and crown cover for combined species of shrubs showed significant differences between the location of lodges and available conditions. Beaver appeared to select sites with greater than 3 stems per 100 points shrub density and greater

Table 3.3. Differences between characteristics of random sites and lodges on the Marias River study area, including test type and significance level. KS = Kolmogrov-Smirnoff two-sample test Chi = Chi-square test.

Variable	Test	df	Value	Significance
Bank				
Slope	KS		1.116	0.166
Aspect	KS		1.434	0.003
Location	Chi	1	2.237	0.135
Configuration	Chi	2	8.435	0.015
Substrate	Chi	1	3.327	0.068
Water/Underwater				
Slope	KS		1.912	0.001
Depth at 1 m	KS		1.753	0.004
Depth at 2 m	KS		1.633	0.010
Configuration	Chi	2	2.627	0.269
Substrate	Chi	1	10.35	0.001
River Width	KS		0.837	0.486
Upland				
Height	KS		0.637	0.811
Configuration	Chi	1	0.541	0.462
Woody Vegetation				
Continuous - Upstream Length	KS		1.076	0.197
Continuous - Downstream Length	KS		0.637	0.811
Continuous - Total Length	KS		0.956	0.320
Shrubs - Combined Species				
Height	KS		1.036	0.234
Density	KS		1.353	0.051
Crown Cover	KS		1.434	0.033
Shrubs - Willow Species				
Height	KS		1.036	0.234
Density	KS		0.916	0.371
Crown Cover	KS		0.996	0.274
Trees - Combined Species				
Number	KS		0.717	0.683
Diameter	KS		0.518	0.951
Crown Cover	KS		0.518	0.951
Trees - Cottonwood/Willow				
Number	KS		0.717	0.683
Diameter	KS		0.515	0.951
Crown Cover	KS		0.515	0.951

Table 3.4. Bonferoni Z tests of significance within categories for random sites versus lodges on the Marias River study area. Values in parentheses are approximate, see text for explanation.

Variable	Bonferoni Z Value	Significance Level *
Bank Aspect		
60 - 180 degrees	(2.79)	++
180 - 300 degrees	(2.80)	-
300 - 60 degrees	(0.38)	NS
Bank Configuration		
Concave	0.69	NS
Flat	3.09	--
Convex	2.04	NS
Underwater Slope		
0 - 10 %	(3.48)	---
> 10 %	(3.48)	+++
Water Depth at 1 m from Shore		
0 - 1 dm	(3.81)	---
> 1 dm	(3.81)	+++
Water Depth at 2 m from Shore		
) - 2 dm	(4.02)	---
> 2 dm	(4.02)	+++
Underwater Substrate		
Soil	5.20	+++
Rock	5.20	---
Shrub Density - Combined Species		
< 3 stems/100 points	(2.80)	-
3 - 20 stems/100 points	(2.69)	+
> 20 stems/100 points	(0.25)	NS
Shrub Crown Cover - Combined Species		
0 - 5 %	(2.90)	--
> 5 %	(2.90)	++

* Significance levels.

+ = use greater than availability
- = use less than availability

+++ or --- $p < 0.001$
++ or -- $p < 0.01$
+ or - $p < 0.05$

than 5% crown cover for lodge construction. Sites with fewer shrubs were used less often than expected. No tree variables were significant. For details of the values, see Table 3.4.

Lake Elwell

Significant differences were observed between lodge and random sites for bank aspect ($p < 0.05$), water depth at 1 m ($p < 0.01$) and 2 m ($p < 0.05$) from shore, underwater substrate ($p < 0.05$), upland height ($p < 0.001$), and upland configuration ($p < 0.001$). All other variables showed no significant difference (Table 3.5).

Lodge sites on Tiber Reservoir varied significantly from availability in some characteristics of the physical site and adjacent areas. Lodges were significantly more common on sites with east to southwest aspects (90 to 210 degrees). Sites with other aspects were used less often than expected.

Lodges were built on sites with soil underwater substrates more often than expected and rocky substrates less often than expected. Beaver selected sites for lodges with water depths greater than 3 dm at 1 m from shore or 6 dm at 2 m from shore. They avoided sites with water depths less than 1.5 dm at 1 m or 3 dm at 2 m. Sites with depths of 1.5 to 3 dm at 1 m or 3 to 6 dm at 2 m did not differ significantly between use and availability.

Lodges were more common on sites with adjacent uplands between 910 and 930 m in elevation or bench-like configurations. Sites with cliff-like uplands over 950 m in elevation were avoided. Sites between 930 and 950 m in elevation showed no significant difference

Table 3.5. Differences between characteristics of random sites and lodges on the Lake Elwell study area, including test type and significance level. KS = Kolmogrov-Smirnoff two-sample test Chi = Chi-square test.

Variable	Test	df	Value	Significance
Bank				
Slope	KS		0.972	0.301
Aspect	KS		1.568	0.015
Location	Chi	1	0.536	0.464
Configuration	Chi	2	2.568	0.277
Substrate	Chi	1	3.548	0.060
Water/Underwater				
Slope	KS		1.337	0.056
Depth at 1 m	KS		1.673	0.007
Depth at 2 m	KS		1.474	0.026
Configuration	Chi	2	0.406	0.816
Substrate	Chi	1	5.368	0.020
Width	KS		1.220	0.102
Upland				
Height	KS		2.064	0.000
Configuration	Chi	1	14.14	0.001
Woody Vegetation				
Continuous - Upstream Length	KS		0.896	0.398
Continuous - Downstream Length	KS		1.165	0.132
Continuous - Total Length	KS		1.066	0.206
Shrubs - Willow Species				
Height	KS		1.045	0.225
Density	KS		0.538	0.934
Crown Cover	KS		0.917	0.370
Trees - Combined Species				
Number	KS		0.438	0.991
Diameter	KS		0.388	0.998
Crown Cover	KS		0.120	1.000

between use and availability. For details of the values, see Table 3.6.

DISCUSSION

On all 3 study areas, beaver constructed hybrid dens, combining features of both the domed lodge and bank burrow. Living quarters were dug into the soil of the bank, as in a burrow. However, the water near shore was too shallow for beaver to construct and maintain an underwater entrance by simply burrowing through the soil. Even if the water was deep, the dynamic action of the flowing water tended to erode entrances. Therefore, beaver piled sticks from the bank several feet into the water. The tunnel extended through the sticks, as in a pond lodge, to a safe and secure exit below the water line. In some cases, beaver even increased the height of the bank by piling sticks and mud over the living quarters. This construction technique allowed beaver to thrive on sites where bank and water conditions prevented construction and maintenance of pure burrows or lodges. Although this reduces the impact of water and bank conditions, there are limits.

Many authors have implicated the lack of suitable den sites in the patterns of distribution and survival of beaver colonies (Collins 1979, Boyce 1981, Bissell and Bown 1987). On the study areas, beaver generally built dens on sites with stable soil banks with at least a minimum water depth near shore at low water. Because conditions varied on all 3 study areas, the factors defining stable banks and suitable water depths varied.

Table 3.6. Bonferoni Z tests of significance within categories for random sites versus lodges on the Lake Elwell study area. Values in parentheses are approximate, see text for explanation.

Variable	Bonferoni Z Value	Significance Level *
Bank Aspect		
90 - 210 degrees	(5.13)	+++
210 - 330 degrees	(3.63)	---
330 - 90 degrees	(2.66)	-
Underwater Substrate		
Soil	4.09	+++
Rock	4.09	---
Water Depth at 1 m from Shore		
< 1.5 dm	(2.59)	-
1.5 - 3 dm	(0.67)	NS
> 3 dm	(2.25)	+
Water Depth at 2 m from Shore		
< 3 dm	(2.59)	-
3 - 6 dm	(0.16)	NS
> 6 dm	(2.57)	+
Upland Height		
910 - 930 m	(4.40)	+++
931 - 950 m	(2.71)	-
> 950 m	(5.04)	---
Upland Configuration		
Cliff	6.73	---
Bench	6.73	+++

* Significance levels.

+ = use greater than availability
- = use less than availability

+++ or --- $p < 0.001$
++ or -- $p < 0.01$
+ or - $p < 0.05$

On all 3 study areas, beaver lodges were found almost exclusively on sites with soil substrates. Under similar conditions, Tabor et al. (1981) found that 46 of the 64 dens located were dug into soil banks. Seven were built of sticks and mud in rock crevices. Collins (1979) described the low water banks of the Snake River in Wyoming as mostly unsuitable for beaver dens, partially due to the cobblestone substrate.

Although the hybrid den style reduces the impact of water depth on beaver use of marginal sites, there are limits; beaver cannot extend the entrance tunnel indefinitely or maintain it on banks exposed to spring ice scour. For sites to be habitable, they should have some minimum depth of water near shore sufficient to insure a passable underwater entrance at low water. The minimum depth will depend on the extent of water level fluctuations on a site.

On the Marias River, beaver tended to select den sites with greater-than-average water depths near shore. The Marias is a generally shallow river. Small changes in water level can lead to the exposure of wide gravel bars and mud flats. Water levels on the Marias River study area are directly controlled by Tiber Dam, immediately upstream. As a flood control facility, Tiber Dam significantly changes the normal seasonal fluctuations on the River. To maintain suitable dens, beaver were forced to search out deep sites. By comparison, the Missouri is a relatively deep river. There was no significant difference in measurements of water depth near shore on lodge and random sites, indicating that average conditions may meet minimal standards. All dams immediately above the Carter

Ferry study area are run-of-the-river facilities, having little effect on the river's water levels.

Beaver at Lake Elwell also appeared to choose deep sites, substantially deeper than at either river site. Because Lake Elwell is a flood control reservoir, water levels fluctuate widely throughout the year. To maintain underwater entrances to the dens during even moderate drawdowns, beaver must select sites with steep slopes and deep water near shore. Tabor et al. (1981) found most beaver dens along the Columbia River on sites with bank slopes greater than 25%. Collins (1979) found that 6 of the 8 sites permanently abandoned by beaver completely lacked low water den sites. Several authors have stated that extensive water level fluctuations, whether natural or human-caused, reduced the suitability of sites for beaver and often led to abandonment (Rutherford 1953, Henry 1967, Martin 1977, Slough and Sadleir 1977, Tabor et al. 1981, Bissell and Bown 1987).

Deep water and soil banks are of little use if they are unstable. Collapsing banks provide little shelter and may kill animals. We would expect beaver to select sites that are relatively stable, not subject to extensive erosion. On rivers, most erosion is caused by flowing water. Although we did not attempt to measure erosion directly, only 1 den on the Carter Ferry study area was dug into a steep and actively eroding cliff, even though such conditions exist throughout the area. Tabor et al. (1981) found 86% of the dens on the Columbia River were on sites with little to no water velocity. Only Bissell and Bown (1987) reported significantly greater use of undercut and eroded banks and less use of flat or convex banks on the Flathead

River. One den was destroyed when the bank caved in. Eroded banks are generally correlated with deep water near shore. Water levels on the Flathead River are influenced by a power peaking dam upstream and a hydroelectric dam downstream. The apparent selection of cutbanks may be an artifact of the need for deep underwater entrances. On both the Missouri and Marias rivers, beaver lodges appeared correlated with some measurements of riparian shrubs and trees. It would be advantageous to live near your food supply. However, shrubs and trees tend to develop on stable, low relief areas. There is no way to tell from my data whether the apparent selection was due to stability or food.

On large reservoirs, wind and waves replace flowing water as the major erosive force. Without protection from waves, reservoirs or large lakes are considered unsuitable for beaver (Slough and Sadleir 1977, Allen 1983, Bissell and Bown 1987). Tabor et al. (1981) found 90% of the dens on the Columbia River were on sites with good to excellent protection from waves.

Lake Elwell is a very large body of water stretching 30 km in a east-west direction. The area experiences strong, persistent, easterly winds on a regular basis. When the wind direction corresponds to the long axis of the reservoir, immense waves are created, scouring any exposed shoreline and leading to extensive erosion. Protection, in the form of shelter from wind and waves, is provided by the land relief. Although the bank aspect of random sites was relatively evenly distributed, beaver showed a strong preference for sites with east to southwest aspects. Sites with such aspects are protected from the impacts of wave erosion. Many of the den sites were also located in the narrow, sinuous channels created when dry coulees were flooded. The very narrow channels act as baffles, further diminishing the wave energy.

SPATIAL AND TEMPORAL USE OF WOODY SHRUBS AND TREES BY BEAVER

METHODS

As food supplies might be a critical factor influencing beaver use of terrestrial areas, I investigated seasonal and spatial use of the major woody food species. Herbaceous vegetation, used by beaver during the growing season, was readily available and probably not limiting. However, woody species, used for both food and construction, were scarce in some areas and might have affected the patterns of habitat use on the study areas.

Permanent plots were established at 6 selected colony sites on the Carter Ferry study area to measure use of woody shrubs. Five, 1 m wide transects were situated perpendicular to the shoreline, 1 each at the lodge center and at 25 and 50 m upstream and downstream. Where lodges were located at one end of, or even several hundred meters from, the nearest woody riparian vegetation, 5 transects were established at 25 m intervals beginning at the closest edge of shrub growth. Each transect was divided into 1 m square plots that were checked monthly for cutting by beaver. On the initial count, the diameter and species were recorded and each stem classified as old cut, new cut, or uncut. All cut stems were marked with paint. During monthly recounts, the species and diameter of newly cut stems were recorded and the cuts marked.

Monthly cutting activity was graphed. Seasonal activity was divided into fall, September through November; winter, December through February; spring, March through May; and summer, June through August. Seasonal values were compared to an even distribution using Chi-square.

Initial survey data were graphed by size class and distance from water for both the combined sites and site 2 alone. Site 2 contained the most extensive willows. Because the length of each transect containing willows varied widely, all values were expressed as density per transect.

The percent of stems cut and raw numbers cut versus the total number available were graphed. Transects were divided into 5 m segments to reduce minor density differences and the results graphed, as were the mean frequencies of cut and uncut willows.

Although shrubs appear to comprise the majority of the beaver's woody diet on the Carter Ferry study area, a variety of trees are also available. Many of these trees showed some evidence of beaver cutting activity, though most were abandoned before the trees were felled. All trees within the 100 m sections of bank chosen for the random sample were classified as to diameter at 0.5 m above ground, species, distance from water, and degree of beaver cutting. Only trees over 7 cm in diameter were used for the analysis. Green ash _Fraxinus pennsylvanica_, juniper _Juniperus scopulorum_, russian olive _Elaeagnus angustifolia_, water birch _Betula occidentalis_, and elm _Ulmus_ sp. were combined into 1 category because they were scarce on the study area and showed little or no beaver use. The Chi-square test was used to determine the effect of tree species on cutting activity and the Bonferoni Z statistic was used to determine which categories were creating the observed significance. Kolmogrov-Smirnoff and Mann-Whitney U tests were used to determine the effect of the continuous variables, diameter and distance from water on beaver cutting. Where distance from water and diameter were significant, Spearman Rank correlation was used to determine correlation between these variables. Diameter, by species, was categorized into approximately 25 percentiles based on total available for each species. Distance from river was divided into 10 m segments. Both results were graphed.

RESULTS

Seasonal Cutting Activity

Site 5 was dropped from all calculations because it was abandoned by beaver at the start of the study and showed no evidence of permanent occupancy throughout. Some cutting, attributed to transients, occurred during the winter on site 5.

Seventy-two percent of the total cutting occurred during the fall, with the peak, 31%, in November, corresponding with the construction of caches. Sites 1, 2, and 3 followed this pattern faithfully. Sites 4 and 6 showed secondary peaks during April and June, respectively. Summer was the most inactive cutting period with only 5% of the total annual cutting, due primarily to activity on site 6. This disparity in seasonal cutting was significant at the $p < 0.001$ level (Figures 4.1 and 4.2).

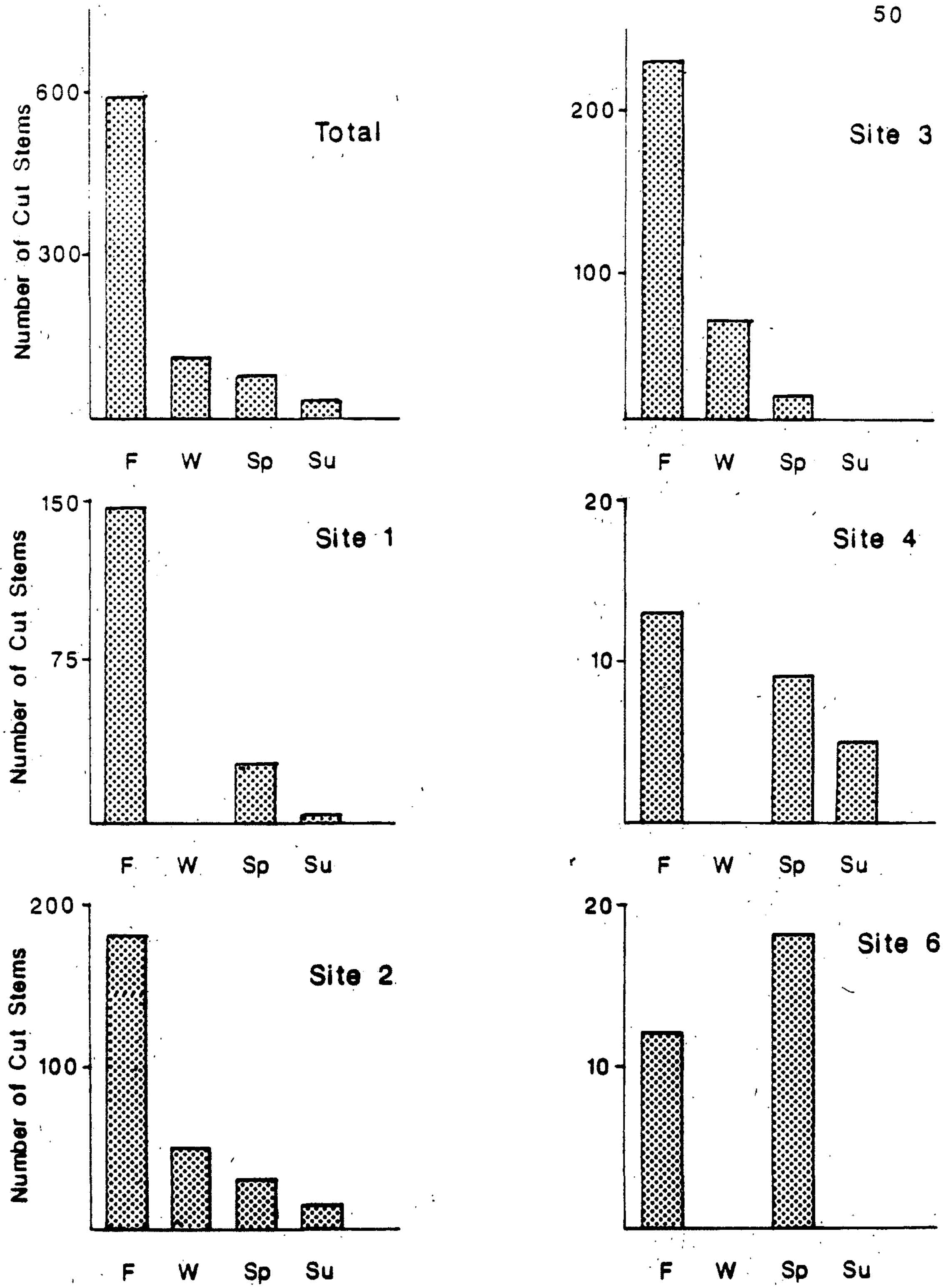


Figure 4.1. Number of willow stems cut by season on permanent plots, by site and combined sites.

