AN INVESTIGATION OF THE FACTORS AFFECTING CARRYING CAPACITY OF SELECTED AREAS IN NEWFOUNDLAND FOR THE BEAVER, CASTOR CANADENSIS CAECATOR BANGS, 1913

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by

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ABSTRACT

Factors which influence the carrying capacity of habitat for beavers, _Castor_ _canadensis_, in Newfoundland were investigated in two study areas of dissimilar habitat types. One area had served previously as a study area for other aspects of beaver ecology and here tagged beavers with known territories were an aid to the present study.

Topography determines the type and availability of water for beaver colonization. Highest densities in Newfoundland are found in areas where many small ponds and streams of gradient less than 3 per cent occur in conjunction with hardwoods. Alder is the most important plant species, both as food and as building material. More than 90 per cent of all tree species cut are in the 1 - 3 inch diameter class. Aquatic vegetation, particularly the water lily, is the major constituent of the beavers' summer diet.

Logging and forest fires are beneficial to beaver since they create conditions necessary for an invasion of hardwoods. Most species of vegetation flooded by beavers are killed in one or two years. Abnormal fluctuating water levels, as found in areas of logging operations, normally precludes beaver occupancy of these areas.

Competition by moose and muskrat on aquatic

vegetation is relatively heavy, but does not adversely effect the beaver. Moose browsing of alder is the only serious competitive influence to beavers and may cause colony abandonment. Main cause of abandonment is lack of food. Harrassment by man or natural predators does not normally have a serious effect on the colony.

Factors determining size of colony territory are: type of water, availability of food, age of colony and intra-specific conflict. These combine to determine the population density of any area. Scarcity of food caused much summer movement in one study area. Census counts from 1958-1963 revealed that beavers adjust their numbers to keep the population in balance with a changing food supply.

Maximum carrying capacity of Newfoundland beaver habitat is probably 1 active lodge per square mile. A carrying capacity index of high, medium and low (1, .5 - 1, and $<$ .5 active lodges per square mile) is suggested. Three habitat types are proposed with the water and food requirements and population potential of each.

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INTRODUCTION

The beaver, Castor canadensis caecator (Bangs) 1913, has been important to the economy of Newfoundland since the beginning of the 19th century. The sale of pelts provided considerable revenue during the early development of the Province. Except for several isolated areas on the Avalon Peninsula, beavers were practically exterminated from the island by 1935 because of excessive trapping and poaching. A live-trap and transfer programme was begun in 1935 when 68 beavers were trapped on the Avalon Peninsula and released in various parts of the Province. During the next ten years 1,000 beavers were live-trapped from the Avalon. The programme proved highly successful. The first trapping season in 23 years was declared in 1946.

Government sponsored research on the biology and economics of the beaver was begun in 1955 and has continued to the present. The object of beaver management is to regulate the beaver population through controlled trapping to provide maximum harvest for trappers. A management programme for beaver can logically be divided into three aspects: (1) determination of the population characteristics of the beaver (reproduction rates, mortality, etc.), (2) carrying capacity investigations, and (3) studies of harvest management.

From 1957-1960, Miller (1960) conducted a three-year study of beaver in a 15 square mile study area in central

Newfoundland. His investigations dealt mainly with the first and third of these divisions. During the summers of 1961 and 1962, and during the fall of 1963 I carried out investigations on the carrying capacity of Newfoundland beaver habitats. The study was conducted in central Newfoundland (including Miller's study area), and on New World Island, (Fig. 1). Other areas of the Province, while not receiving the detailed investigation of the two major study areas, were visited in connection with this study. These areas also appear in Fig. 1.

Carrying capacity (maximum number of animals which can be maintained indefinitely on a given area - Wildlife Investigational Techniques, 1963) of any area for beaver may be generally considered a matter of available food, available water and size of individual territories of each beaver colony. Also contained within these broad categories are many interrelated factors.

I classified this study into the following categories:

(1) Habitat Relationships

(2) Vegetation Studies

(3) Population Studies

I have similarily divided the reporting of my results into these categories.

DESCRIPTION OF STUDY AREAS

GRAND FALLS

Topography and Cover

Soils in the 15 square mile study area are generally coarse textured podzols developed from bouldery undulating material (Shaw, *et al.*, 1955). Rock outcroppings are common and in some locations form small narrow ridges. The gradual rolling topography varies from 100 feet above sea level with several elevations reaching 450 feet. Numerous bogs are spread throughout the area. Three main stream systems drain the area.

The northern part of the area, which escaped an extensive fire in 1922 supports dense stands of tall white birch, *Betula papyrifera* Marsh, on the ridges. White spruce, *Picea glauca* (Moench) Voss, intermingles with the white birch down the slopes. Aspen, *Populus tremuloides* Michx., is found in small patches on some of the slopes, together with pin-cherry, *Prunus pennsylvanica* L., willows, *Salix* spp., and red maple, *Acer rubrum* L. Balsam fir, *Abies balsamea* (L.) Mill., is not common. Black spruce, *Picea mariana* (Mill.) BSP., and tamarack, *Larix laricina* (Du Roi) K. Koch, comprises most of the crown cover in the lowlands, mixed occasionally with a few white birch and white pine, *Pinus strobus* L. The intermediate cover is predominately alder, *Alnus rugosa* (Du Roi) Spreng, and *Alnus crispa* (Ait.), white spruce, black spruce and tamarack. Wild pear, Amelanchier bartramiana (Tausch) Roemer and viburnum, Viburnum cassinoides L., are common intermediate cover plants. Other shrubs of importance are hazelnut, Corylus cornuta Marsh, cranberry viburnum, Viburnum trilobum Marsh, and redosier dogwood, Cornus stolonifera Michx.

In the southern portion of the study area white spruce regenerated following the 1937 fire. Tall dead white pine are scattered throughout the area.

Ground cover consists mainly of the Ericaceaus plants - leatherleaf, Chamaedaphne calyculata (L.) Moench, sheep laurel, Kalmia angustifolia L., pale laurel, Kalmia polifolia Wang., labrador tea, Ledum groenlandicum Oeder, rhodora, Rhododendron canadense (L.) Torr., and blueberry, Vaccinium angustifolium Ait. Other important plants are sweetgale, Myrica Gale L., spirea, Spiraea latifolia (Ait) Borkh., shrubby cinquefoil, Potentilla fruticosa L., sedge, Carex rostrata Stokes, bullrush, Scirpus spp., rush, Juncus spp., water birch, Betula michauxii (Spach), and the pitcher plant, Sarracenia purpurea L. Many species of lichens and mosses are also found.

Aquatic plants are plentiful and are found in all the major ponds and lakes and in the slow waters of the brooks.

Numerous small ponds and a network of streams makes this area excellent beaver habitat (Table 1).

The Grand Falls study area may be considered a wilderness area. It is accessible only by rough foot trails. Several small fishing cabins are scattered throughout the area and these cabins are infrequently but regularly used during fishing and hunting seasons . Other than this, there is no disturbance of the wildlife of the area.

NEW WORLD ISLAND

Topography and Cover

New World Island with an area of 69 square miles, consists largely of folded and faulted sedimentary and volcanic rock (Williams, 1963). There are many rough small hills, small ponds, short streams and large areas of bog and exposed rock. The topography is one of roughness and irregularity. No point on the island is more than two miles from the sea. The highest elevation is 300 feet above sea level.

There are no large forests on the island. Small, usually stunted, spruce and fir occur over much of the island and form a very dense growth, with an occasional interspersion of birch, on the slopes of the hills. On level ground and around edges of numerous bogs, less dense growth occurs. Aspen is rare on the island. Birch is available in limited quantities. Hardwoods are generally less abundant than in the Grand Falls study area.

Alder comprises the major intermediate cover but is less abundant than in the Grand Falls area. Dogwood and wild pear are also important cover shrubs. Only dogwood occurs more frequently than in the Grand Falls area.