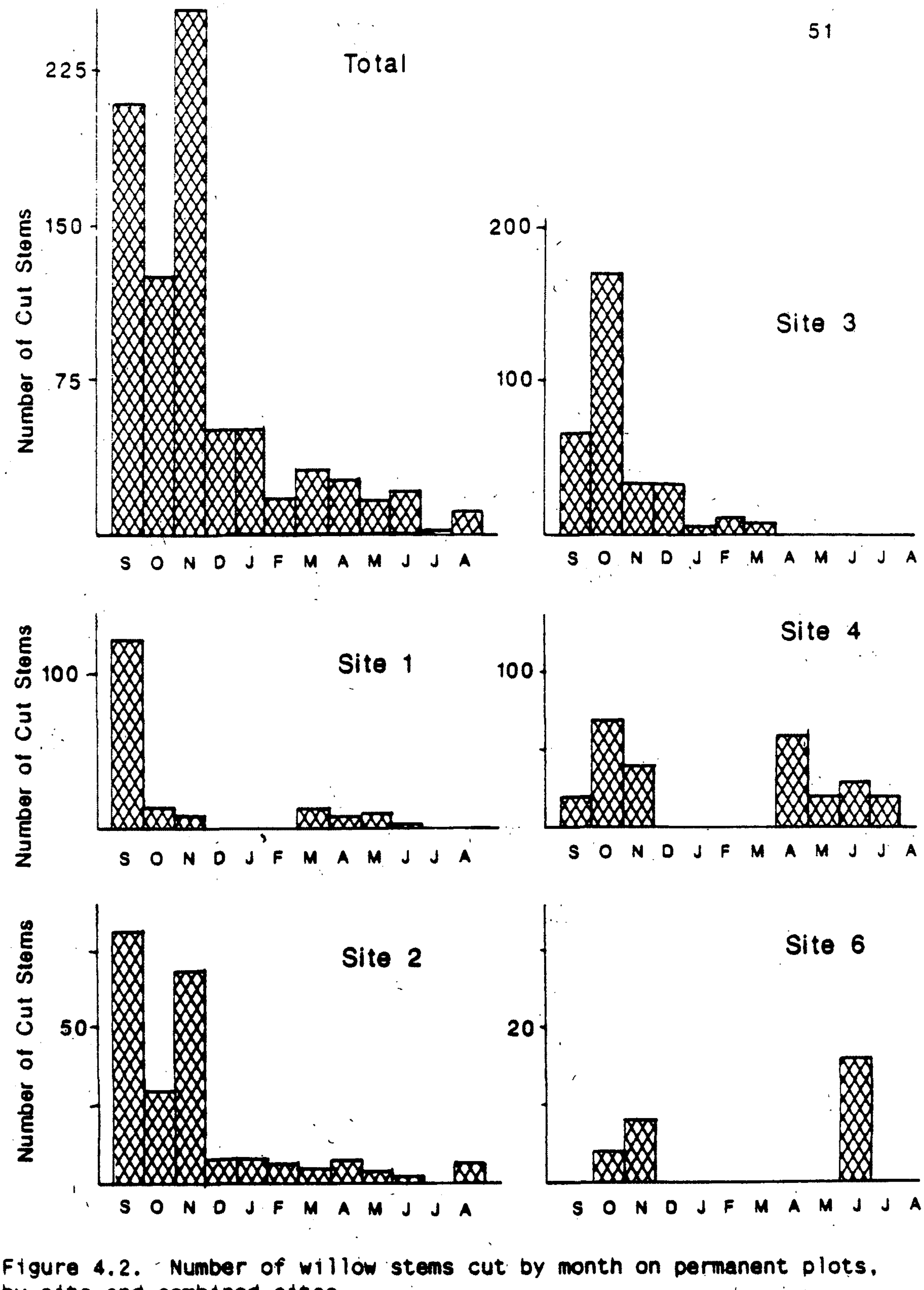


Figure 4.2. Number of willow stems cut by month on permanent plots, by site and combined sites.

No attempt was made to quantify seasonal cutting activity on trees. Very few trees were cut in the entire study area throughout the study and none on the permanent plots.

Spatial Cutting Activity

Shrubs - Beaver cut a higher proportion of the willows in each size class as close to the water as available (Figures 4.3 to 4.6). Because of natural riverbank succession, smaller willows were more common near the shore and willows with >2 cm diameter were most common at 20 m inland. More than 50% of the available willows 0.5 to 1 cm in diameter were cut within 5 m of shore, 1 to 2 cm in diameter within 10 m of shore, and >2 cm within 18 m of shore. This corresponds with the variance in availability. The mode for available stems of 0.5 to 1 cm was 3 m inland, 1 to 2 cm was 12 m inland, and >2 cm was 22 m inland.

Microhabitat differences resulted in occasional large differences between the availability of willow in adjacent plots, often the result of flood debris or erosion. Therefore, densities were pooled in 5 m increments. The pattern remained the same (Figure 4.7).

Using the mean frequency of cut and the mean frequency of uncut stems, the pattern again remains intact (Figure 4.8). The proportion of the cutting activity in each 5 m segment was greatest near the shore. The proportion of the remaining uncut stems was greatest further from shore. Most of the cutting activity occurred within the first 5 m for stems 0.5 to 1 cm in diameter, and 11 to 14 m for stems greater than 1 cm in diameter.

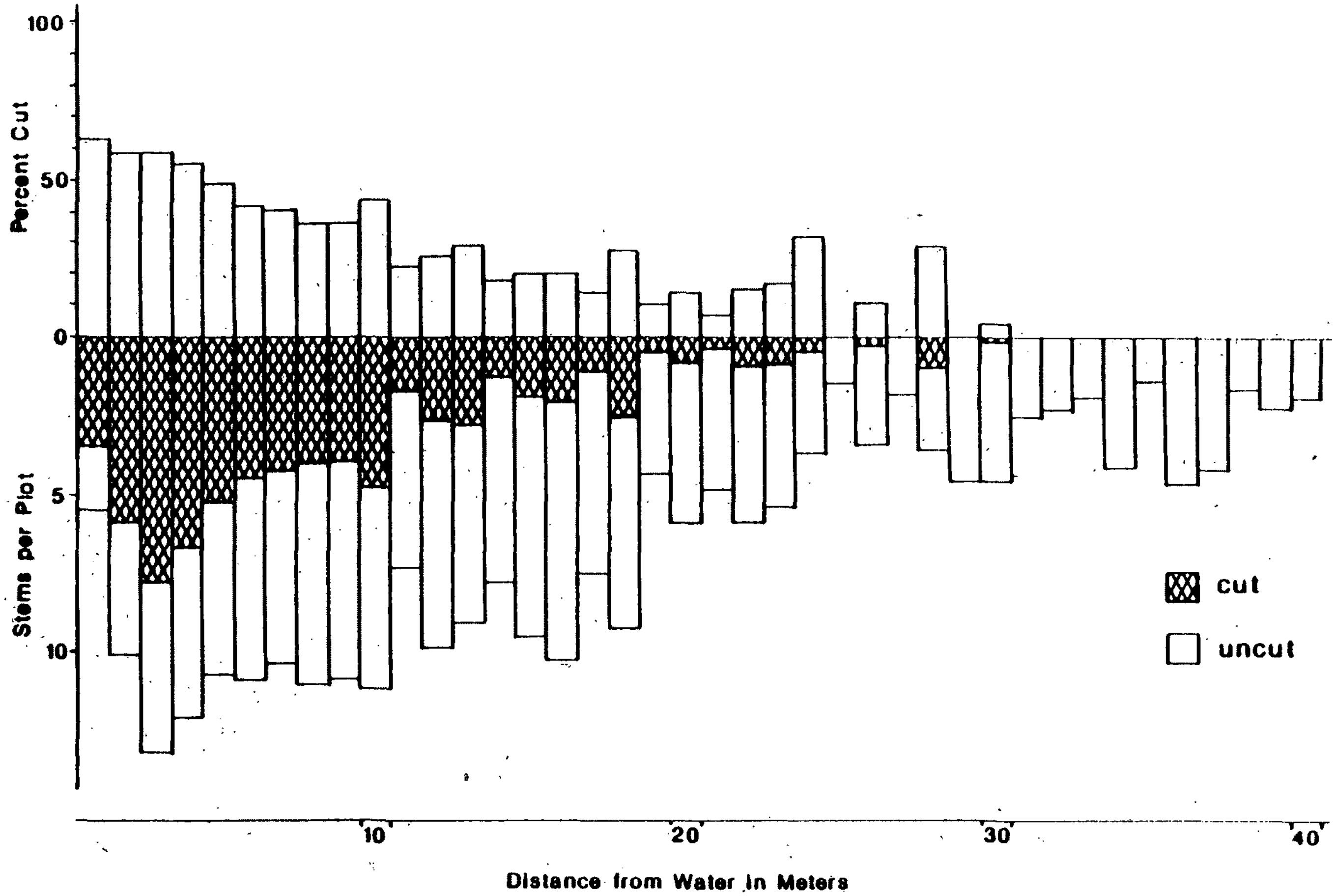


Figure 4.3. Mean stem density and beaver use of willows of 0.5 to 1 cm in diameter by distance from water, for all sites combined.

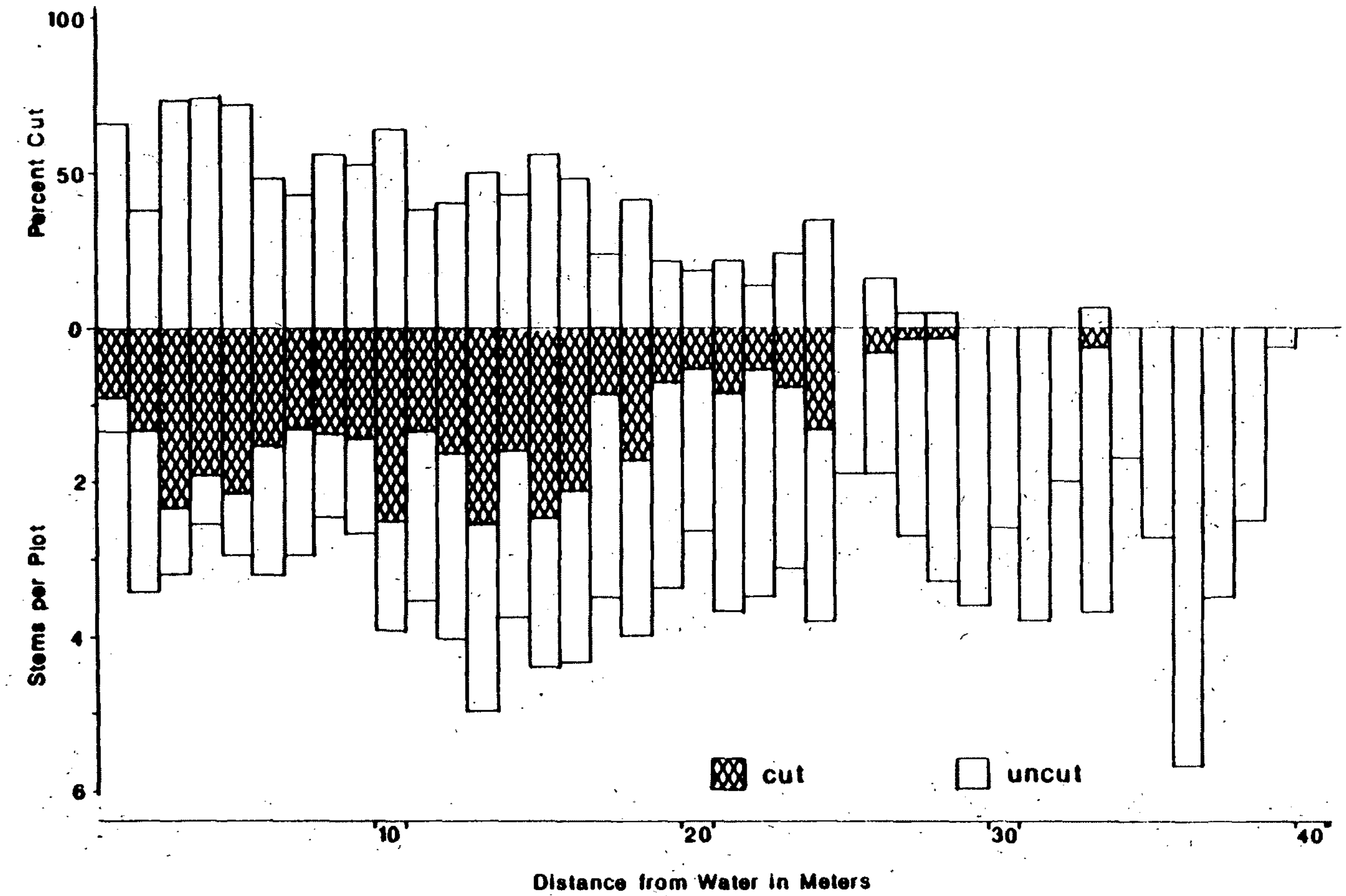


Figure 4.4. Mean stem density and beaver use of willows of 1 to 2 cm in diameter by distance from water, for all sites combined.

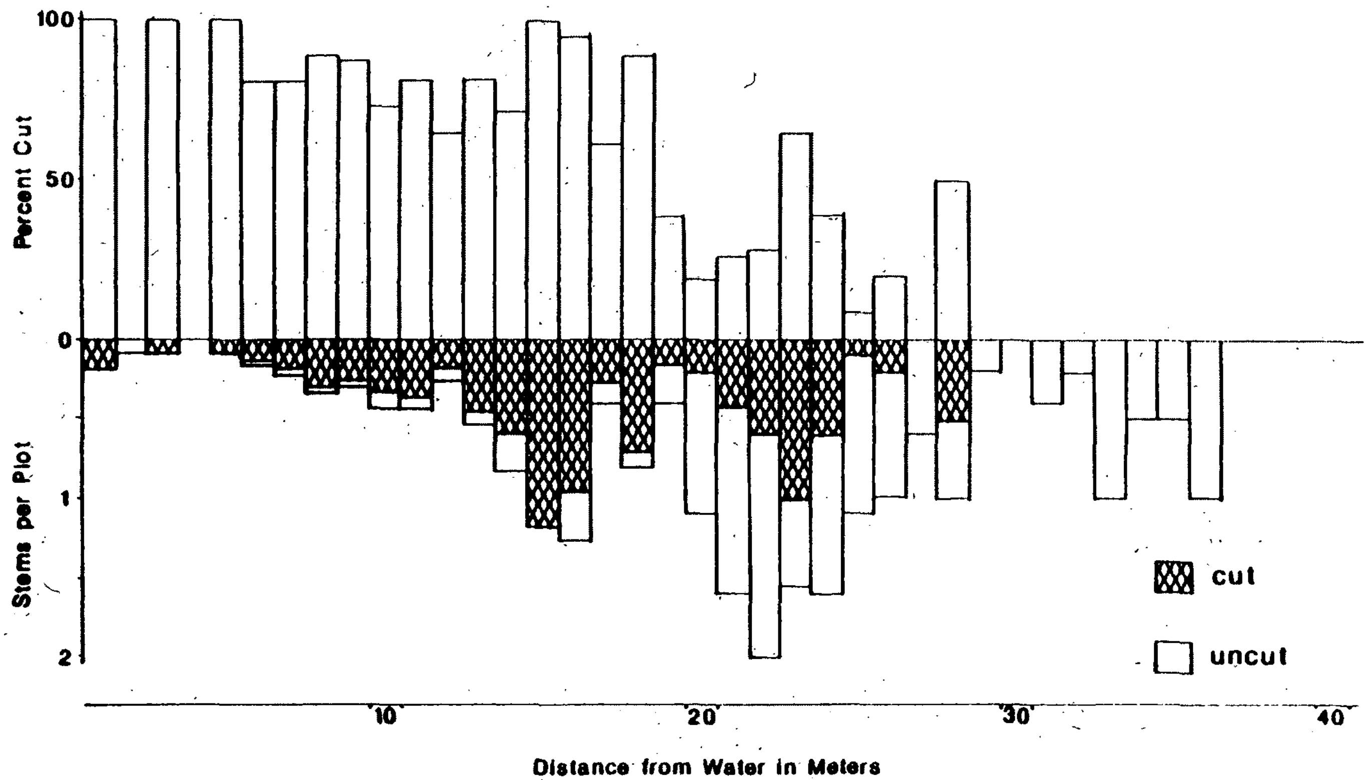


Figure 4.5. Mean stem density and beaver use of willows of greater than 2 cm in diameter by distance from water, for all sites combined.

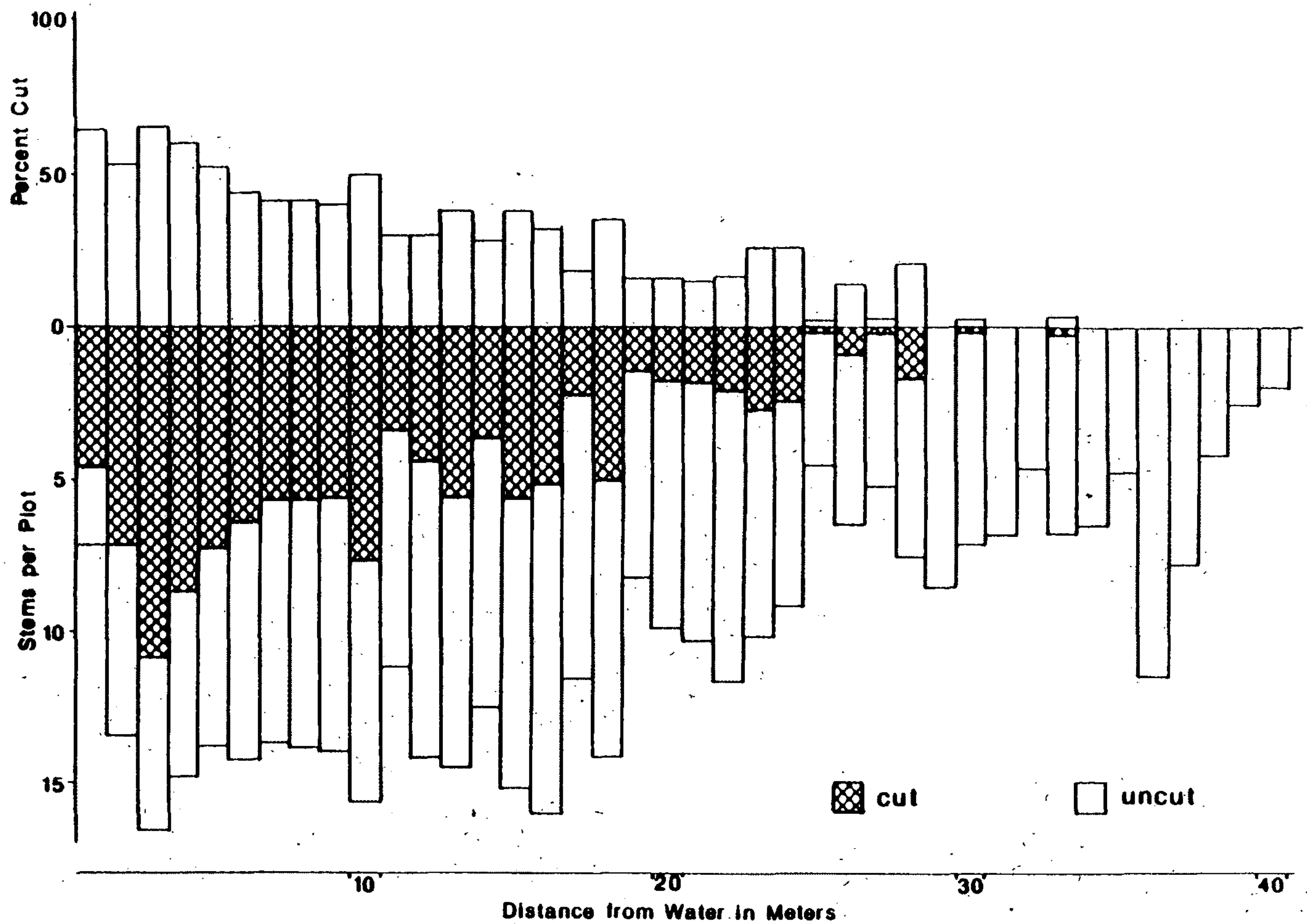


Figure 4.6. Mean stem density and beaver use of willows by distance from water, for all sites and diameters combined.

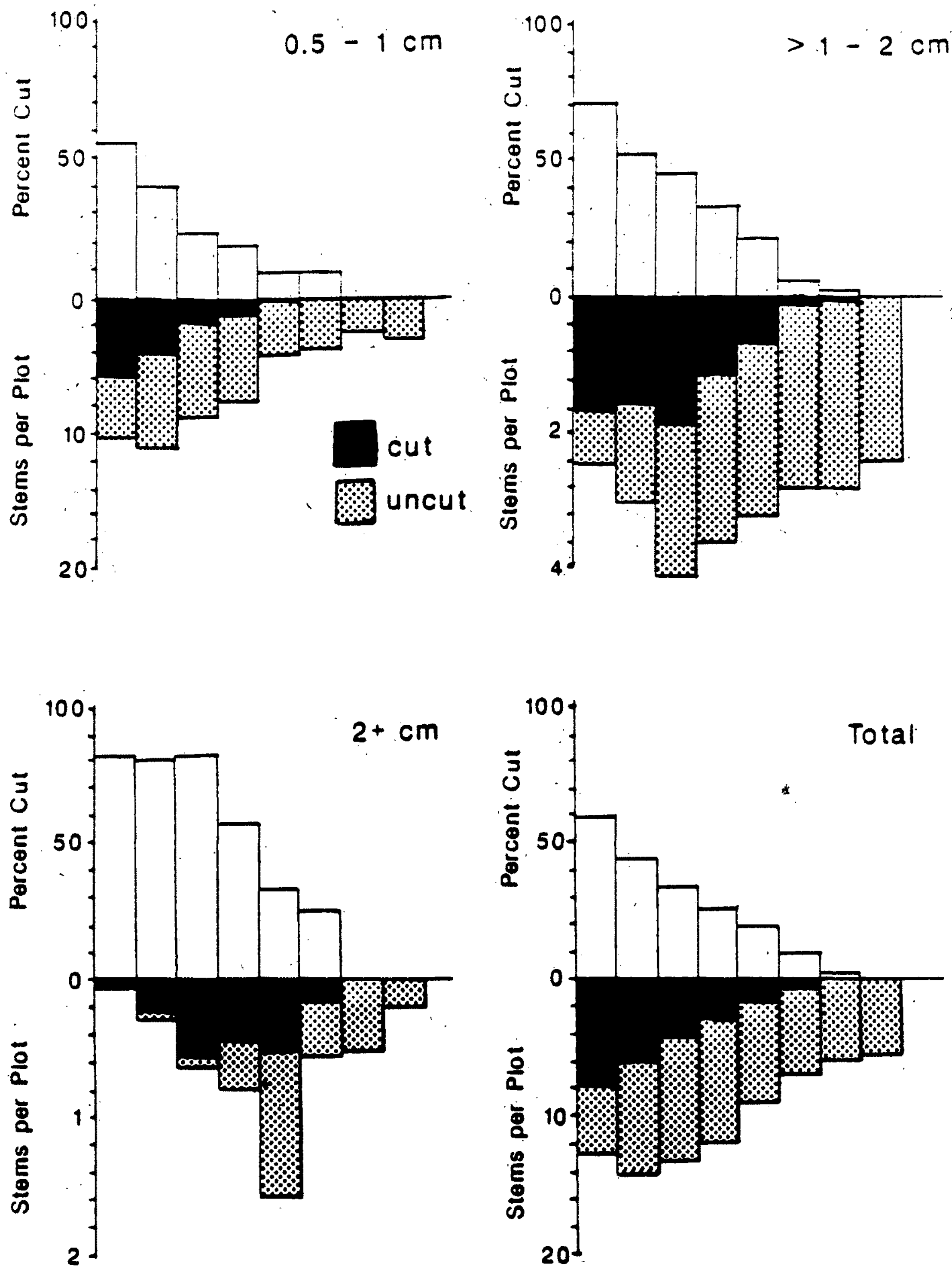


Figure 4.7. Mean stem density and beaver use of willows for all sites combined by distance from water in 5 m segments.

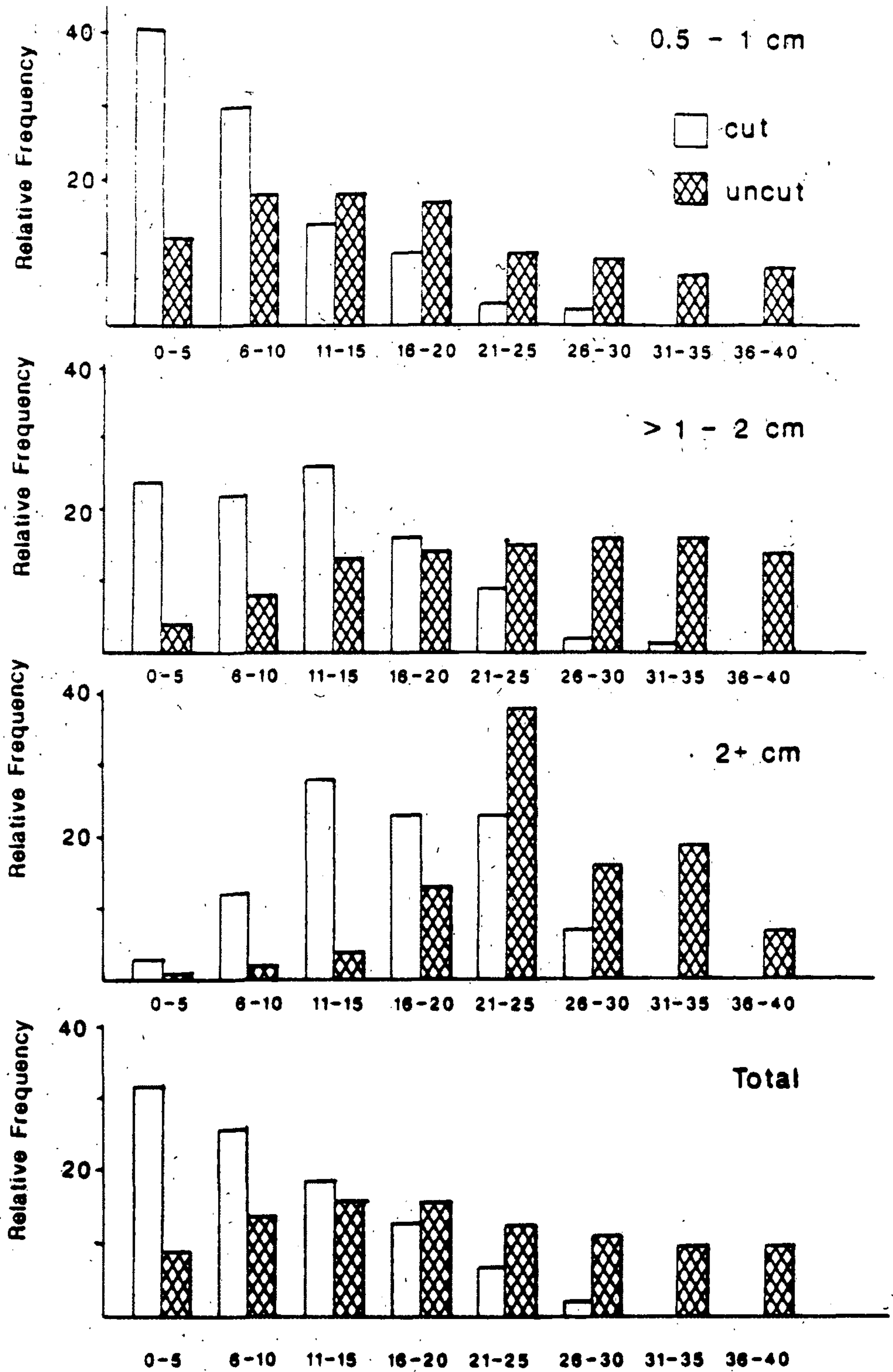


Figure 4.8. Relative frequency of cut and uncut willow stems for all sites combined.

Site 2 provided the greatest density and length of willow on any transect. Therefore, I analyzed it separately to remove any confounding effects of averaging across sites. Still, the general pattern held (Figures 4.9 to 4.12). For 0.5- to 1-cm diameter class, beaver cut the highest proportion within the first meter while the mode of available stems was at 9 m from shore. Most 1 to 2 cm diameter willows were cut within the second meter, but the modes were 11 and 19 m. Beaver cut all but 1 of the available willows of >2 cm within 18 m of the shoreline while the mode of the availability was 21 m. Again, plots were combined into 5 m segments to remove microhabitat effects and the pattern remained (Figure 4.13).

<u>Trees</u> - Willow trees comprised 27% of the available trees but 36% of the trees showing beaver cutting activity, a significantly higher use than available ($p < 0.05$, Figure 4.14). Cottonwoods and chokecherry were cut by beaver in the same proportion as available. Boxelder and the remaining species were cut less often than expected (Table 4.1).

When all species were considered together, there was a significant difference between the diameter of cut and available trees. Trees less than 9 cm in diameter were cut more often than expected while those over 18 cm in diameter were cut less often than expected ($p < 0.001$). When species were considered separately, significant differences were seen for cottonwood. Beaver cut cottonwoods over 36 cm in diameter less often than expected ($p < 0.001$) (Figure 4.15). No significant differences were found among chokecherry, boxelder, or other species.

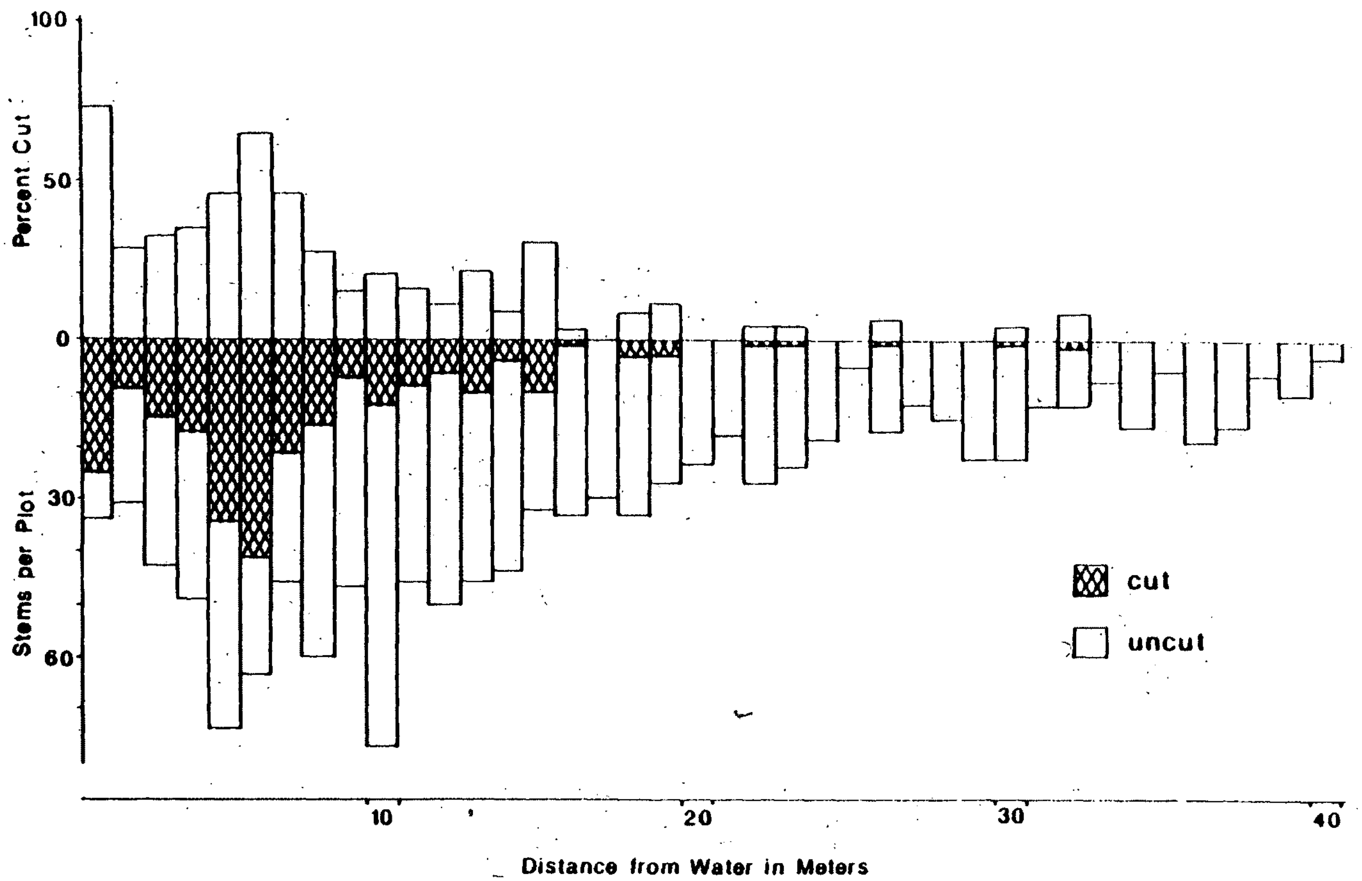


Figure 4.9. Mean stem density and beaver use of willows of 0.5 to 1 cm in diameter by distance from water, for Site 2.