Ground cover throughout the island is comprised mainly of Ericaceaus vegetation. Sedges, rushes, mosses and lichens are common. Aquatic plants are found in the ponds but are usually not found in the streams because of the fast water.

Most of the streams are unsuitable habitat for beaver because of fast water. Ponds represent the only available beaver habitat. Table I presents the type and availability of water.

Approximately 5,000 people live in the 31 communities scattered around the coastline of New World Island. One much travelled secondary gravel highroad traverses the island. The usual practice of cultivating vegetable gardens and grazing animals on every available grassy field is found here. The wide-spread cutting of trees for fuel has caused a general degradation of many former forested areas.

METHODS OF STUDY

The names of plants and animals appearing in this thesis are from Gray (1908), Fassett (1940), Rouleau (1956), Bangs (1913), Cameron (1958) and Peters and Burleigh (1951).

(A) Habitat Relationships

Type and Availability of Water

To determine the availability of water in the study areas, a small fixed wing aircraft was used, flying grid lines ¼ mile apart at approximately 60 miles per hour. The number of lakes (> .5 miles long), ponds (< .5 miles long) and bogs were recorded on aerial photographs and 1:50,000 topographical maps. Colony locations were plotted on the photos and maps. Stream mileage was measured from the maps following the plotting of exact stream origins while flying.

Stream Gradient

Stream gradient was calculated from contoured 1:50,000 topographical maps. The gradient of short streams was measured in the field using a Brunton compass (pocket transit) and standard leveling techniques.

Fluctuating Water Levels

To determine the extent of beaver colonization on logging rivers, two rivers were flown with the light aircraft. The flight lines followed the course of the river from its mouth to its headwaters. Five flight lines were flown for each river, one to observe the river and the others to observe the zero to .25 miles and .25 to .5 mile-wide strips along each side of the river. The locations of beaver lodges were plotted on 1:50,000 topographical maps.

Certain sections of the rivers and some of the ponds were also covered by canoe to determine if signs of former beaver occupancy, not observable from the air, were present.

Permission to operate one of the dams and gates of a logging system was given by the Anglo-Newfoundland-Development Company Limited. The dam was closed for a week and the rise in lake level measured by a long calibrated pole inserted in the lake bottom. The head of water was then released by opening the dam.

Effects of Logging on Forest Succession

Forest composition in old logged areas, new logged areas and unlogged areas all within one general forest type, was recorded from aircraft circling above the area long enough to determine the general forest composition below. Photographs were taken and studied later. Composition of the forests regenerating in some old logged areas was also determined by ground transects.

Effects of Fire on Forest Succession

The tree species regenerating after fire was studied by determining the species composition in two areas of the Grand Falls study area burnt in 1922 and 1937. Another area south of Lewisporte had been burnt in 1954 and transects through this area gave the composition of the regenerating forest soon after fire.

Colony Abandonment

Three possible causes of colony abandonment were investigated:

1. Lack of food,
2. Competition for food,
3. Harassment by man or natural enemies

(1) Lack of Food

The method of approach to the investigation of food utilization and availability is similar to that used by Hall (1960) in California. At 100 feet intervals around two inactive colonies, transects 10 feet wide were run from the water at right angles into the forest for a distance of 600 feet. (Six hundred feet was chosen because food is rarely obtained at distances greater than this.) Each transect was subdivided into 10 foot blocks. This permitted an analysis of distance from water to intensity of cutting relationship.

For each 10 foot square of each transect, the following information was recorded - number and stump diameter of each species present, - number and stump diameter of each species cut, - number of each species which had been browsed by moose, *Alces alces americana* Clinton and snowshoe hare, *Lepus americanus struthopus* (Bangs) 1913.

The two inactive colonies studied were chosen deliberately because of their isolation.

(2) Competition for Food

General field observations determined which of the species of animals using vegetation as food were competitors for beaver food.

The individual transect method described under lack of food, gave the intensity of moose and snowshoe hare browsing on beaver food. In addition to the investigations for the two inactive colonies, five active colonies, chosen randomly, were similarly studied.

(B) Vegetation Studies

Cover Mapping of Study Areas

Using the light aircraft and flying transects .25 miles apart at speeds of approximately 60 miles per hour and altitudes of 200 to 500 feet, I compiled cover maps of the study areas. Cover categories were: bare ground, bog, closed canopy aspen, closed canopy birch, mixed hardwoods, hardwoods-conifers and conifers. The preliminary flight mapping was done on 1:50,000 topographical map sheets. Drafted maps were later produced and are presented in Figures 2 and 3.

Food Habits and Factors of Utilization

Factors of food utilization investigated were:

1. Availability
2. Stocking and forest type
3. Diameter size preference
4. Distance from water
5. Slope of ground
6. Competition

Availability

Availability of food was studied by counting the available and utilized stems of each food species present in ten-foot wide block transects as already described under Colony Abandonment of Section A. The total stems of a species cut was expressed as: (a) percentage of that species cut, (b) percentage of the total cut.

Stocking and Forest Type

The intensity of cutting in areas of closed canopy aspen, closed canopy birch, mixed hardwoods and hardwood conifers, was determined by stem counts of utilized and available trees of a species. These studies were by 1/100 acre plots.

Diameter Size Preference

To determine the diameter of trees, a d.b.h. (diameter breast high) tape was used. The diameters then can be read directly from the tape when the tape is placed around the circumference of the tree. The measurements were made at the base.

Distance From Water

Distances from water to all observed regular cutting areas were measured along the food trail route. Distances from the water to sites of single or very limited cutting outside the regular cutting sites were measured in a straight line in the absence of a well-defined food trail.

A 100-foot cloth tape was used for measuring. Data recorded was: - distance from water,

- species cut
- diameter size cut

Slope of the Ground

The slope of all food trails to regular cutting areas was measured by Brunton compass. The clope of ground traversed in cases of single or limited cutting was measured. Data recorded was: - slope of ground

- species cut
- diameter size cut

Competition

General observation indicated whether competition for food influenced the beaver's choice of food. A more detailed investigation of the effects of moose competition was possible by counting stumps of the tree species cut in the Grand Falls area (where moose are plentiful) and by stump counts on New World Island (where there are no moose).

Seasonal Foods

A quantitative study of aspen utilization was carried out by painting stumps in the feeding areas with a spray can of red automobile paint. Periodic visits were made to these areas to record and paint new cuttings.

Summer foods utilized were investigated by:

- weekly visits to each colony to record the new cuttings.
- recording species and frequency of occurrence of chewed scraps of vegetation floating on the water of the colony.

Thirty complete water lily plants were dug from the pond bottom in depths up to four feet by reaching over the side of a canoe or standing in the water. The plants were measured, weighed and the leaves counted to assess their potential as a beaver food.

Winter foods were determined by tree cutting counts and by investigation of winter food piles.

Effects of Flooding on Vegetation

Miller (1960) had two known-age colonies in the Grand Falls study area, I located another. During the period of my investigation I paid monthly visits to these colonies and recorded any new deaths in the flooded vegetation to determine the time required to water kill various tree species.

(C) Population Studies

Size of Colony Territory

Factors investigated as possibly influencing territory size were:

- topography, water type and availability
- vegetation
- intra-specific conflicts
- inter-specific conflicts
- age of colony

Topography, Water Type and Availability

Area of colony territory was determined by observation of cutting sites, food trails and location of dams repaired by the beavers. Miller (1960) had determined many colony areas by live trapping. Measurement (by 100 foot cloth tape) was made of colonies on streams, ponds and lakes. The availability of extra water (in the form of stream sections or adjacent ponds), for territory expansion was recorded. In the case of stream colonies the distance to the next stream colony was measured. Overland distances between colonies was measured.