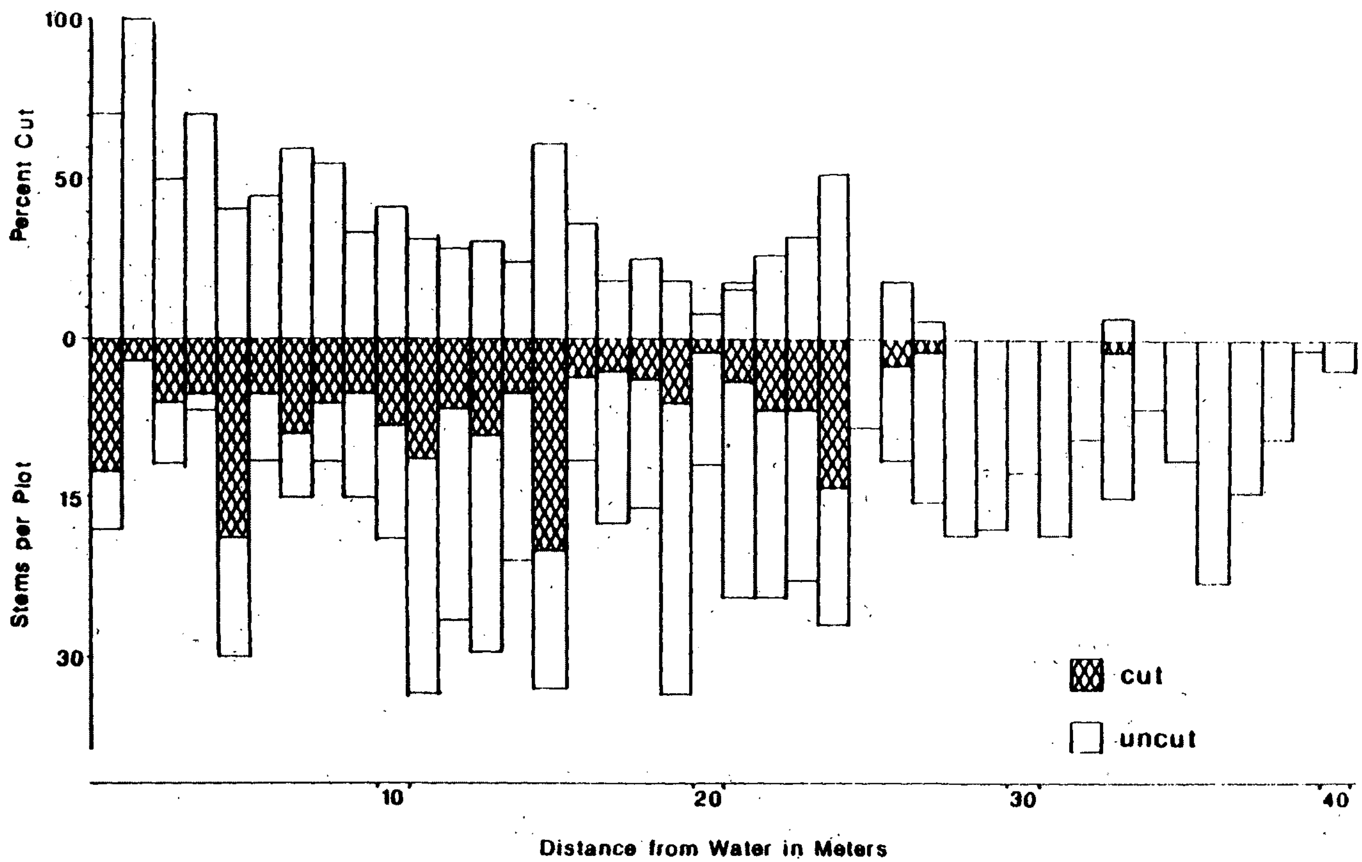


Figure 4.10. Mean stem density and beaver use of willows of 1 to 2 cm in diameter by distance from water, for Site 2.

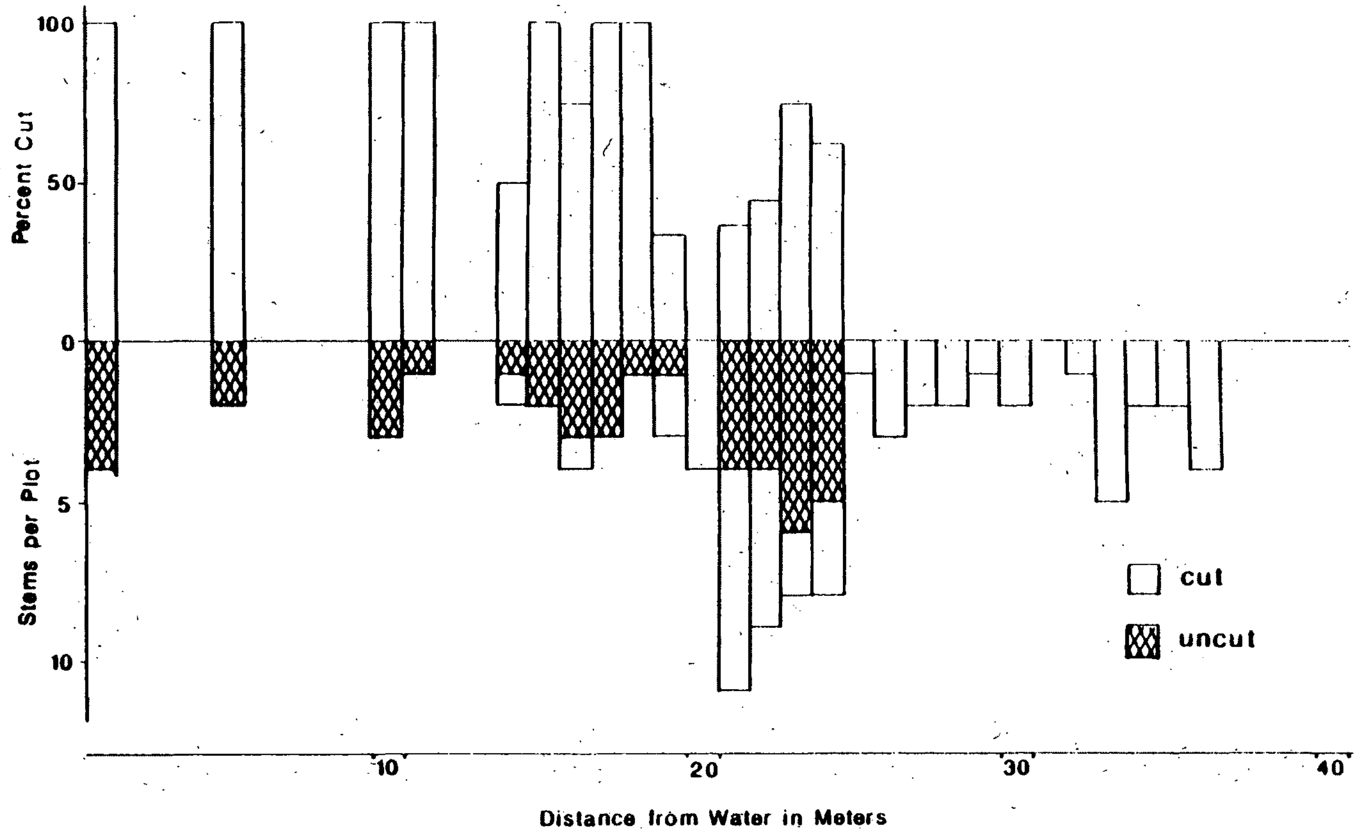


Figure 4.11. Mean stem density and beaver use of willows of greater than 2 cm in diameter by distance from water, for Site 2.

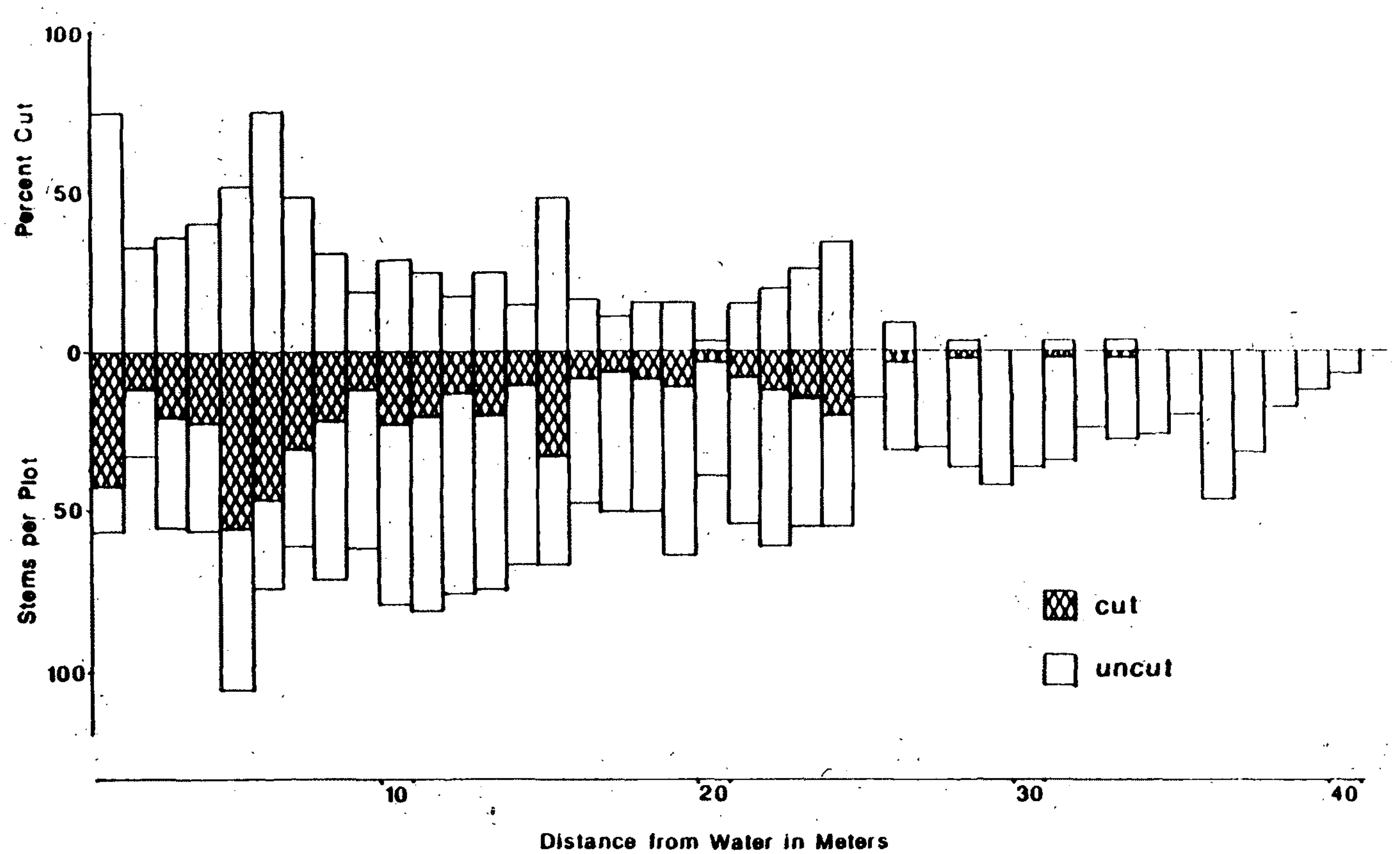


Figure 4.12. Mean stem density and beaver use of willows by distance from water, for Site 2 with all diameters combined.

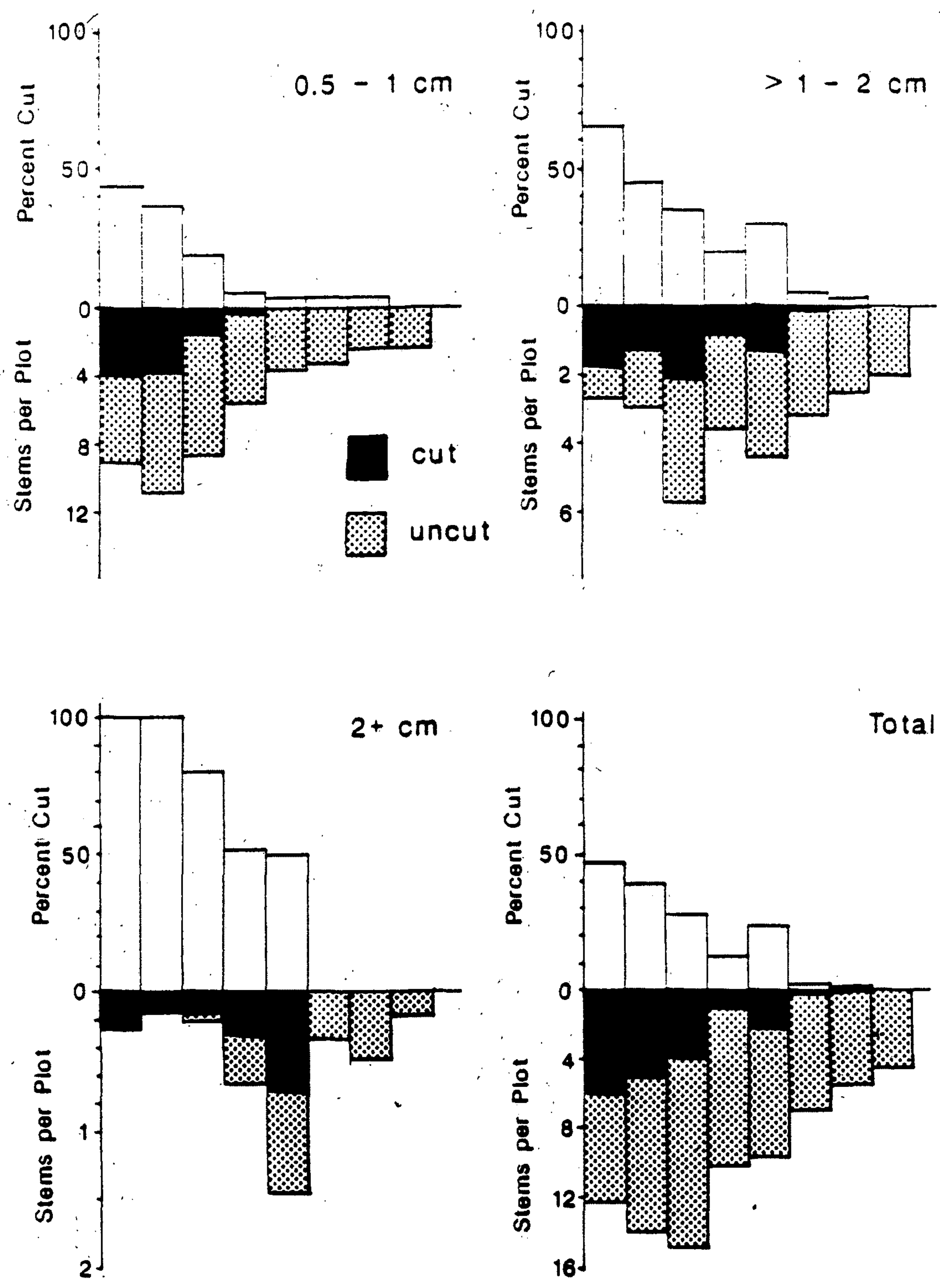


Figure 4.13. Mean stem density and beaver use of willows on Site 2 by distance from water in 5 m segments.

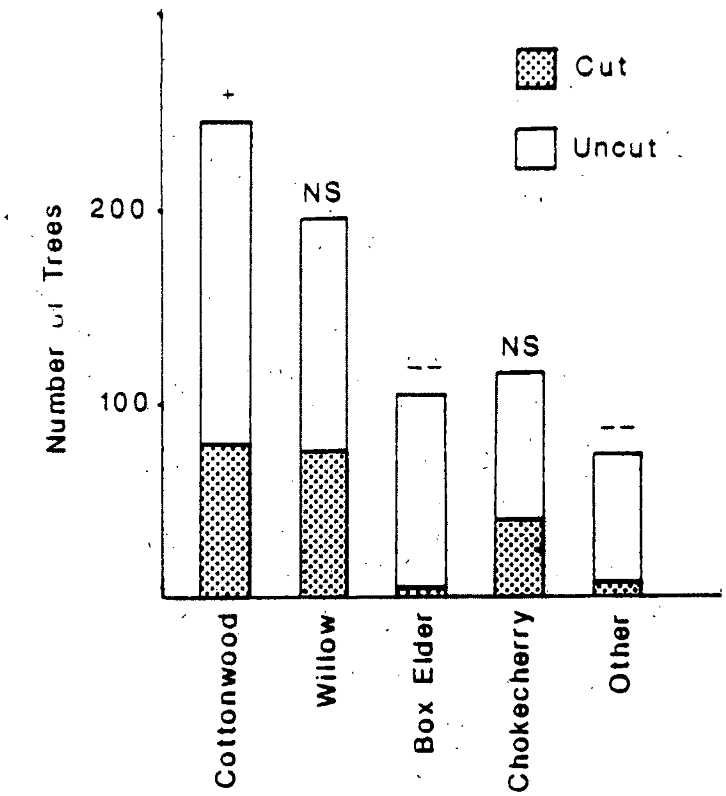


Figure 4.14. Number of cut and uncut trees with diameter > 7.5 cm by species on the Carter Ferry study area. + = greater than expected use, - = less than expected use. ++ or -- = $p < 0.01$, + or - = $p < 0.05$, NS = not significant.

Table 4.1. Beaver use and availability of tree species on the Carter Ferry study area.

Species	Available # Stems	Available % Total	Cut #	Cut % Cut	% of Total Cut	Significance Level *
Cottonwood	244	33.3	79	32.4	38.2	NS
Willow	195	26.6	75	38.5	36.2	+
Box elder	105	14.3	5	4.8	2.4	--
Chokecherry	115	15.7	40	34.8	19.3	NS
Other	74	10.1	8	10.8	3.9	--
Total	733		207			

* Significance levels.

+ = use greater than availability
- = use less than availability

++ or -- $p < 0.01$
+ or - $p < 0.05$

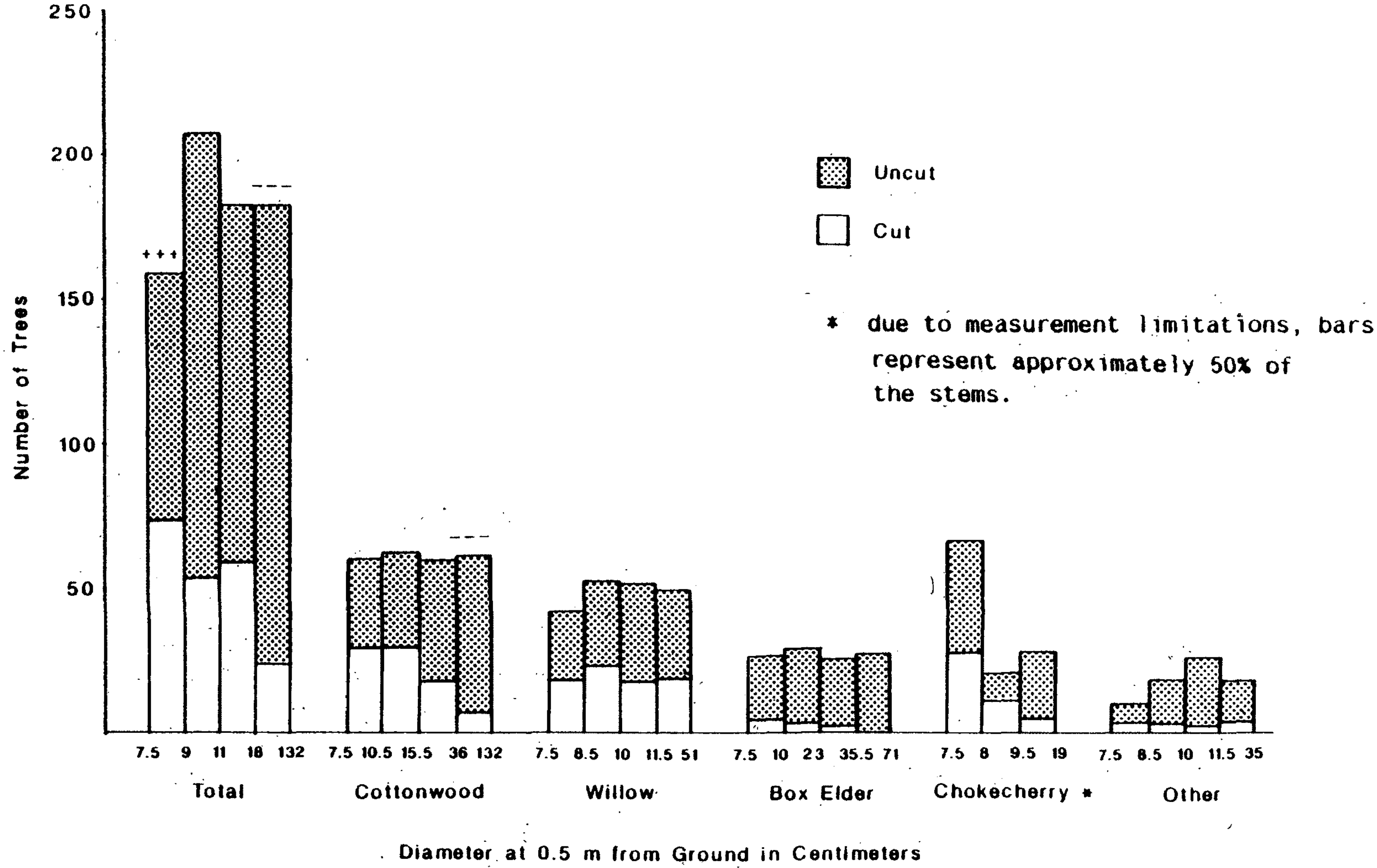


Figure 4.15. Number of cut and uncut trees by species and diameter. Categories are approximately 25 percentiles based on total stems unless otherwise noted.

For distance from river, with all species combined, beaver cut trees further from the water than expected ($p < 0.001$). When divided by species, beaver cut cottonwoods further from the river than expected ($p < 0.001$). There were no significant differences between use and availability for all other species (Figure 4.16).

DISCUSSION

Seasonal Cutting Activity

The bulk of the cutting activity by beaver occurred during the fall, coincident with the construction of winter food caches. The secondary peaks seen on site 4 and 6 were attributed to additional building activity. Beaver on site 4 spent April repairing damage sustained by their lodge during spring floods. The colony at site 6 built a new lodge during June within 250 m of the old lodge that had collapsed during the spring.

The winter of 1983-84 was fairly mild by central Montana standards. Shelf ice developed along the main river channel during cold spells, but rarely exceeded 5 m in width. Backwater areas froze solid. The lack of substantial ice or snow allowed beaver to continue to cut fresh willows throughout the winter.

Spatial Cutting Activity

Shrubs - Beaver are probably more susceptible to predation on land than in the water, hence the motivation to build dams and ponds.

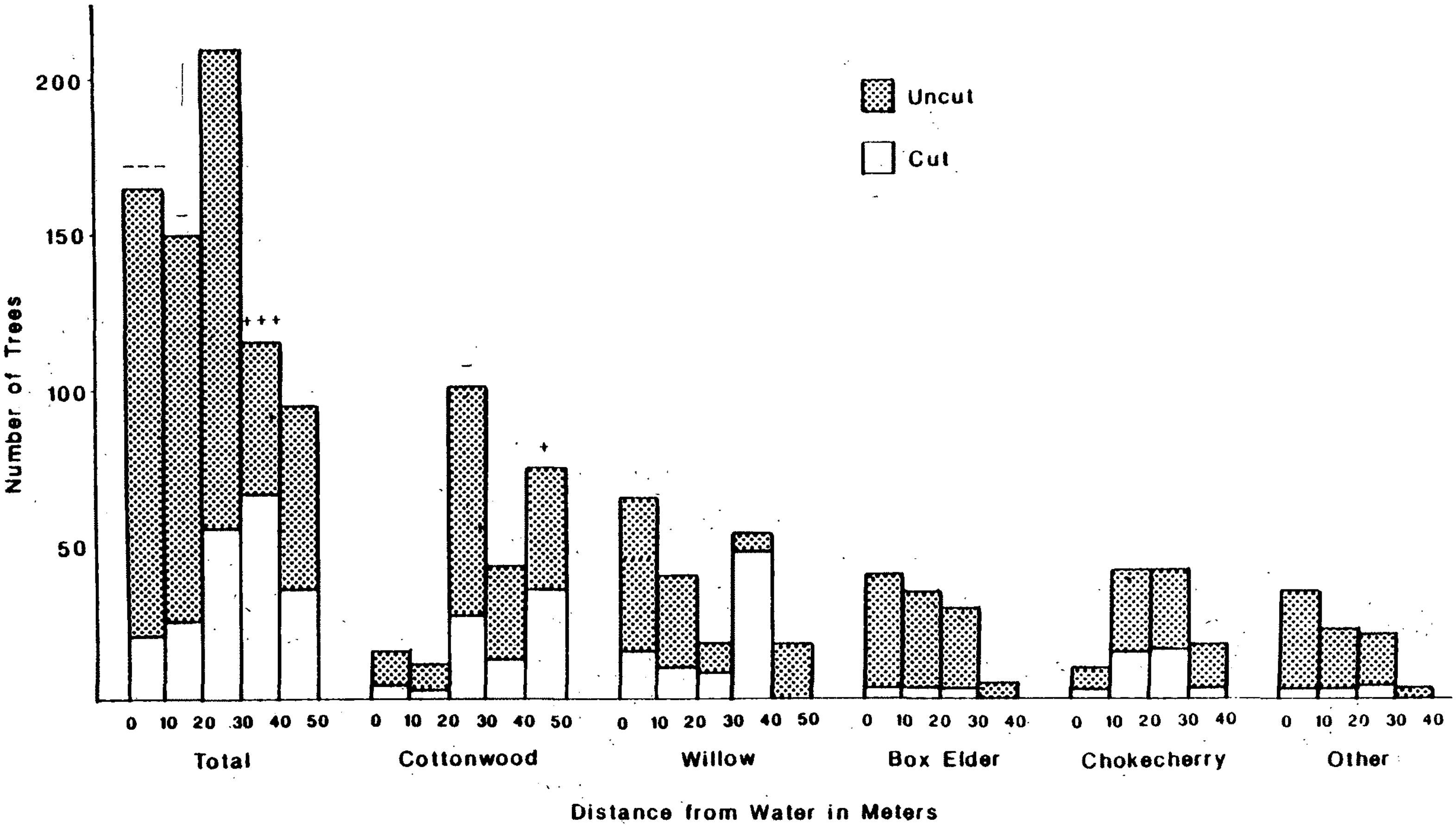


Figure 4.16. Number of cut and uncut trees by species and distance from water in 10 m segments.

Therefore, the chance of predation should increase with both distance from water and time spent on land. If so, we would expect beaver to develop feeding strategies aimed at maximizing the food gathered per unit time spent in terrestrial habitats. To do so requires balancing the food species preference, distance from the water, and size of the item as it relates to the time required to cut the item, process it into manageable pieces, and the total amount of food yielded. These factors may be used to explain the pattern of cutting observed on the Carter Ferry study area.

Beaver feeding activity and selectivity varies by plant species (Jenkins 1980). Beaver expend greater effort for highly preferred species, such as aspen. The study area provided a generally uniform availability of shrub and tree species, of which willow and cottonwood were the most commonly available and used by beaver.

Beaver have been observed to travel long distances from water to harvest highly preferred species. Maximum travel distances of over 100 m are commonly reported (Bradt 1938, Hiner 1967, Northcott 1971, Jenkins 1980) with over 700 m reported by Brenner (1967). Even so, most cutting occurs within 30 m of the shore (Hall 1970, Jenkins 1980). Virtually all willows on the study area lay within 40 m of the water's edge and were therefore considered available to the beaver. In addition, evidence of beaver cutting was found on many of the cottonwood trees that lay inland of the willows.

Most willows within the study area grow on point bars or deposition areas, leading to a characteristic shrub distribution. Areas farthest inland represent the oldest, driest, and most stable ground and contain the largest, presumably oldest, willows. Areas near the water's edge are the youngest and receive the most damage from seasonal flooding or winter ice. These areas contain the smallest willows. All willows on the study area were less than 10 cm in diameter and could be easily cut by beaver in a single session.

Larger willows, though further from the water, contain a much greater volume of bark per plant due to the extensive branching when compared to the smaller plants (0.5 to 1 cm diameter) which often consist of a single whip. The larger plants also contain greater numbers of leaves and growing shoots, an important summer and early fall food source (Aleksiuk 1970). Therefore, the larger willows may well yield more food per cutting effort.

No willows were large enough to require subdivision before hauling to the water. Handling time, representing a possible increased risk of predation, would be similar for all size classes. In addition, there is no need to make multiple trips to haul a single item to the water. Therefore, given the choice, cutting larger diameter willows would be the most cost effective.

Given the above, the pattern of cutting observed, smaller willows near shore and larger ones further inland, is not surprising. It is more surprising that beaver were observed to cut some small stems at distances of 25 m or more from shore. This activity is a function of the beaver's method of foraging. Beaver tend to utilize established trails from the water's edge to cutting areas. Willows near these trails are cut extensively, yet surrounding areas remain untouched; only occasionally did beaver create a clear-cut pattern. Small willows may be cut along these trails at great distances from shore out of convenience or when larger items become snagged on the small willows growing alongside the trails. Most trails were essentially perpendicular to the shoreline. Therefore, activity on a single transect varied widely depending on whether it intersected a feeding trail.

Trees - Numerous authors have reported an apparent preference by beaver for particular tree species. The preferred species may vary depending on availability, but usually include members of the Salicaceae Family, aspen, willows, and cottonwoods. Alder (Alnus sp.) are often included, though they are avoided in some areas (Aldous 1938, Towsend 1953, Northcott 1964, Henry 1967, Northcott 1971, Slough 1978, Swenson and Knapp 1980, and Tabor et al. 1981). On the Carter Ferry study area, beaver appeared to prefer willows, utilizing them more than expected based on availability. Although cottonwood is often considered a preferred species, the 3 species of cottonwood tree on the area were not utilized more than expected.

Beaver are capable of cutting down very large trees, though they appear to be selective of size under some conditions. On the study area, beaver concentrated on the smaller trees. Although cottonwoods reached 132 cm in diameter, no trees over 77 cm were cut by beaver. Size selection by beaver may be due to avoidance of the very large trees. To cut large trees, beaver must spend extended time on the bank, both felling the tree and reducing the branches to manageable size, exposing themselves to predation. By concentrating on the smaller trees, the beaver can reduce exposure time.

Chabreck (1958) reported no apparent selectivity in diameter class, although more than half the cut stems were in the 1 inch (2.5 cm) class and none were over 5 inches (12.7 cm). Henry (1967) reported most cut stems less than 3 inches in diameter (7.6 cm). Jenkins (1980) found selectivity in size of beaver cuttings related to species and distance from water.

At Carter Ferry, beaver cut cottonwoods further from the water than expected. If beaver are more vulnerable to predation on land, as discussed in the shrub section, we would not expect them to travel any further than necessary to cut trees without some overriding factor. Jenkins (1980) reported a decrease in the mean diameter of trees cut as distance from water increased. This conforms to a "time-minimization" strategy for feeding. Why did beaver travel further than necessary on the study area? If the preferred size class of trees predominated further inland, beaver might travel past less suitable trees. However, I found no significant correlation between diameter and distance from water for cottonwoods and a positive correlation for willow. The answer may lie in the distribution of trees throughout the study area. Most riparian trees on the area are found in narrow strips inland of the willow shrubs. Distances are generally greater than 25 m inland. Therefore, beaver have no choice in many areas but to travel this distance inland to cut trees. In those few places with extensive groves of trees near the water, willow shrubs are generally absent. Because beaver expend much of their cutting efforts on willow shrubs, they may spend less time in areas without shrubs, providing less opportunity to cut those trees. The apparent selection for longer distances may be an artifact of averaging data over widely different conditions.

Beaver on the Carter Ferry study area showed generally weak selection for species, distance from water, or diameter of trees, perhaps because they had little need of large woody materials. Beaver on the main river do not construct dams. The only structures they build that require large materials are bank lodges, and these structures are generally small. Large woody debris is common along the river and beaver made use of the ready supply. Several lodges contained readily available materials, such as driftwood boards. Because willow shrubs were abundant, beaver had little need to cut large trees for food. Given the greater risk probably associated with harvesting large trees, the cutting of large trees observed on the study area may have been simply opportunistic or instinctive work by beaver while in the area cutting willow shrubs. This hypothesis is supported by the numerous trees partially cut and abandoned by beaver.

DENSITY, LOCATION, AND SIZE OF BEAVER COLONIES

METHODS

In addition to collecting habitat-use information, efforts were made to determine beaver populations on the study areas. Exact quantification of beaver populations is a 2 step process, involving a count of active beaver colonies and a measurement or estimate of the number of individuals per colony. An active beaver colony is distinguished by the presence of a winter food cache. In northern climates, beaver tend to build only a single winter cache per colony (Hay 1958). The Carter Ferry study area was searched by boat for active colonies during the fall of 1982. Aerial searches were conducted on all study areas and additional sections of the Missouri and Marias rivers during the fall and winter of 1983-84 and 1984-85. All surveys were flown using a Super Cub flying approximately 100 km per hour at 100 m above the river or reservoir shoreline. Extensive ice during the winter of 1984-85 forced a reduction in the area surveyed. Care was taken to observe all the shoreline carefully. Shoreline and river channel length was measured from USGS Quad maps using an Apple Computer Graphics Table and digitizing software. The number of caches located was divided by the total length of shoreline and river channel to determine colony density.

All caches found along the Missouri River were classified as to type of adjacent upland or water channel, including islands, backwater channels, main banks with adjacent floodplains, and main banks with adjacent steep uplands or cliffs. Steep uplands were defined as any area with at least 30 m of rise within 100 m of the shore, most were substantially steeper. All shoreline between Morony Dam and Dauphine Rapids was classified as above and the total in length of each category calculated. Bonferoni Z tests were used to determine significant differences between availability and use in each category.

Selected colonies were live-trapped using Hancock Beaver Traps baited with castor and bait sticks. Beaver were immobolized with Vetalar (ketamine hydrochloride) and Acepromazine as described by Lancia et al. (1978). Animals were weighed, and the overall length, tail width, tail length, and skull breadth at the zygomatic arch were recorded (Patric and Webb 1960). Sex was determined by external palpation (Osborn 1955). Each beaver was marked with a unique combination of colored plastic rototags, 1 in each ear, to allow individual identification. Beaver were kept in holding cages until they had completely recovered from the drug to prevent drowning. Trapping was conducted during the fall of 1983 and spring of 1984 on the Carter Ferry study area, and the spring of 1984 on Lake Elwell. Trappers who returned ear tags were contacted to determine trapping location. No carcasses were recovered.

RESULTS

Colony Density

Densities of active beaver colonies varied widely between areas, especially when comparing rivers to reservoirs. On the Missouri

River, densities ranged from 0.03 to 0.31 colonies per kilometer of shoreline with an average of 0.15 (Table 5.1). For the Marias River below Tiber Dam, densities ranged from 0.10 to 0.23 colonies per kilometer of shoreline with an average of 0.18 (Table 5.2). Variance between densities on reservoirs was even greater, ranging from no colonies to 0.17 per kilometer of shoreline (Tables 5.3 and 5.4).

Cache Location

Of the 90 caches located along the Missouri River in the winter of 1983-84, 44 (50%) were associated with islands while only 21% of the shoreline was classified as island, a difference significant at the $p < 0.001$ level (Tables 5.5 and 5.6). Only 7 caches (8%) were associated with main banks with adjacent steep uplands although 28% of the shoreline was so classified, also significant at the $p < 0.001$ level. Main banks with adjacent floodplains or benches were associated with 30 caches (34% of the total) and represented 47% of the available shoreline. Backwater channels contained 8 caches (9% of the total) and represented 3% of the available shoreline. Neither was significant at the $p < 0.05$ level (Figure 5.1).

Colony Size

Nine beaver were live-trapped at 3 sites on the Carter Ferry study area, 2 in the fall of 1983 and 7 in the spring of 1984 (Table 5.7). Two additional individuals were taken by commercial trappers in the fall of 1983. During the winter of 1983-84, 11 beaver were

Table 5.1. Densities of beaver caches along the Missouri River in central Montana during the winters of 1983-84 and 1984-85. Densities are expressed as number of caches per shoreline and river length.