Vegetation

For each measured colony the surrounding forest composition was determined by ground transects. Food species present were recorded.

Intra-Specific Conflicts

General observation suggested the degree of tolerance one beaver family has for another.

Inter-Specific Conflicts

Size of beaver territories in areas where moose are found was compared with territory size in moose free areas.

Age of Colony

The known-age colonies in the Grand Falls study area were re-measured each year to determine the amount of territory expansion.

Movement of Tagged Beavers

Miller had live trapped and tagged beaver in the Grand Falls study area from 1957-60. The study area was completely trapped out in the spring and summer of 1962. Bailey live traps were used. The tagged beavers were killed since many of them were of known age and valuable for further investigation. A compilation was made of the movement data of 14 tagged beavers. The untagged animals were released outside the study area. One group of five was released on an island.

Population Stability

The light aircraft was used to conduct the fall census of the Grand Falls study area from 1958 to 1963. The area received 100 percent coverage. The area is small enough (15 square miles) to permit a water-course census method. It is often necessary to circle above heavily populated areas to ensure accuracy in plotting all inactive and active beaver lodges. Lodges were plotted on 1:50,000 topographical map sheets.

RESULTS

(A) Habitat Relationships

Type and Availability of Water

The water type most colonized on New World Island is the pond. Sixty-three percent of the colonies are located on ponds. In the Grand Falls study area 67 percent are on streams. Table I shows the relation of water type and availability to colony location.

Fluctuating Water Levels

The Rattling Brook main river system is approximately 50 miles long. The Noel Paul River system is 60 miles long. The distribution of beaver lodges along these river systems (Table 2) indicates that abnormal fluctuation of water levels is a deterrent to beaver colonization.

Effects of Fire and Logging on Forest Succession

Succession after logging is often favourable to beavers. After fire it is nearly always favourable. The extent of the fire, or area logged, and composition of other adjacent forest types is the qualifying factor. Table 3 presents the regeneration pattern. Table 4 lists the stable and unstable forest types normally occurring in Newfoundland.

Colony Abandonment:

The availability of food species as shown for the two inactive colonies (Table 5) suggests that normally the food supply is at a very low state before abandonment occurs. Table 5 should be compared with Table 9.

Table 1

Water Type and Availability, and Colony Location

in Grand Falls Study Area and New World Island, 1960

Area	Stream Miles Available	Colonies on Streams	Ponds Available	Colonies on Ponds	Lakes Available	Colonies on Lakes	Bogs Available	Colonies on Bogs
Grand Falls	23	16	47	4	5	3	4 sq.mi.	1
New World Island	30	4	120	31	30	14	15 sq.mi.	0

Grand Falls: - 67% on streams; 17% on ponds; 12% on lakes; 4% on bogs

- average stream gradient = 1%

New World Island: - 8% on streams; 63% on ponds; 29% on lakes, 0% on bogs

- average stream gradient = 4.5%

Table 2

Colony Location on Logging River Systems

in Central Newfoundland

		Lodge Location				Approximate
River System	In River	¼ mile from river		½ mile from river		Stream Miles
		In Brooks	In Ponds	In Brooks	In Ponds	
Rattling	2	17	9	3	2	50
Noel Paul	1	4	1	1	0	60

Table 3

Regeneration After Fire and Logging

Forest Type	After Logging	Remarks	After Fire	Remarks
Balsam fir	Original Forest	Virtually the Original Forest	Hardwoods and spruce	If spruce forest nearby
Black Spruce	Original Forest	Inferior, some Birch	Original	Usually the Original
Hardwoods	Original or fir	If fir Forest Nearby	Original	Usually the original
Dwarf Shrub Bogs	Original	Almost Always	Original	Almost Original
Alder Swamps	Original	Always	Original	Always

Table 4

Stability of Forest Types in Newfoundland

Stable Types	Unstable Types
Black Spruce	Undifferentiated hardwoods
Balsam Fir	Black spruce on wet soil
Alder Swamp	Kalmia - Black Spruce
Dwarf Shrub Bog	Kalmia Barrens
Birch Forests	Carex - Balsam Fir

Competition for Food

The snowshoe hare may be dismissed as a competitor. The muskrat, Ondatra zibethica obscura (Bangs) 1913, utilizes some of the aquatic food of beavers but is not considered an important competitor. The moose is a definite food competitor and probably a cause of colony abandonment.

Alder is the only tree species browsed by moose which is sufficiently abundant and utilized by beavers to be a factor in colony abandonment in the areas investigated.

Table 6 indicates the food species of beaver which are utilized by moose and muskrat. All foods sampled by beavers are included.

Table 7 indicates the single observation of moose browsing on aspen.

Table 5

Woody Plant Utilization at 2 Inactive Colonies
in Grand Falls Study Area

Species	Stump Size Class (Inches) 1	2	3	4	5	6	7	Total Stems Utilized	% of Total Utilized	Former Total Stems Utilized	% Available Stems Utilized
Alnus crispa and *A. rugosa*	1292	450	152	2				1896	90.9	2348	80.1
Populus tremuloides	16	34	14	6	3	3		76	3.8	76	100
Betula papyrifera	34	12	7	3	1			57	2.8	386	14.8
Acer rubrum	4	3	1					8	0.3	97	8.3
Salix sp.	18	2	2					22	1.1	28	78.2
Prunus pennsylvanica	2	1	1					4	---	16	25.0
Viburnum trilobum	2	4	6					12	0.6	270	4.4
Abies balsamea	1	1						2	---	328	0.6
Picea mariana	5	3	1					9	0.5	970	0.9
Totals	1374	510	184	11	4	3	0	2086	100.0		
Percentage	65.7	25.1	9.1	0.1	-	-	-				

Table 8 indicates the degree of moose and snowshoe hare browsing on some of the terrestrial food species of beaver at the five active and two inactive colonies for which the food utilization studies of Tables 5 and 6 were conducted.

(B) Vegetation Studies

Food Habits and Factors of Utilization

(1) Availability

The availability and utilization of woody plants at five colonies in the Grand Falls study area and on New World Island is tabulated in Tables 9 and 10.

(2) Stocking and Forest Type

Utilization of alder is normally not affected by forest type, alder stands usually being present near the water irrespective of local forest type. Utilization of other tree species varies with the forest type. This is especially true of aspen and birch. (Table 11).

(3) Diameter Size Preference

Tables 9 and 10 indicate that tree diameter sizes from one to three inches are preferred regardless of species.

(4) Distance from Water and Slope of Ground

Aspen is the only tree species for which great distances and/or difficult slopes are traversed. All other cutting is within 200 feet of the water. (Table 12).

Table 6

Competition by Moose and Muskrat on Beaver Food

Eaten by Beaver	Moose	Muskrat
Betula michauxii		
Betula papyrifera	x	
Picea glauca		
Populus tremuloides	x	
Prunus pennsylvanica	x	
Salix sp.	x	x
Acer rubrum	x	
Abies balsamea	x	
Picea mariana		
Alnus rugosa		
Alnus crispa	x	
Amelanchier bartramiana	x	
Viburnum cassinoides	x	
Viburnum trilobum		
Corylus cornuta	x	
Cornus stolonifera	x	x
Chamaedophne calyculata		
Kalmia angustifolia		
Kalmia polifolia		
Ledum groenlandicum		
Rhododendron canadense		
Vaccinium angustifolium		
Myrica Gale		x
Spiraea latifolia		
Potentilla fruticosa		x
Carex rostrata	x	x
Scirpus sp.		x
Juncus sp.		x
Potamogeton sp.	x	x
Nuphar variegatum	x	x
Nuphar microphyllum	x	x
Nuphar tuberosa	x	x
Nuphaea odorata	x	x
Sarracenia purpurea	x	x

% beaver foods utilized by moose - 53%
% beaver foods utilized by muskrat - 38%

% beaver food utilized by moose and muskrat - 65%
% food utilized by all three - 26%

Table 7

Moose Browsing and Beaver Utilization

of Aspen at One Colony in the Grand Falls

Study Area

Stump Diameter (Inches)	Total Availability	Utilized		Cut but not utilized		Unutilized	
		Number	No. moose browsed	Number	No. moose browsed	Number	No. moose browsed
1	5	0	0	0	0	5	0
2	17	6	0	1	1	10	2
3	23	10	0	3	1	10	3
4	7	3	0	1	1	3	0
5	3	0	0	1	0	2	0

Table 8

Moose and Snowshoe Hare Browsing on Beaver Foods at 5 Active and 2 Inactive Colonies in the Grand Falls Study Area

Species	Number of stems available	Number moose browsed	% moose browsed	Number S. hare browsed	% S. hare browsed	
Alnus crispa	5659	1352	23.9	345	6.1	Five Active Colonies
Populus tremuloides	199	24	12.2	2	1.2	
Betula papyrifera	974	209	21.4	36	3.7	
Acer rubrum	254	43	17.1	0	0	
Salix sp.	67	22	32.4	3	4.2	
Prunus pennsylvanica	42	3	6.7	0	0	
Viburnum cassinoides	713	277	38.8	9	1.3	
Cornus stolonifera	127	19	15	4	3	
Corylus cornuta	284	57	20	7	2	
Alnus crispa	452	398	88.2	14	3.2	Two Inactive Colonies
Populus tremuloides	0	---	----	--	---	
Betula papyrifera	329	112	34.1	4	1.1	
Acer rubrum	89	16	18.2	0	0	
Salix sp.	6	6	100.0	2	33.3	
Prunus pennsylvanica	12	---	----	0	0	
Viburnum cassinoides	258	111	43.3	2	0.8	
Cornus stolonifera	97	73	75	4	4	
Corylus cornuta	185	139	75	7	4	

Table 9

Woody Plant Utilization at 5 Active Beaver Colonies in Grand Falls Study Area

Species	Stump Size Class (Inches) 1	2	3	4	5	6	7	Total stems utilized	% of total utilized	Total stems available	% available stems utilized
Alnus crispa and A. rugosa	1355	237	42					1634	82.8	5659	28.7
Populus tremuloides	18	64	37	11	3	2	1	136	6.9	199	64.9
Betula papyrifera	40	26	29	10	4	1	3	113	5.7	974	11.6
Acer rubrum	7	11						18	0.9	254	7.1
Salix sp.	12	2						14	0.7	67	20.8
Prunus pennsylvanica	1		4	6				11	0.6	42	26.3
Viburnum trilobum	8	21						29	1.5	713	4.1
Abies balsamea	1	2	1					4	0.2	875	0.4
Picea mariana	5	7	1					13	0.7	2348	0.6
Total	1447	370	114	27	7	3	4	1972	100.0	11,131	
Percentage	73.3	18.7	5.8	1.4	0.4	0.2	0.2		100.0		

Refer to Table 11 for aspen cutting in various forest types.

Table 10

Woody Plant Utilization at 5 Active Beaver Colonies on New World Island

Species	Stump Size Class (Inches) 1	2	3	4	5	6	7	Total stems utilized	% of total utilized	Total stems available	% available stems utilized
Alnus crispa and A. rugosa	673	123	22	2				820	83.9	1329	61.7
Populus tremuloides	11	2						13	1.5	14	89.8
Betula papyrifera	12	24	8					44	4.6	75	58.3
Salix sp.	28	11						39	4.0	55	71.2
Prunus pennsylvanica		3	1					4	0.1	8	50.0
Cornus stolonifera	10	32						42	4.4	62	67.7
Abies balsamea	2	4						6	0.1	298	2.0
Picea mariana	8	5						13	1.4	415	3.2
Total	744	204	31	2				981	100.0	2,256	
Percent	75.3	20.8	3.7	0.2					100.0		

Table 11

Tree Cutting in Four Forest Types
in Grand Falls Study Area

Forest Type	Percentage Utilization			
	Aspen	Birch	Other Hardwoods	Conifers
Old closed canopy aspen	100	-	-	-
New " " "	45	-	-	-
Old closed canopy birch	100	2	-	-
New " " "	85	2	-	-
Old mixed hardwoods	100	1	1	-
New " "	83	1	1	-
Old hardwoods-conifers	100	-	7	0.5
New " "	100	-	7	0.3

Table 12

Maximum Distance from Water and Maximum Slope
of Ground of Observed Beaver Cutting

Species	Max. dist. from water (ft.)	Max. slope of ground (degrees)
Aspen	652	75
Cherry	326	15
Alder	140	40
Birch	135	15
Others	100	15

(5) Competition

Competition from moose or muskrat does not appear to influence the beaver's diet. Compare Tables 9 and 10.

Seasonal Foods

Limited tree cutting is done during the summer. Aquatic vegetation and small shrubs appear to be most heavily utilized as summer foods.

Stumps in the cutting areas of three colonies were painted. One of the colonies made no further use of the feeding area. In the second colony, 12 aspen and one birch were cut during the summer. Nineteen aspen were cut at the third colony in the early fall. Table 13 indicates the cutting data for these two colonies.

Table 13

Aspen and Birch Cutting at Two Colonies in Grand Falls Study Area

Colony	Species		Stump Diameter (Inches) 1	2	3	4	5	6
Colony A (summer cutting)	Aspen	Available	11	18	7	6	3	3
		Utilized	--	7	3	-	1	1
	Birch	Available	29	63	50	21	11	3
		Utilized	1	--	--	--	--	-
Colony Y_1 (fall cutting)	Aspen	Available	5	17	23	7	3	-
		Utilized	-	6	10	3	-	-
	Birch	Available	1	8	3	5	2	-
		Utilized	-	-	-	-	-	-

Table 14 lists the species and frequency of chewed scraps of vegetation that were floating on the water of colonies from three areas. The two species of *Nuphar* rank first in occurrence. The size studies of *N. variegatum* and *N. microphyllum* are shown in Table 15.

Table 14

Average Occurrence of Chewed Vegetation on Colony Water for 6 Visits

Species	Fragments per Colony Grand Falls	New World Island	Avalon Peninsula
Nuphar variegatum (root)	4	10	10
Nuphar microphyllum (root)	2	8	4
Alnus crispa	5	7	4
Alnus rugosa	5	5	6
Carex rostrata	6	12	12
Myrica Gale	2	5	3
Rhododendron canadense	2	3	3
Vaccinium angustifolium	2	4	6
Sarracenia purpurea	4	2	5
Betula papyrifera	2	0	1
Juncus sp.	1	1	1
Viburnum cassinoides	2	1	1
Acer rubrum	2	0	1
Prunus pennsylvanica	1	0	1
Populus tremuloides	2	0	0
Picea glauca	1	2	2

The woody plant utilization of the beaver colony as shown in Tables 9 and 10 is a general representation of winter diet since little summer cutting of trees occurs. The composition of fall browse piles is shown in Table 16.