CACHE COUNT - MISSOURI RIVER

1983-84	Caches	Shoreline km	Caches/ Shore km	River km	Caches/ River km
Morony Dam to Carter Ferry	8	61.2	0.13	26.2	0.30
Belt Creek #	0	4.5	----	2.2	----
Highwood Creek #	6	16.0	0.38	8.0	0.75
Carter Ferry to Fort Benton	16	78.4	0.20	25.3	0.63
Fort Benton to Loma Ferry	18	101.8	0.18	33.0	0.54
Loma to Coal Banks Landing	19	103.7	0.18	35.5	0.54
Coal Banks to Pilot Rock	12	41.5	0.31	15.7	0.76
Pilot Rock to Slaughter River	3	94.6	0.03	40.6	0.07
Slaughter River to PN Ferry	6	51.8	0.11	19.7	0.30
PN Ferry to Dauphine Rapids	7	53.9	0.13	21.6	0.32
TOTAL	90	586.9	0.15	217.6	0.41

1984-85					
Morony Dam to Carter Ferry	5	61.2	0.08	26.2	0.19
Carter to Cottonwood Bottom *	7	53.7	0.13	16.2	0.43
TOTAL	12	116.0	0.10	42.6	0.28

Not included in total.

* Stopped 9 km short of Fort Benton due to ice jam.

Table 5.2. Densities of beaver caches along the Marias River in central Montana during the winters of 1983-84 and 1984-85. Densities are expressed as numbers per shoreline and river length.

CACHE COUNT - MARIAS RIVER

1983-84	Caches	Shoreline km	Caches/ Shore km	River km	Caches/ River km
Tiber Dam to Circle Bridge	21	92.8	0.23	39.4	0.53
Circle to Eightmile Coulee	6	57.9	0.10	25.8	0.23
TOTAL	27	150.7	0.18	65.2	0.42

1984-85	Caches	Shoreline km	Caches/ Shore km	River km	Caches/ River km
Tiber Dam to Circle Bridge	20	92.8	0.22	39.4	0.51
Circle to Eightmile Coulee	7	57.9	0.12	25.8	0.27
TOTAL	27	150.7	0.18	65.2	0.42

Table 5.3. Densities of beaver caches on reservoirs along the Missouri River in central Montana during the winter of 1983-84. Densities are expressed as number of colonies per length of shoreline and estimated length of river channel before inundation.

CACHE COUNT - MISSOURI RIVER RESERVOIRS

1983-84	Caches	Shoreline km	Caches/ Shore km	Channel km	Caches/ Channel km
Morony Reservoir	1	17	0.06	7	0.14
Ryan Reservoir	1	6	0.17	3	0.33
Cochrane Reservoir	0	13	----	4	----
Rainbow Reservoir	2	13	0.15	5	0.20
TOTAL	4	49	0.082	19	0.21
Holter Lake	2	100	0.020	47	0.042
Hauser Lake	0	76	-----	26	-----
Canyon Ferry Reservoir	4	164	0.024	54	0.074
TOTAL	6	340	0.018	127	0.047

Table 5.4. Densities of beaver caches on Lake Elwell in central Montana during the winters of 1983-84 and 1984-85. Densities are expressed as number of colonies per shoreline length and estimated length of river channel prior to inundation.

CACHE COUNT - LAKE ELWELL (TIBER DAM)

1983-84	Caches	Shoreline km	Caches/ Shore km	Channel km	Caches/ Channel km
Marias Arm	13	228	0.06	68	0.19
Willow Creek Arm	7	67	0.10	16	0.44
TOTAL	20	295	0.07	84	0.24
1984-85					
Marias Arm	12	228	0.05	68	0.18
Willow Creek Arm	5	67	0.08	16	0.31
TOTAL	17	295	0.06	84	0.20

Table 5.5. Shoreline composition and location of beaver caches along the Missouri River between Morony Dam and Dauphine Rapids, winter 1983-84.

Bank Type	Shoreline km	Shoreline % Total	Beaver Caches Number	Beaver Caches % Total	Significance Level
Main - Steep	165	28	7	8	---
Main - Bench	277	47	30	34	NS
Island	126	21	44	49	+++
Backwater	18	3	8	9	NS
TOTAL	587		90		

Significance levels.

+ = use greater than availability
- = use less than availability

+++ or --- $p < 0.001$
NS not significant

Table 5.6. Classification of shoreline type for segments of the Missouri River, displayed as percent of each segment, and beaver cache densities.

Section	Main Steep	Main Bench	Island	Back-water	Caches/ Shoreline km
Morony Dam to Carter Ferry	46	45	9	0	0.13
Carter Ferry to Fort Benton	29	41	24	6	0.20
Fort Benton to Loma Ferry	15	41	35	9	0.18
Loma to Coal Banks Landing	23	46	30	1	0.18
Coal Banks to Pilot Rock	21	52	26	0	0.31
Pilot Rock to Slaughter R.	42	50	8	0	0.03
Slaughter River to PN Ferry	30	49	13	8	0.11
PN Ferry to Dauphine Rapids	21	64	15	0	0.13
TOTAL RIVER	28	47	22	3	0.15

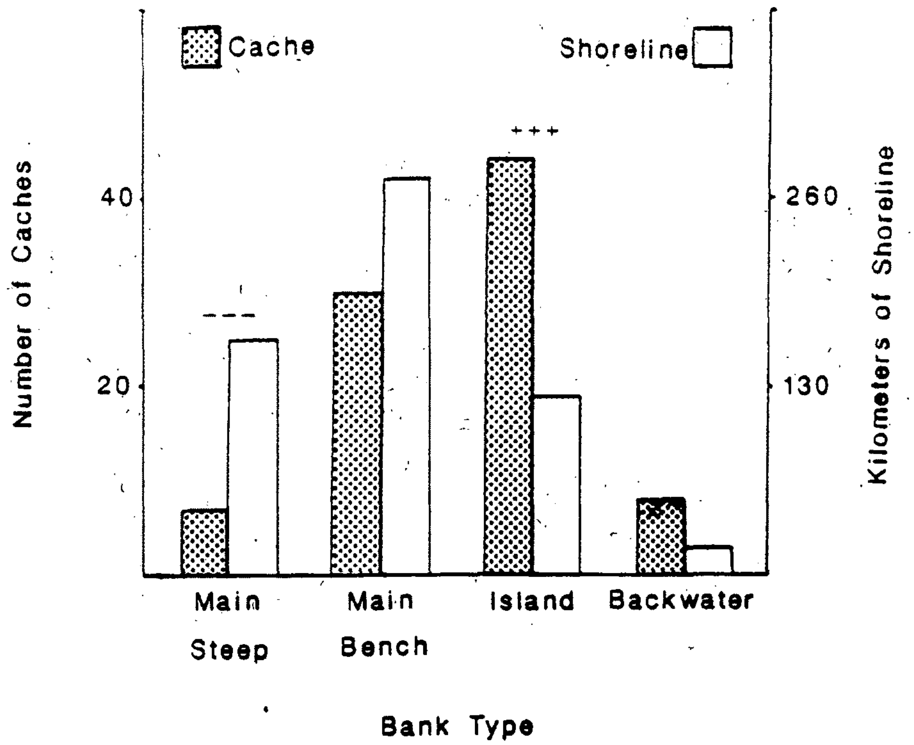


Figure 5.1. Comparison of the number of caches (n = 90) and length of available shoreline (n = 587 km) by bank type. Significance + = greater than expected use, - = less than expected use. +++ or --- $p < 0.001$.

Table 5.7. Measurements of beaver trapped and marked on the Carter Ferry and Lake Elwell study areas, including date captured and estimated age. Weights are given in kilograms, length, width, and width of zygomatic arch in cm.

#	Colony Number	Date Caught	Sex	Weight	Total Length	Tail Width	Tail Length	Zygo Arch	Est. Age
Carter Ferry									
1	1	11-4-83	F	6.4	75	8.3	19.9	7.05	Kit
2	1	11-5-83	F	6.0	78	7.0	21.5	7.83	Kit
3	1	11-83	-	31	--	---	----	----	Adult
4	1	11-83	-	30	--	---	----	----	Adult
5 *	1	4-2-84	F	15.9	104	12.8	26.3	9.21	Adult
6	1	4-9-84	M	14.1	95	12.8	26.9	----	2 yr
7	2	3-24-84	F	7.2	81	9.6	20.2	8.04	Kit
8	2	3-25-84	F	15.9	104	13.5	25.6	10.10	Adult
9	2	4-18-84	F	14.5	102	12.5	25.0	8.95	2 yr
10	3	4-16-84	F	20.0	106	14.7	24.4	----	Adult
11	3	4-19-84	F	12.7	97	11.5	26.3	8.30	1 yr
Lake Elwell									
1	1	4-30-84	F	20.0	109	16.0	28.2	10.21	Adult
2	2	4-30-84	M	14.1	103	13.1	24.7	9.55	2 yr
3	2	5-2-84	F	18.1	105	14.4	26.6	9.97	Adult

* Lost ear tags when recaptured on 4-10-84.

taken by a second trapper from 3 locations within the study area. The same trapper took 11 more during the winter of 1984-85, including several marked ones. I was unable to examine carcasses of these animals. Three beaver were captured and marked on Lake Elwell. None of these tags have been returned

No known age specimens were available from the area. Ages of trapped beaver were estimated by comparing values presented in the literature for each age class for weight, tail size, and width of zygomatic arch by Osborn (1953), Towsend (1953), Buckley and Libby (1955), and Patric and Webb (1960) with measurements of the captured animals. Age was calculated separately for each measurement and author. The values presented in Table 5.7 are strictly estimates: however, in most cases, most techniques yielded the same estimated age, increasing confidence in the results.

Five marked beaver were trapped by commercial beaver trappers since late 1984 (Table 5.8). Three were trapped within 2 km of their original capture site, 2 within 1 year of the original capture. One beaver, trapped in 1984 as a yearling 23 km below Morony Dam, was retrapped in December of 1987 on a tributary to the reservoir above the dam. This represents a direct line distance of 20.2 km or 33 km of waterway. To travel between these sites, the animal would have had to negotiate the cliffs or housing area at Morony Dam, or several kilometers of open farmland.

Table 5.8. Date of recapture and distance from release point for marked beaver taken by commercial trappers.

Beaver Number	Date of 1st Capture	Date of Recapture	Distance Moved	Comments
2	11-5-83	11-21-85	< 2 km	Weight 13 kg, Age 1 1/2
7	3-24-84	Fall 84	< 2 km	
6	4-9-84	Fall 84	unknown	
10	4-16-84	Fall 84	< 1 km	1 front leg missing, healed and fur covered
11	4-19-87	12-17-87	32 km	Trapped on tributary to river above Morony Dam

DISCUSSION

Colony Density

As with any technique, aerial cache counts are not without problems. Payne (1981) compared cache counts derived from ground searches, trapper information, and aerial counts from several different aircraft in Newfoundland. Counts conducted by Super Cub missed 39% of the caches. Hay (1958) found no difference between aerial and ground counts of caches. Swenson et al. (1983) reported aerial cache counts on rivers in central Montana ranged from 70 to 100% accurate. The low values were from areas with extensive overhanging vegetation.

On the Carter Ferry study area, no caches were located during ground searches that were not seen from the air. One small cache on Morony Reservoir was hidden by rocks and was not seen during the aerial count. Conditions on the study areas were generally excellent for spotting caches. Banks were seldom undercut and vegetation was usually sparse along the winter shoreline. The width of the river allowed good viewing along both banks.

Aerial counts of beaver colonies are further complicated if some active colonies do not build caches. Hay (1958) stated that beaver on the plains in Colorado frequently failed to build caches, though he reported no data to support this. Bissell and Bown (1987) reported 2 apparently active colonies with no food cache on the Flathead River in northwest Montana. On the Carter Ferry study area we maintained close contact with the various colonies and I feel that all active colonies built caches. Some caches were fairly small and past observers may have failed to recognize these as beaver caches.

In most studies, beaver densities are reported as number of colonies per length of water channel, or, in areas of extensive wetlands, as colonies per land area. For large lakes or reservoirs, where no well defined channel exists, densities are reported as colonies per length of shoreline. All 3 methods work for their respective conditions, are easily calculated, and allow comparisons between populations in different areas under comparable water conditions. Unfortunately, because each is related to a different measure of availability, we cannot compare between rivers, wetlands, and lakes or reservoirs. Even with different types of rivers, such as single channel or braided, comparing simple numbers per river mile may be misleading.

Beaver are shoreline animals. The area immediately adjacent to the land-water interface provides food, shelter, and protection, particularly on rivers, lakes, and reservoirs. Woody shoreline vegetation provides essential seasonal food, such as willows and cottonwoods, as well as building materials. On large bodies of water, beaver are dependent on the shoreline for shelter, be it a bank burrow, combination burrow and lodge, or as an anchor for a domed lodge. Although not all shoreline is suitable for the growth of the beaver's preferred food plants or the construction of burrows, the length of available shoreline is a better indicator of habitat availability than channel length or acres of land. Recent advances in technology allow easy calculation of shoreline length in even highly convoluted situations. By reporting colony densities by shoreline distance, we may compare densities in all types of habitat.

For the above reasons, I have reported densities of beaver colonies by length of available shoreline for all areas. I have included the values for colonies per channel length on river segments to allow comparison with previous studies. For reservoirs, colony density was also expressed by length of channel that existed under pre-dam conditions for comparison with nearby rivers.

Several authors have reported values for the density of beaver colonies under conditions similar to the study areas. Values vary from a low of 0.06 colonies per river kilometer on a stabilized section of the Missouri River in South Dakota (Vanden Berge and Vohs 1977) to 1.8 colonies per river kilometer on the upper Yellowstone (Swenson et al. 1983). Martin (1977) reported densities of beaver colonies on 11 stretches of the Yellowstone River from 0.31 to 1.24 colonies per river kilometer. Values for the current study on the Missouri River range from 0.07 to 0.76 colonies per river kilometer and for the Marias River from 0.11 to 0.53 colonies per river kilometer, both within the reported extremes.

The wide variation in colony density along the Missouri River may be due in part to differences in the river configuration and habitat quality. The lowest densities occurred between Pilot Rock and Slaughter River, a section known locally as the White Cliffs after the extensive sandstone cliffs that flank much of the river. This section has little in the way of floodplain or island habitat suitable to beaver use (Table 5.9)

Only 1 study has reported colony densities on reservoirs or large lakes, and this for only part of the lake. Bissell and Bown (1986) found 0.07 and 0.14 colonies per kilometer of shoreline at the north end of Flathead Lake in northwest Montana. Reservoirs on the Missouri River contained from no colonies to 0.17 colonies per kilometer of shoreline, while Lake Elwell contained 0.2 to 0.24 colonies per kilometer of shoreline.

Three of the 4 reservoirs immediately above the Carter Ferry study area, Morony, Ryan, and Rainbow, showed colony densities within the variation shown on the Missouri River, though at the lower end. The area between Morony Dam and Great Falls is a naturally steep and rocky section of the River and probably never supported high beaver densities. Given the rocky nature of the shoreline, the presence of any beaver is surprising. All 3 reservoirs are run-of-the-river projects, so extensive water level changes are uncommon and of short duration. There is little to no human access or shoreline development on any of the 4 reservoirs.

Of the 3 reservoirs surveyed near Helena, no beaver were found on Hauser Lake, and only 2 colonies on Holter Lake. Both are fairly rocky, though no more so than the Great Falls reservoirs, and are also run-of-the-river facilities. Both have extensive seasonal recreational use and some shoreline development concentrated in the low-relief areas. Four colonies were found on Canyon Ferry Reservoir, including 1 on an inlet and 2 at the head of the reservoir. Canyon

Table 5.9. Kilometers of available shoreline for segments of the Missouri River in central Montana by upland or channel classification.

River Section	Main-Steep	Main-Bench	Island	Back-water	Total
Morony Dam to Carter Ferry	28.5	27.4	5.3	0.0	61.2
Carter Ferry to Fort Benton	22.9	31.8	18.8	4.9	78.4
Fort Benton to Loma Ferry	15.5	42.0	35.8	8.5	101.8
Loma to Coal Banks Landing	24.1	47.5	31.3	0.8	103.7
Coal Banks to Pilot Rock	8.9	21.7	10.9	0.0	41.5
Pilot Rock to Slaughter River	39.3	47.2	8.1	0.0	94.6
Slaughter River to PN Ferry	15.6	25.3	6.9	4.0	51.8
PN Ferry to Dauphine Rapids	11.1	34.5	8.3	0.0	53.9
Total	165.9	277.4	125.3	18.3	586.9

Ferry is a flood control and irrigation reservoir, experiencing extensive yearly drawdowns. Between 1970 and 1983, the reservoir had an average yearly drawdown of 4.6 m and a maximum yearly drop of 7.3 m. Subimpoundments have been created at the head of the reservoir to reduce dust and the 2 colonies in that area may be utilizing these more stable water areas.

Densities on Lake Elwell range from 0.05 on the main arm to 0.10 colonies per kilometer of shoreline on the Willow Creek arm. These are generally lower than the Marias River directly below the dam, although the habitat appears to have been similar prior to the dam's construction. The existing shoreline is highly convoluted, generally steep, and subject to extensive erosion, limiting beaver habitat. Tiber Dam is a flood control facility, experiencing periodic and extensive changes in water levels.

From the standpoint of mitigation, the most interesting question is whether the current populations on Lake Elwell are comparable to the pre-dam conditions. If current conditions on the Marias River below Tiber Dam are comparable to the pre-inundation conditions above, we can estimate pre-dam populations of beaver. Maps and conservations with long-time residents suggest that conditions above and below the dam were similar prior to construction, although the dam does stabilize current water levels on the river below. Whether this has a positive or negative effect on beaver populations is unknown. Approximately 68 km of the Marias River channel was flooded by Tiber Dam. Using an average of 0.42 colonies per kilometer of channel, we can estimate that 28 colonies were originally displaced by the dam.

Currently, the main reservoir contains 12 to 13 colonies, or less than half the estimated pre-dam population.