Table 15

Size Studies of *Nuphar variegatum* and *N. Microphyllum* in Grand Falls area

Species	Average root length (in.)	Variation	Avg. root diam. (in.)	Var.	Avg. No. leaves	Var.	Avg. leaf length (in.)	Var.	Avg. root wt. (lb.)	Var.
Nuphar variegatum	21	12-27	2½	1½ to 4	9	6 to 14	6	2 to 10	4	1½ to 6
Nuphar microphyllum	19	10-25	1	1 to 2	9	6 to 14	3	1 to 4	2	1½ to 3

Table 16

Average Browse Pile Composition in Grand Falls
Area and New World Island
(Number of browse piles per area = 15)

Species	Percentage In Grand Falls	Percentage In New World Island
Alnus crispa and *A. rugosa*	60.0	70.0
Betula papyrifera	20.0	20.0
Viburnum cassinoides	3.0	--
Salix sp.	6.0	4.0
Prunus pennsylvanica	1.0	--
Populus tremuloides	4.0	0.5
Acer rubrum	1.0	--
Cornus stolonifera	--	3.0
Myrica Gale	1.0	--
Rhododendron canadense	1.0	1.0
Vaccinium angustifolium	2.0	1.0
Picea glauca	1.0	0.5

Table 17

Time Required to Water-Kill Vegetation

Vegetation	Majority of Individuals killed	Individuals may Withstand Flooding
Gramineae	1 yr.	------
Ericaceae and other shrubs	1 yr.	2 yrs.
Picea glauca and *P. mariana*	1 yr.	2 yrs.
Abies balsamea	1 yr.	------
Populus tremuloides	1 yr.	2 yrs.
Betula papyrifera	1 yr.	2 yrs.
Acer rubrum	2 yrs.	4 yrs.*
Alnus crispa and *A. rugosa*	2 yrs.	5 yrs.*
Salix sp.	2 yrs.	5 yrs.*

*From Payne (1961)

Effects of Flooding on Vegetation

The length of time required to water-kill some species of vegetation is tabulated in Table 17.

(C) Population Studies

Size of Colony Territory

Topography, Water Type and Availability

It appears that stream colony territories are normally smaller than pond colonies. A combination of one or more small ponds and a section of stream represents the usual type of colony in areas of favourable beaver habitat. This type of colony territory is generally larger than both the stream colony and the pond colony. By determining the type of water available, topography is a governing factor in territory size.

Tables 18 and 19 show the type and size of some colonies from both study areas. The tables also indicate whether or not uninhabited water was available for territory expansion.

Vegetation

Vegetation composition of surrounding forest is not a factor in size of colony territory where topography is unfavourable to expansion, as on New World Island. Where topography permits easy expansion of territory, as in the Grand Falls area, vegetation is probably a factor of territory size. Colonies which have access to unlimited alder and abundant hardwoods are generally smaller than colony territories where these are less abundant.

Tables 18 and 19 show the forest compositions of the colonies measured.

Intra-Specific Conflict

This is a factor of territory size. One beaver colony will not tolerate another colony in its territory. Table 20 shows the land and water distance between 16 colonies in the Grand Falls study area. All measurements except Colony Y_1 are by Miller.

Age of Colony

Age is normally a factor of territory size. The youngest colonies in the Grand Falls study area are the smallest. Territorial expansion of two colonies is shown in Table 21.

Movement

Table 22 shows the movement data of 14 tagged beavers over a five-year period in the Grand Falls study area. From this table and also from Figure 5, it appears that beavers are reluctant to occupy the same pond for more than two successive winters. I believe that most movement in this area is a search for food.

Table 18

Forest Cover, Age, Size and Type of 16 Beaver Colonies (Grand Falls)

Colony	Type of Colony	Length (yds.)	Water for Expansion	Age (yrs.)	Forest Composition (%)				
					Aspen	Birch	Other Hdws.	Conifers	Alder Rating
A	2 ponds + stream sections	572	stream	4	1	11	12	76	Excellent
F	1 pond + stream sections	803	stream	5+	<1	9	14	77	Excellent
G	stream	352	stream	3	<1	7	10	83	Excellent
H	1 pond + stream section	1400	stream	5+	<1	4	9	87	Excellent
M	stream	147	stream	2	<1	2	5	93	Good
O	2 ponds + stream sections	847	stream	5+	<1	8	11	81	Good
P	5 ponds + stream sections	1845	stream	5+	<1	10	11	79	Excellent
Q	2 lakes + stream sections	1584	stream	5+	<1	8	10	82	Good
R	2 ponds + stream sections	704	stream	5+	<1	7	12	81	Excellent
S	1 lake + stream section	2200	stream	5+	<1	3	5	92	Fair
U	2 lakes + stream sections	1408	stream	5+	<1	10	8	82	Good
V	2 ponds + stream sections	1441	none	5+	<1	10	12	78	Excellent
W	2 ponds + stream sections	880	none	5+	<1	9	11	80	Good
X	3 ponds * stream sections	1210	stream	5+	<1	7	9	84	Excellent
Y	3 ponds + stream sections	1286	stream	5+	<1	6	8	86	Good
Y_1	stream section	160	stream	1	<1	9	6	85	Excellent

Average number of tree stems per colony (by transects spaced 100 feet) = 5566

Alder rating (by transects spaced 100 feet) - Excellent - 1500 stems
Good - 1000 stems
Fair - 500 stems

Table 19

Forest Cover, Age, Size and Type of 10 Beaver Colonies (New World Island)

Colony	Type of Colony	Length (Yds.)	Water for Expansion	Age (yrs)	Forest Composition (%)				
					Aspen	Birch	Other Hdws.	Conifers	Alder Rating
1	1 pond	650	none	3+	-	<1	3	97	Excellent
2	1 pond	200	stream	3+	-	<1	4	96	Fair
3	1 pond	475	none	3+	-	<1	2	98	Good
4	1 lake	1200	none	3+	<1	2	4	94	Excellent
5	1 pond	550	stream	3+	-	1	2	97	Excellent
6	1 pond	450	stream	3+	-	<1	1	99	Excellent
7	1 pond	375	none	3+	-	<1	<1	99	Good
8	1 pond	830	none	3+	-	<1	3	97	Fair
9	1 pond	155	none	3+	-	<1	1	99	Fair
10	1 pond	375	none	3+	-	<1	<1	99	Excellent

Average number of tree stems per colony (by transects spaced 100 feet) = 452

Alder rating (by transects spaced 100 feet) - Excellent - 500 stems
Good - 300 stems
Fair - 150 stems

Table 20

Territory Size and Distance between
Territories of 16 Beaver Colonies
Grand Falls Study Area

Colony	Territory length (yds.)	Distance to Nearest Colony (yds.)			Number of Beaver in Colony (1960)
		Downstream	Upstream	Overland	
A	572	-	704	528	4
F	803	-	1144	55	2+
G	352	1144	1276	308	3
H	1408	1276	748	484	4
M	110	-	792	55	3
O	847	1056	308	341	6
P	1848	308	484	341	3
Q	1584	1002	-	110	7
R	704	484	396	180	6
S	2200	224	420	0	7
U	1408	396	187	264	3
V	1441	187	-	0	4+
W	880	0	-	143	4
X	1210	-	-	55	5
Y	1286	-	-	55	3+
Y_1	160	420	1720	870	2 (in 1961)

Table 21

Territorial Expansion of Two Beaver Colonies
in Grand Falls Study Area

Colony	Length (Yds.)			Type of Colony
	1960	1961	1962	
Colony M	110	147	195	Small stream
Colony Y_1	-	160	250	Large stream

Table 22

Movement and measurement data of 14 beavers trapped in Grand Falls study area in spring and summer, 1962

Tags	Capture dates	Ponds where captured	Colony	Sex	Age	Weight (lbs.)	Total lgth. (in.)	Tail lgth. (in)	Tail wdth. (in.)	Stream dist. moved	Land dist. moved
234	6-8-60	1372	x			18	33.50	9.50	3.50		
263	6-4-62	1372	x	F	A	26	38.50	9.75	4.25	0 mi.	0 mi.
370	8-5-60	1321	M	M							
371	4-25-62	1322	F		2 yr	15.25	39	9	3.50	3500 ft	1000 ft
269	7-29-59	1347	Q	F	kit	4	18	5	2		
270	6-20-60	1346	Q		yr	16	31.25	9	3.75		
402	8-31-60	1347	Q			20	33.25	9.50	4		
230	4-25-62	1353			adul	(Eaten in trap, Lynx)				1200 ft	1200 ft
398	8-31-60	1347	Q	M	kit	6.50	25.75	6.75	2.50		
399	4-25-62	1353			A	13.25	33	9	3.50	1200 ft	1200 ft
272	7-12-60	1322	F	F	A	30	38.75	11.50	4.25		
	4-26-62		Y_1			28	42	10.50	4.50	5.75 mi	3.50 mi

Table 22 (cont'd)

165	7-4-58	1357	S	M	yr	15	27.50	8.50	3.25	.25 mi.	0
226	7-24-59	1355	S		2 yr	26	34.50	10	4	0	0
265	6-11-60	1357	S		A	28.50	38	10	4.50	.25 mi.	0
423	9-15-60	1358	S		4 yr	33.50	39	10	4.75	.25 mi.	0
	5-4-62	1357	S		5 yr	29.50	39.50	10	4.75	.25 mi.	0
158	6-25-58	1347	Q	M	A	38	37.50	10.75	5	3.25 mi.	.75 mi.
227	7-29-59	1355	S			39	41	11	5	.50 mi.	.50 mi.
275	6-16-60	1357	S			40	40.50	11	5.25	0	0
	5-4-62	1357	S			36.25	40.50	11	5.25	2.75 mi.	600 ft.
163	6-27-58	1357	S	F	A	29	33.50	10	4.50		
317	7-29-59	1356	S			33	38.50	11	5	.50 mi.	0
318	7-14-60	1357	S			39	41.25	11.50	5.25	.50 mi.	0
	5-4-62	1357	S			37	42.50	10.50	5.25	0	0
262	6-8-60	1370	X	M	A	36	42	12	4.50		
	5-?-62	1371	X			31	42	10.50	4.25	1000 ft	400 ft
155	6-21-58	1357	S	F	A	36	36	10	5		
313	7-14-60	1357	S			39	42	10.75	5.50		
314	5-?-62	1357	S			40.50	41	10.50	5.50	0	0
172	7-12-58	1340	0	F	A	35	36	10	4.75		
384	8-7-60	1340	0			40	41	11.25	5.50		
384	5-22-62	1341	0			37	40	10.25	5	1200 ft	1200 ft

Table 22 (cont'd)

182	7-23-58	1323	G	F	A	32	36.50	10.50	5.25		
210	7-15-59	1323	G			32	42	10.25	5		
	5-24-62	1323	G			34	40	10.25	5	0	0
340	8-1-60	1323	G	F	kit	8	25	7	2.75		
341	9-13-60	1323	G			10.50	26.50	7	3		
	5-24-62	1323	G		2 yr	21	33.50	9	4.50	0	0
152	6-18-58	1357	S	M	2 yr	26	34.50	9.75	4.50		
219	7-20-59	1352	P		3 yr	35	41	10.75	5	1.75 mi.	1.50 mi.
352	7-18-60	1308	A		4 yr	35.50	40	10.75	5.50	3.25 mi.	1.25 mi.
353	5-25-62	1352	P		5 yr	33	41	10.25	5	3.74 mi.	1.25 mi.

Stability of the Population

Beaver populations in Newfoundland are not stable where the animals rely on aspen or birch to any appreciable extent. Unfavourable (rough) topography may however, sometimes force stability upon a population.

Fall census counts of the closed Grand Falls study area over a five-year period indicate that beavers adjust their numbers to balance a continually changing food supply. Table 23 shows the population figures in Grand Falls.

Table 23

Population in Grand Falls
Study Area 1958-1963

	Year					
	1958	1959	1960	1961	1962(1)	1963
No. of active colonies	20	23	24	18	14	12
Colonies per sq.mi.	1.3	1.5	1.6	1.2	0.9	0.8
No. of beavers*	93	106	110	83	64	55
Beavers per sq.mi.	6.2	7.1	7.3	5.5	4.3	3.7

*Based on 4.6 beavers per colony

(1) Area trapped out in spring and summer of 1962

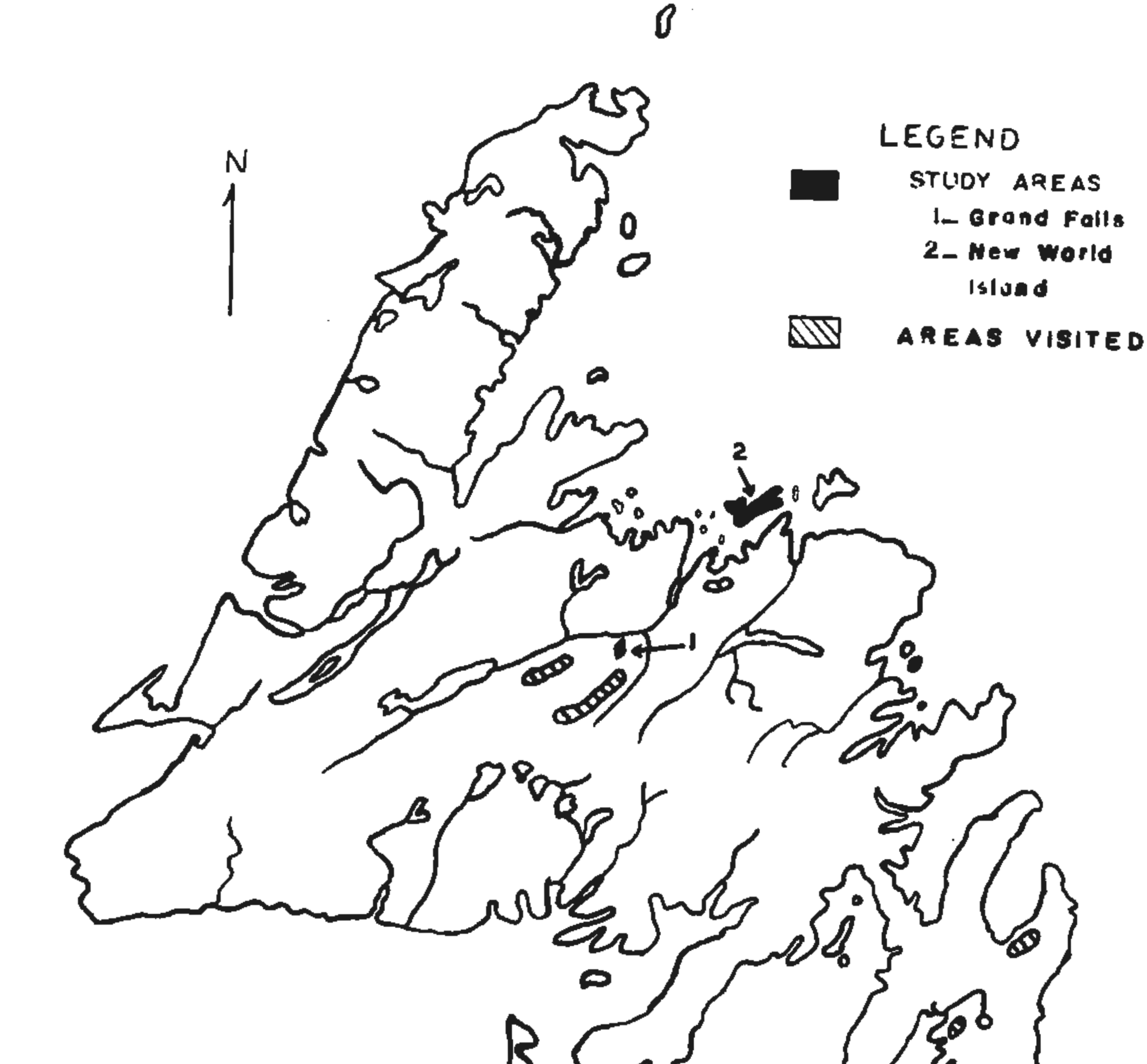


Fig. 1 - Map of Newfoundland showing areas of field investigations.