Cache Location

The extensive cache counts conducted on the Missouri River during 1983-84 allowed comparison of the general location of caches with available shoreline conditions. Martin (1977) noted a extensive use of islands and braided river segments for caching on the Yellowstone and Bighorn Rivers, but no statistically significant difference between use and availability. On the Missouri River, caches were found significantly less often than expected on main river banks with steep uplands and more often than expected on islands.

Main banks with relatively steep uplands are the result of erosion. These banks are characterized by relatively fast and deep water near shore, making it difficult for beaver to anchor a cache, and generally unstable banks unsuitable for denning. During the 3 years of the study, I examined 5 caches adjacent to cliffs. All were associated with large rocks dislodged from the cliff. These rocks provided anchor points for the cache and protection from the full force of the water's energy. All 5 were within 0.5 km of ample food sources, often directly across the river. Only 2 had visible dens nearby, 1 dug into the loose soil of the cliff and 1 built of sticks wedged into a crevice in the rocks. The other 3 dens were not located.

All islands surveyed were built by deposition, resulting in generally low relief and loose bank material. Most contained extensive stands of willows, cottonwoods, and chokecherries. Much of the cottonwood regeneration observed on the Carter Ferry study area occurred on the upstream end of 2 of the large islands. The young cottonwoods were heavily used by beaver. In addition to a ready food supply, the loose soil of the islands provided excellent opportunities for denning. Most islands contained areas sheltered from the main flow of the river, protecting caches and dens.

Colony Size

Poor trapping conditions, coupled with increased commercial trapping pressure made our live trapping efforts only marginally successful. Two new trappers set up on the Carter Ferry study area during the study, a fact I learned only after the second season so I was unable to examine any carcasses.

A typical beaver colony is often perceived as a mated pair, young of the year, and yearlings born the previous year (Bradt 1938), yet many authors report variations ranging from single animals to groups containing additional adults or 2-year-olds (Bradt 1938, Towsend 1953, Taylor 1970, Bergerud and Miller 1977). Some of these variations may be due to differences in the definition of a colony.

Live trapping on the study areas was not intensive enough to determine total colony composition or size. However, the capture of kits at 2 colonies indicates that reproductively active colonies do exist, and at least 1 colony approached the typical pattern

(Table 5.10). The unrecorded removal of beaver by commercial trappers further clouded true colony composition.

Most studies of sex ratios in beaver reveal generally equal proportions at all ages (Osborn 1953, Henry and Bookhout 1969, Vanden Berge and Vohs 1977, Svendsen 1980). The apparent preponderance of females found in the Carter Ferry study area may be due to the personnel's inexperience in determining sex.

The number of individuals per beaver colony varies widely between areas, habitats, and even years. In an intensive study of colonies in Michigan, Bradt (1938) found from a single individual to 12 beaver per colony, with an average of 5.1. Swenson et al (1983) found average colony sizes of 5.2 to 9.2 on the Yellowstone and Tongue rivers in Montana. Of particular interest, they noted a drop from 9.1 to 6.1 beaver per colony in the same area over 2 years. Again, live trapping on the study areas was not sufficient to determine true colony size.

With the advent of marking of beaver in the 1950's, extensive information has been gathered on their movements. Many early studies focused on the movements of transplanted beaver. Beaver are capable of extensive movements, sometimes involving considerable overland travel. Hibbard (1958) reported that 1 transplanted beaver in North Dakota traversed 107 km (straight line) or 238 km of waterway, with an average travel for 18 recaptured individuals of 14.5 km of waterway. Berghofer (1961) reported movements of transplanted beaver in New Mexico of 6 to 51 km, including individuals that moved over a 3600 m divide, 4 major watersheds, and 1 who traversed at least 22 km of rough, dry land. Knudsen and Hale (1965) found no movement by more

Table 5.10. Minimal age structure and composition of selected beaver colonies as determined by live-trapping.

Colony Number	Adults	Subadults	Kits	Total
Carter Ferry				
1 (Fall 83)	2*	0	2	4
1 (Spring 84)	1	1	0	2
2	1	1	1	3
3	1	1	0	2
Lake Elwell				
1	1	0	0	1
2	1	1	0	2

* taken by a commercial trapper.

than 67% of the beaver marked during transplanting in Wisconsin with a maximum travel distance of 48 km (straight line). Beer (1955) reported a maximum natural movement of 50 km (straight line) or 65 km by water by beaver released at a capture site in Minnesota. Leege (1968) reported no movement by 34% of the 87 beaver recaptured after release at their original trap sites in Idaho. More than 21% moved more than 1.6 km, with an average straight line distance of 8.5 km and a maximum of 18 km. The longest recorded movement of a beaver released at its capture site was 241 km (Libby 1957).

Most beaver on the Carter Ferry study area were retrapped within 2 km of their release point. All were released at the point of capture. One yearling, captured in April of 1984, was taken by a trapper in December of 1987, 33 km by water from it's release point. Although the total distance traveled is not remarkable, the animal must have traversed several miles of cropland, negotiated the cliffs north of Morony Dam, or traveled through a dog-infested housing area at the south end of the dam.

IMPACT OF DAMS AND MITIGATION OPPORTUNITIES

IMPACTS OF DAMS

On rivers and reservoirs, evidence of beaver use of terrestrial habitat is common in areas with riparian shrubs and trees but unusual elsewhere. Shrubs and trees represent much of the beaver's food year-round, providing bark and cambium from fall to spring and leaves or buds during the summer. As expected, sites with shrubs and trees, and banks with characteristics conducive for shrub or tree development, are used more often than sites without.

Because beaver are unable to dam rivers and reservoirs, they do not create the classic domed lodge standing isolated in open water. Free-standing lodges would be lost to floods or ice scour almost every year. Instead, beaver rely on dens or hybrid den/lodge attached to the shore. Such dens are usually built on stable soil banks that are somewhat sheltered from floods and ice scour.

To determine the impact of dams on beaver and riparian vegetation, we must examine how dams alter the characteristics of the riparian zone. Three areas are affected by dams: the head of the reservoir pool and upstream; the reservoir shoreline; and the river below the dam.

All rivers and streams carry sediment, either in suspension or as bed load. The amount of sediment is controlled by the waterway's gradient and rate of flow. As a river enters the standing water of the reservoir, the flow rate decreases and sediments are deposited, forming a delta. Deltas tend to grow upstream, causing a decrease in channel gradient, reduced channel cross section, and increased flood occurrence (Glymph 1973, Baxter 1977, Thompson 1981, Sanchez 1982). The delta is heavily subirrigated, often sprouting dense thickets of willows and cattails (Typha sp). Such areas provide excellent beaver food, but because of their shallow nature, provide few den sites. Small drawdowns in reservoir levels lead to large expanses of mud flats. Any lodge or den would be totally exposed by even minor changes in water levels.

Dams cause substantial changes in habitat on the reservoir proper. With closure of the dam, low lying habitat along the waterway is flooded, destroying many riverine riparian zones (Heinzenkrecht and Paterson 1978, Thompson 1981). The resulting reservoir tends to have a greater length of shoreline than the pre-dam conditions or even a comparable natural lake (Baxter 1977), a characteristic which would seem advantageous to a riparian species like beaver. However, many reservoir shorelines are steep and rocky, providing little habitat for beaver, or their food species (Heinzenkrecht and Paterson 1978, Thompson 1981).

One of the most striking differences between natural and impounded waters is the change in the magnitude and timing of water level fluctuations on the reservoir. The degree of this change depends on the purpose and operation of the dam. Run-of-the-river dams may cause little to no change in fluctuations. Some hydroelectric facilities, particularly those designed to provide peaking power, cause diurnal fluctuations. Irrigation and flood control dams change seasonal fluctuation patterns, typically filling during the spring and early summer, followed by drawdown each winter. In the west, many reservoirs serve multiple purposes, commonly including some flood control.

Fluctuations on the reservoirs covered in this study varied widely. At Canyon Ferry Reservoir, a general purpose facility including flood control and irrigation, annual fluctuations in water levels between 1961 and 1986 averaged 5.1 m with a minimum of 1.9 m and a maximum of 10.2 m. Hauser and Holter dams, directly below Canyon Ferry, are run-of-the-river facilities used for power generation and recreation. Between 1961 and 1986, annual fluctuations on Holter Lake varied from 0.5 m to 5.6 m with an average of 2.2 m. Fluctuations of more than 2 m are sporadic. For the same time period, annual fluctuations on Hauser Lake varied from 0.1 to 5 m with an average of 1.7 m. Again, large fluctuations were uncommon.

Tiber Dam, on the Marias River, is primarily a flood control facility. Annual water level fluctuations from 1957 to 1986 varied from a maximum of 10.3 m to only 1.4 m with an average of 5.0 m.

Fluctuations on the 5 run-of-the-river dams near Great Falls on the Missouri River ranged from 0.5 to 4.5 m in 1983. The 4.5 m fluctuation was due to repair work.

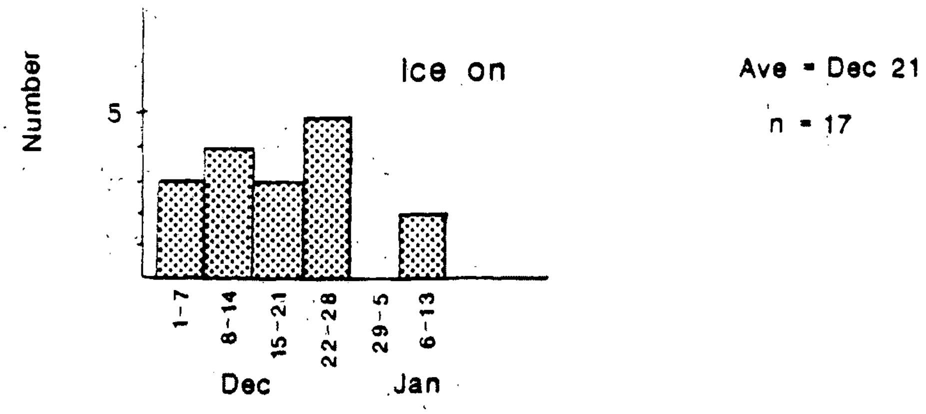
The direct impacts of fluctuations may be extensive. The effect of fluctuations is somewhat dependent on the bottom contours of shoreline areas (Heinzenkrecht and Paterson 1978). Shallow areas are dewatered by minor level changes while steep slopes may retain their basic shape and character despite large fluctuations. Seasonal changes on some flood control reservoirs are extreme. Lake Koocanusa, in Northwest Montana, varies by up to 50 m each year (Thompson 1981). Under such extensive fluctuation regimes, beaver cannot maintain underwater entrances to any den or lodge.

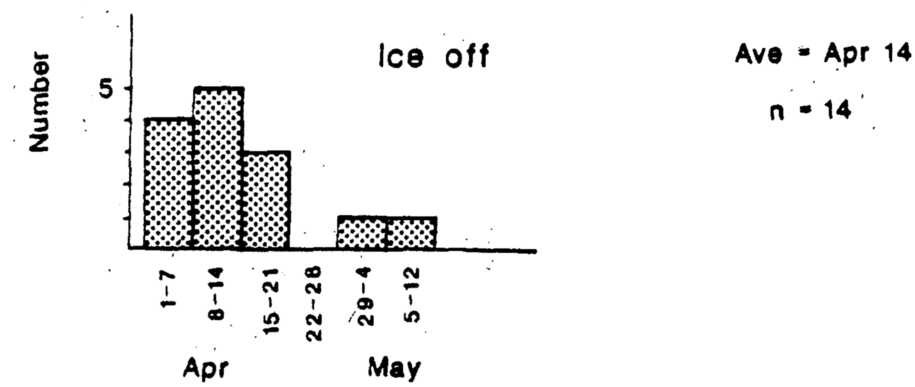
The change in magnitude and timing of fluctuations may, in turn, affect vegetative development of the riparian zones on reservoirs when compared to rivers. Rapid fluctuations or large-scale drawdowns tend to inhibit the establishment of perennial riparian species and favor annuals (Fowler 1978). The effect is greatest when major fluctuations occur during the growing season (Thompson 1981).

Large reservoirs are particularly susceptible to massive erosion caused by wind and wave action. Large flooded areas and windy climates can lead to intense wind-wave regimes, which in turn leads to shoreline erosion and bank failure. The degree and impact of erosion is determined by topography and substrate. Headlands and exposed sites are quickly eroded, and the material redistributed into sheltered areas (Halstead 1973). Massive erosion is common along reservoirs with loose, cohesionless banks (Mikhailov et al. 1982). Weathering alone can cause erosion with certain types of clayey soils (Mikhailov et al. 1982). Mass failures on rock-edged reservoirs depend on the structure, orientation, and composition of the rock (Innerhoffer and Loacker 1982). Shoreline erosion leads to the development of unstable cliffs on exposed sites and general retreat of such cliffs inland (Halstead 1973). The erosion of ravine mouths due to changing water levels may lead to further headwall erosion in those ravines (Mikhailov et al. 1982). Any erosion reduces riparian vegetation and decreases the opportunities for beaver to maintain bank dens.

Reservoirs in northern climates tend to freeze over during winter (Thompson 1981). Ice prevents terrestrial animals from using the water and semi-aquatic species, such as beaver, from easy access to terrestrial foods. Beaver are adapted to survive long periods under ice, but other species, such as waterfowl and bald eagles, will be excluded from using the area during the ice-covered periods. On Lake Elwell, dates of ice formation and break up were recorded for some of the years between 1958 and 1964. Ice formation was generally complete by late December and lasted into late spring. For the 13 years in which the total duration could be determined, the average duration was 109 days (Figure 6.1). Ice break up and scouring in spring, particularly on run-of-the-river reservoirs, may inhibit or destroy riparian vegetation.

Although often overlooked in discussions of reservoir impacts, associated human development may create long-term detrimental impacts on wildlife. Impounded water tends to attract human settlement and development, which can lead to deforestation, overgrazing, and removal of animals when in conflict with human uses (Blairs 1972, Williams 1973, Heinzenkrecht and Paterson 1978). Even moderate grazing may destroy newly developed woody vegetation. Where reservoirs become resort areas, the beaver's cutting of trees and shrubs is in direct conflict with human aesthetic values.





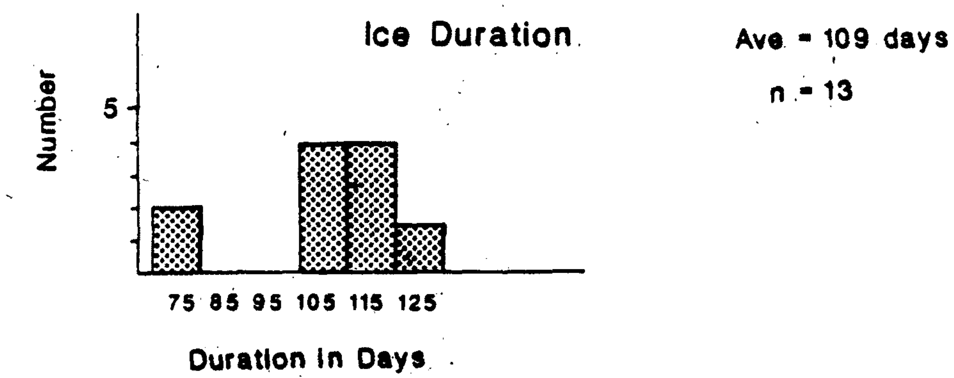


Figure 6.1. Dates of ice formation, melt off, and duration for Lake Elwell, 1958 to 1984.

The impact of dams on the river below may be as great or greater than on the reservoir proper. As on the reservoir, the main effects relate to changes in erosion/deposition and fluctuations.

As mentioned earlier, water, upon entering the reservoir, looses much of its sediment load. The longer the water remains within the reservoir, the clearer it becomes. Water released below any dam carries a sediment load well below the capacity of the now-flowing water. The river will quickly re-establish the sediment load balance, causing erosion, channel degradation, and headwall cutting in tributaries (Boundrant and Livesey 1973, Glymph 1973, Taylor 1978, Thompson 1981, Harrison and Mellema 1982). The river scours its bed for material, removing the finer materials until only large materials are left. When all materials are too large to be moved by the river's flow, the channel becomes armored and erosion extends downstream (Taylor 1978, Harrison and Mellema 1982). Through this process, impacts of the dam may be felt far downstream. Taylor (1978) reported that erosion below Hoover Dam had extended more than 1.6 km (1 mile) downstream after only 6 months and erosion below Parker Dam had extended 96 to 160 km (60 - 100 miles) downstream since closure.

Downstream erosion tends to deepen main channels, restricting flow to those channels and eliminating braided channels, meanders, and even some islands. These areas represent some of the most productive riparian habitat. Deep cutting of channels reduces opportunities for bank denning and lowers water tables, reducing growth of riparian plants (Fenner et al. 1985, Harris et al. 1985, Swenson and Mullins 1985).

Dams often affect water levels and fluctuations downstream. With initial closure of the dam, there is a drastic decrease in instream flow, often remaining at legal minimums year-round. Depending on the size of the reservoir, this may continue for years. Increased evaporation, seepage into porous layers, interbasin transfers, and irrigation cause permanent losses to the river's flow (Heinzenkrecht and Paterson 1978).

After the reservoir is full, operation of the dam continues to alter the river's natural flow regime by changing the timing and amplitude of water level fluctuations. The degree of change depends on the purpose of the dam. Run-of-the-river dams, by definition, have little effect on downstream flows. Most other dams have at least some flood control or irrigation objective. By design, these facilities reduce the incidence and magnitude of floods downstream (Ridley and Steele 1975, Thompson 1981, Harrison and Mellema 1982, Fenner et al. 1985). Some reservoirs also increase low flows, usually related to minimum flow requirements. For example, Harrison and Mellema (1982) reported that, before the development of flood control reservoirs on the Missouri River, flows ranged from 209 to 29,000 cubic meters per second. Now, the low remains the same but peaks reach only 1700 cubic meters per second. During the 1964 flood on the Marias River, the maximum flow above Tiber Dam reaches 241,000 cfs while below the Dam, the flow only reaches 10,100 cfs (Figure 6.2). Reduced flooding should improve denning success for beaver.