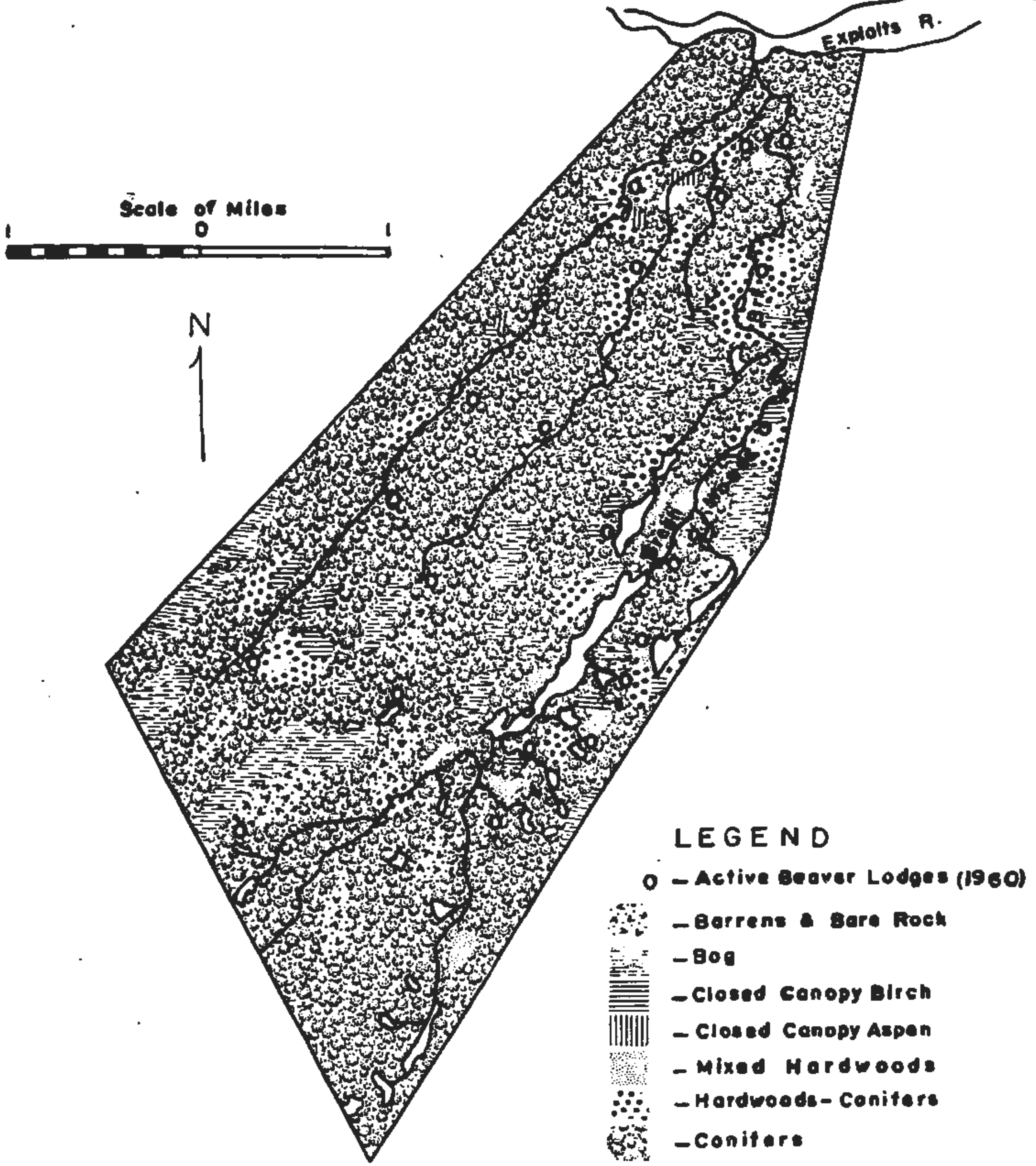


Fig. 2 - Cover map, Grand Falls study area

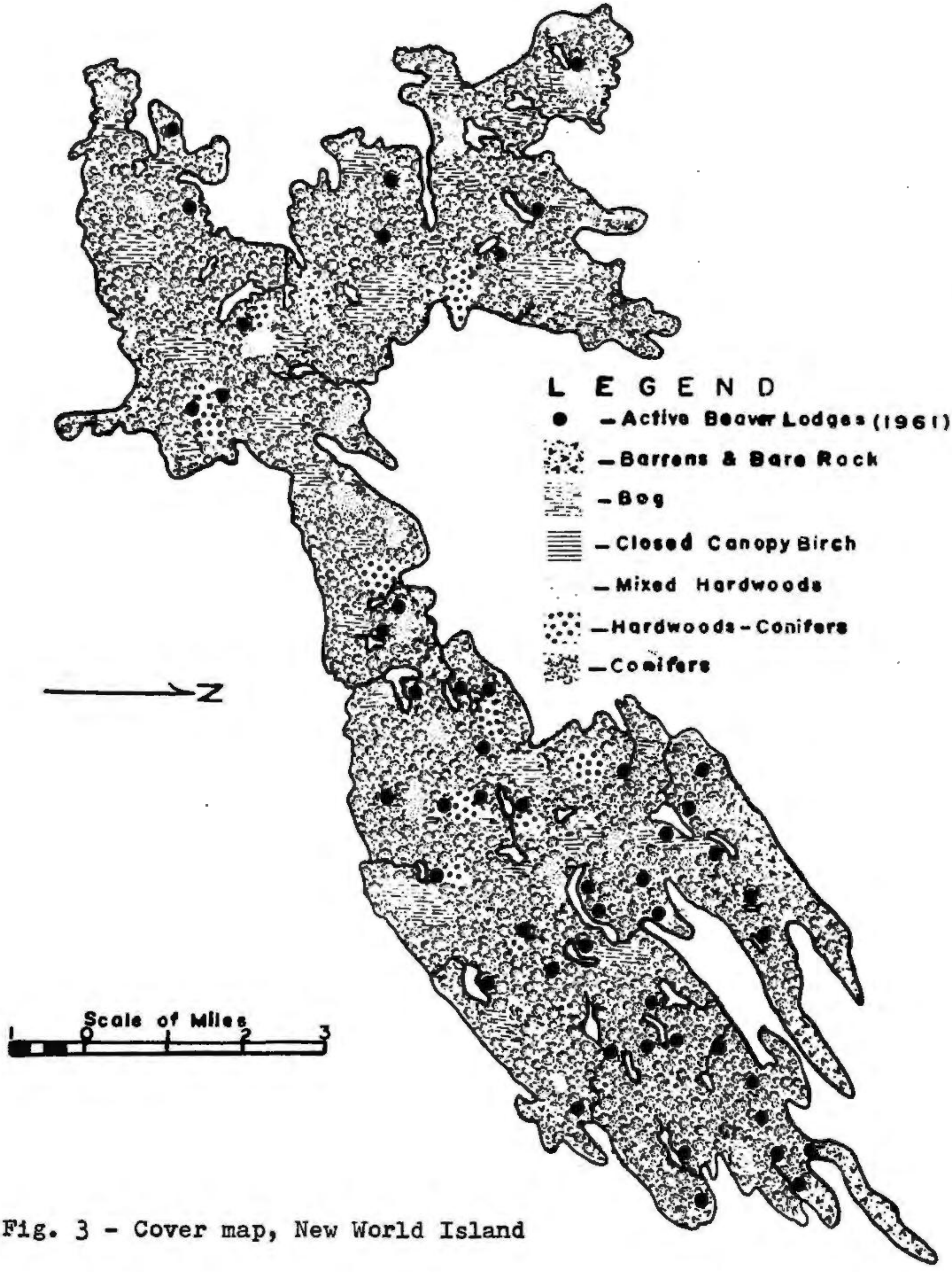


Fig. 3 - Cover map, New World Island