Eighteen major dams effect water flows on the Missouri River above Fort Benton, Montana. Natural fluctuations in water levels tend

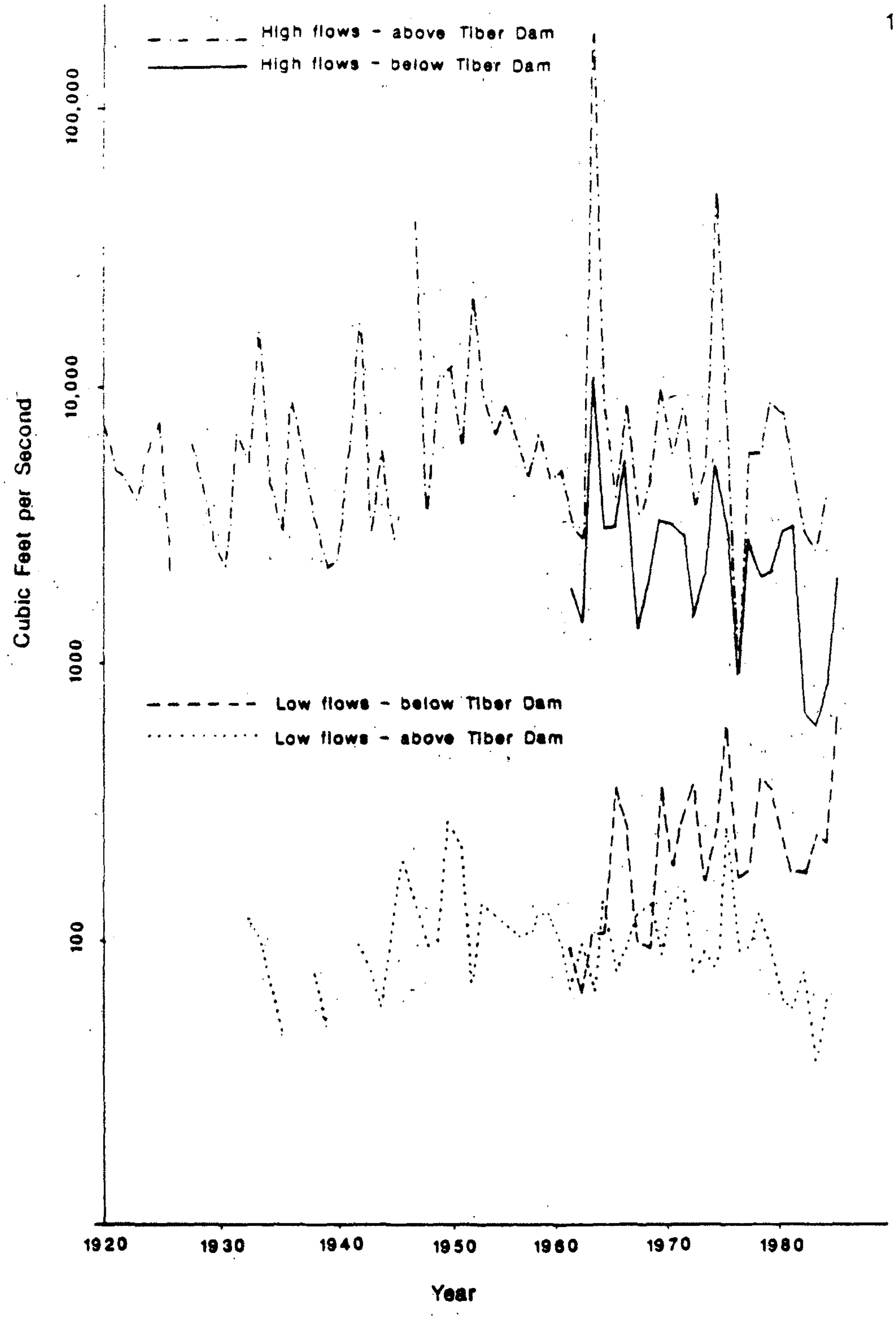


Figure 6.2. Annual maximum and minimum flows for the Marias River at Shelby above Tiber Dam, and Chester, below the Dam in cubic feet per second.

to mask the actual impact of these dams on high and low flows. However, Figure 6.3 shows a general increase in low flows and decrease in high flows as more dams were constructed along the River.

Changes in flooding may have major effects on woody riparian vegetation. Floodplain forests are often considered pulse-stabilized systems. Such areas are held in a state of continual disclimax by periodic flooding, which provides optimal habitat for the establishment of willows and cottonwoods (Baxter 1977, Thompson 1981, Fenner et al. 1985). These species reproduce poorly where they are the overstory dominate. By reducing flood peaks, thereby reducing scouring and the creation of deposition areas, dams may reduce the growth and increase mortality of seedlings and saplings of such species (Thompson 1981, Harris et al. 1985, Swenson and Mullins 1985).

Dams also alter the timing of seasonal fluctuations. In Montana, rivers typically show a discharge peak in May or June, followed by lows in late summer to winter, depending on rainfall. Below dams, discharge peaks are often delayed and may remain high into or through the summer season. The seeds of some riparian trees, such as the Fremont cottonwood (Populus fremontii), remain viable for a very short time and require newly exposed moist sites to germinate. Fenner et al. (1985) demonstrated that the timing of seed release in the Fremont cottonwood corresponds to the optimal time in the Salt River's natural water cycle for seedling germination. The existing dams alter the water level regime downstream, maintaining high water through the germination period thereby severely restricting opportunities for cottonwood reproduction.

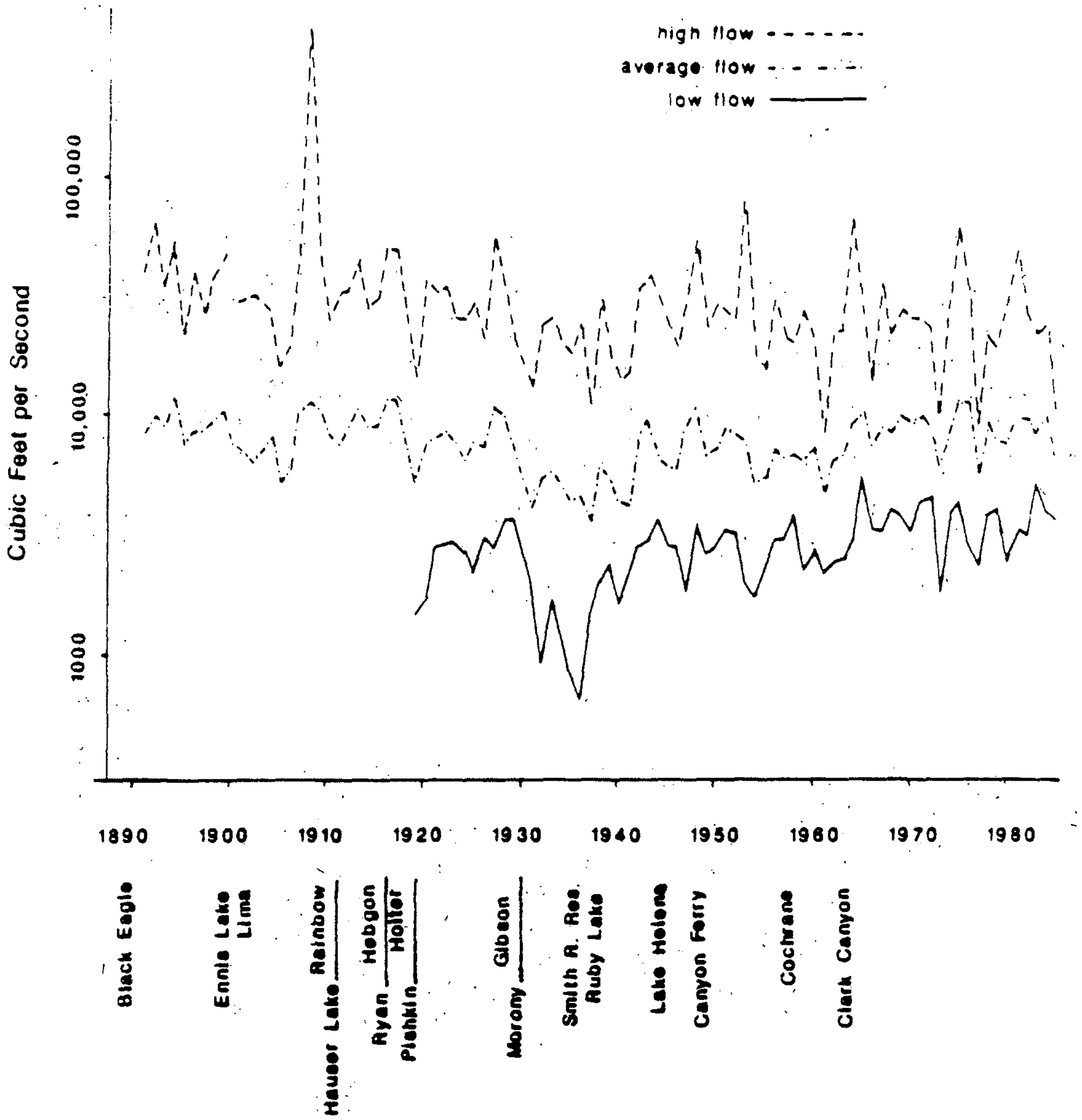


Figure 6.3. Annual maximum, minimum, and average flows on the Missouri River at Fort Benton, Montana, in cubic feet per second with the date of construction for major upstream dams.

Some dams create substantial fluctuations in downstream rivers on a daily, or even hourly, basis. Such fluctuations are uncommon on unimpounded rivers with forested headwaters. Libby Dam, in Northwest Montana, exhibits downstream fluctuations 10 to 12 times greater than pre-impoundment conditions. At some power peaking facilities, such variations may occur several times each day (Thompson 1981).

The impacts discussed above represent only those changes caused by dams in riverine systems that affect beavers or their riparian food source. Any change which destabilizes banks, reduces woody riparian vegetation, or creates violent short-term fluctuations in water levels will reduce the suitability for beaver.

MITIGATION STRATEGIES

Mitigation proposals can be divided into 2 basic types, on-site and off-site. On-site mitigation involves recreating the conditions necessary for a species' or community's survival within, or directly adjacent to, the project boundaries. Off-site mitigation often involves purchasing, protecting, or occasionally enhancing wildlife habitat at some distance from the project. This is a viable approach to wildlife management but does little to replace losses to local populations. It should be utilized only when conditions preclude on-site mitigation. Therefore, the following discussion concentrates on on-site proposals.

The primary negative impact of dams and reservoirs on beaver habitat relates to the loss of stable denning sites and riparian vegetation. The following mitigation proposals are designed to mitigate one or both of these problems.

Under certain conditions, simply replanting riparian zones along the reservoir shoreline may be possible. Most riparian shrubs and trees require high levels of soil moisture within reach of their roots during at least the growing season to survive (Broadfoot 1973, Fenner et al. 1984, Harris et al. 1985). Where low flat shorelines combine with relatively stable water levels, vegetation may be successfully replanted. Swenson and Mullins (1985) and York (1985) had the best results with large, pole-size cuttings taken when the trees were in a dormant state. Poles were planted to the depth of the water table during the growing season. Fresh growth is attractive to cattle and beaver. Both should be excluded to the degree possible until the stands are well established.

Where slopes are too steep to provide suitable subirrigated zones of usable width, slopes could be terraced. Smaller riparian shrubs, such as willows, could be planted on the first terraces, large shrubs or trees planted to an appropriate depth on higher terraces, and more drought tolerant species on the highest terraces. Again, beaver and cattle should be excluded until the plants are well established. For new dams, vegetation might be planted prior to filling the reservoir, although it will be necessary to irrigate the plantings until the water level rises.

The impact of reservoir level fluctuations on vegetation and beaver denning could be mitigated by controlling the amplitude or timing of such fluctuations (Seaman 1973). The yearly amplitude of water level fluctuations on reservoirs is directly controlled by the reservoir's operating mandate. In many cases, altering the fluctuation by an appreciable amount is unfeasible on the reservoir as a whole. However, it might be possible to alter timing to conform more closely to natural conditions.

While we often cannot alter water level fluctuations on an entire reservoir, we might stabilize levels in localized areas by taking a lesson from the beaver. Beaver control water levels on streams and ponds by building dams. Small dikes or dams could be built across the mouths of streams or coulees that enter the reservoir, near their original river entry. The dams would rise to the level just below normal full pool elevation. At full pool, the area would be flooded. As reservoir levels dropped, water would remain trapped behind the dam. With perennial streams, the level might remain stable throughout the year (Figure 6.4). In areas with high soil erosion, such as the arid farmlands of central Montana, these miniature reservoirs would fill with sediment. Dams could be designed to allow periodic flushing or the area could be allowed to develop riparian shrubs and trees as a food source. A series of small dams could be built along perennial streams, the lower ones providing den sites, the upper ones food.

On large reservoirs in windy climates, wind and wave erosion may be the major limiting factor for both vegetation and den sites. Erosion causes problems for all aspects of reservoir management. When designing new facilities, wind direction and reservoir shape should be carefully evaluated. On existing facilities, or where no other options exist, erosion may be reduced by creating natural analogs to

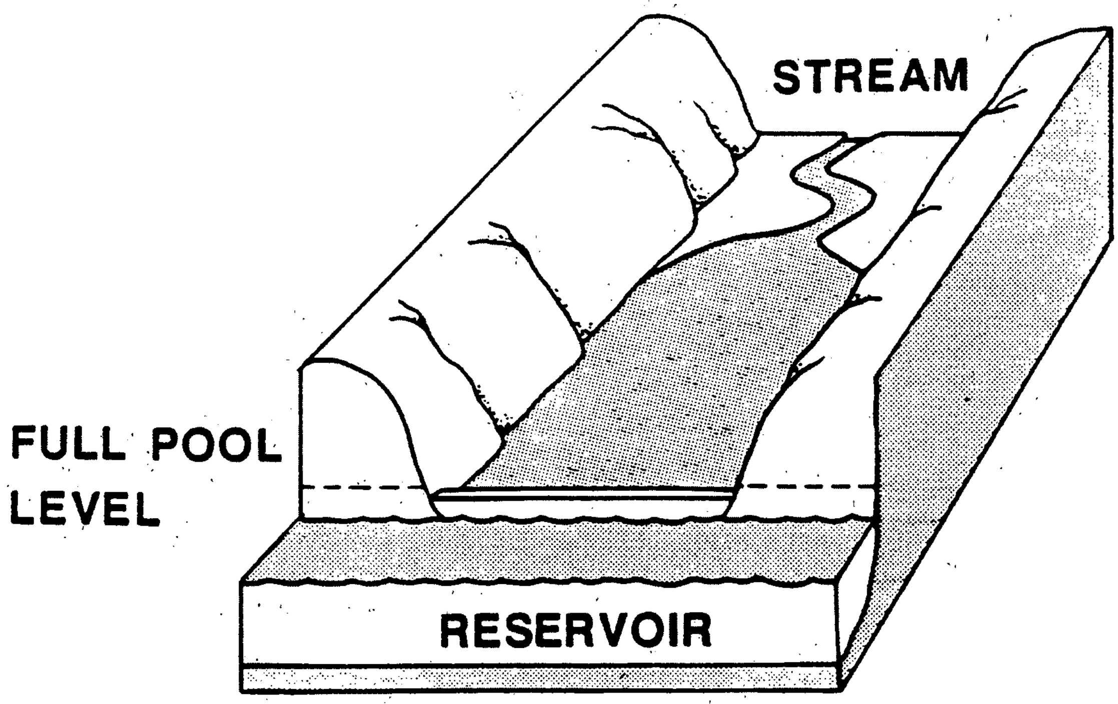


Figure 6.4. Potential for use of dikes or small dams to stabilize water levels on side channels of reservoirs.

the coastal barrier islands (Mikhailov et al. 1982). Such islands can be designed to require low maintenance. Barrier islands dissipate the wave's energy, protecting the shoreline.

When increased human use is in conflict with wildlife values, a variety of solutions exist. If wildlife is the primary interest, the entire reservoir could be closed to human use. Realistically, this is seldom possible. In some areas, human use is restricted during critical periods, such as for waterfowl nesting. Coordination between recreation and wildlife mitigation plans could reduce conflicts in sensitive areas. Reserves could be created along reservoirs to reduce conflicts with humans.

Grazing can have severe impacts on riparian vegetation and bank stability. Cattle are drawn to water and to the shade provided by trees and shrubs. On the plains, this may be the only shade available. Even lightly stocked range may have problems with cattle in riparian zones because of the tendency for livestock to congregate in such areas. To maintain healthy riparian zones, it may be necessary to fence the shoreline, while providing water and shade away from the reservoir.

Downstream impacts may be mitigated by controlling the magnitude and timing of releases from the dam. Major short-term fluctuations, as seen below power peaking facilities, may be controlled during critical seasons. Where the lack of flooding has reduced the survival of riparian trees and shrubs, artificial floods could be created. Releases could be designed to cause moderate flooding on downstream floodplains at appropriate times of the year. Unfortunately, human development on floodplains will prevent artificial flooding in most areas.

Reservoir mitigation is an infant field, with little yet in the way of completed projects to evaluate. We can look to a few natural examples for preliminary ideas. As these ideas are refined and implemented, we can begin to assess the success of particular programs. Because of our lack of knowledge, including evaluation procedures in all mitigation plans is important so we may learn from success and failure. Beaver again provide an excellent indicator for evaluating riparian zone mitigation. This is not to imply that beaver are a panacea. They are useful for only one aspect of reservoir biology, shoreline conditions. They should be part of a package of indicators for different aspects of reservoir mitigation.

While not the final answer, beaver can provide a valuable addition to our tools for wildlife habitat management. As agencies become more involved in developing, implementing, and evaluating mitigation plans, the use of beaver as a mitigation indicator species should be seriously considered.

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