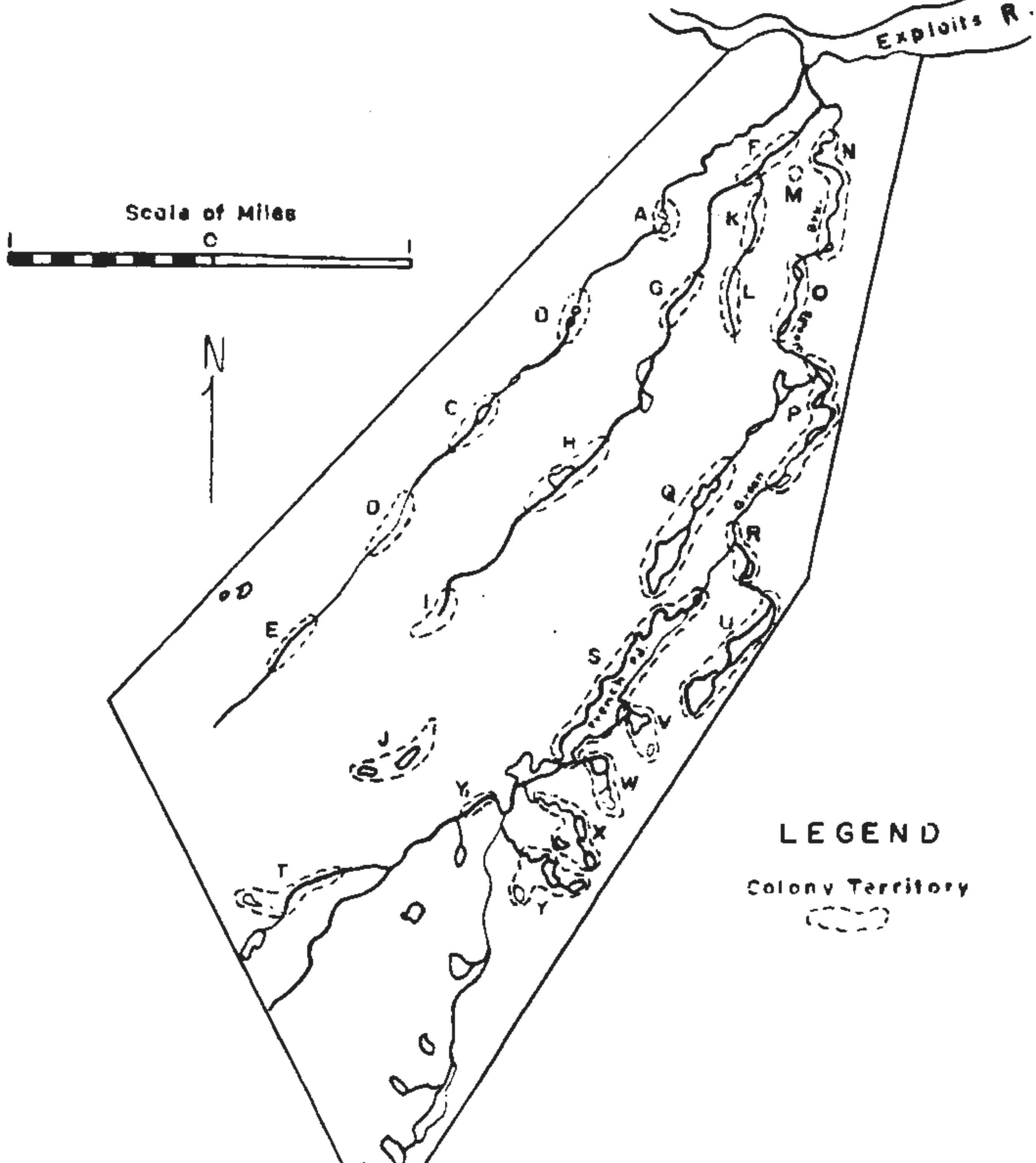


Fig. 4 - Colony Territories, Grand Falls Study Area

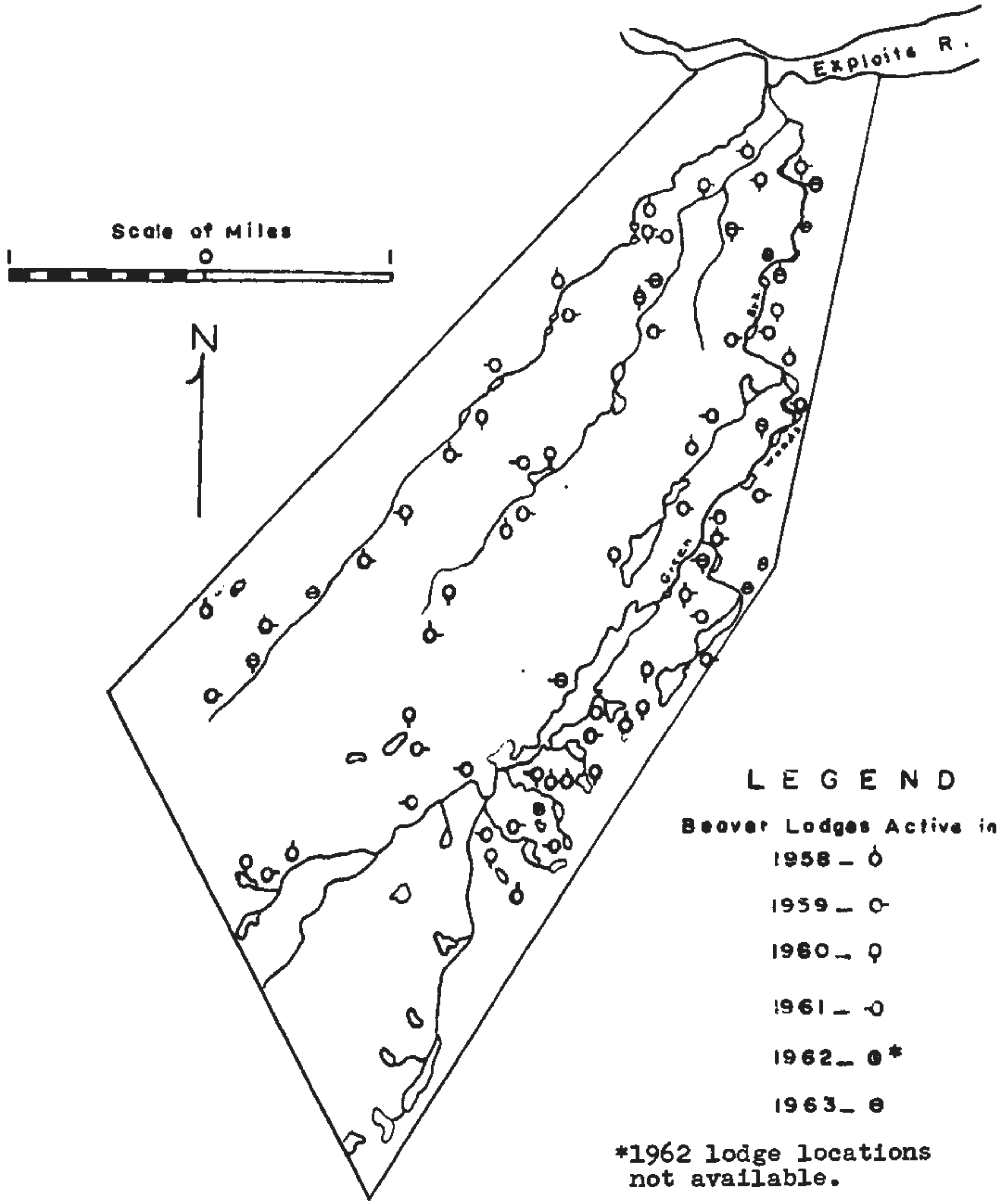
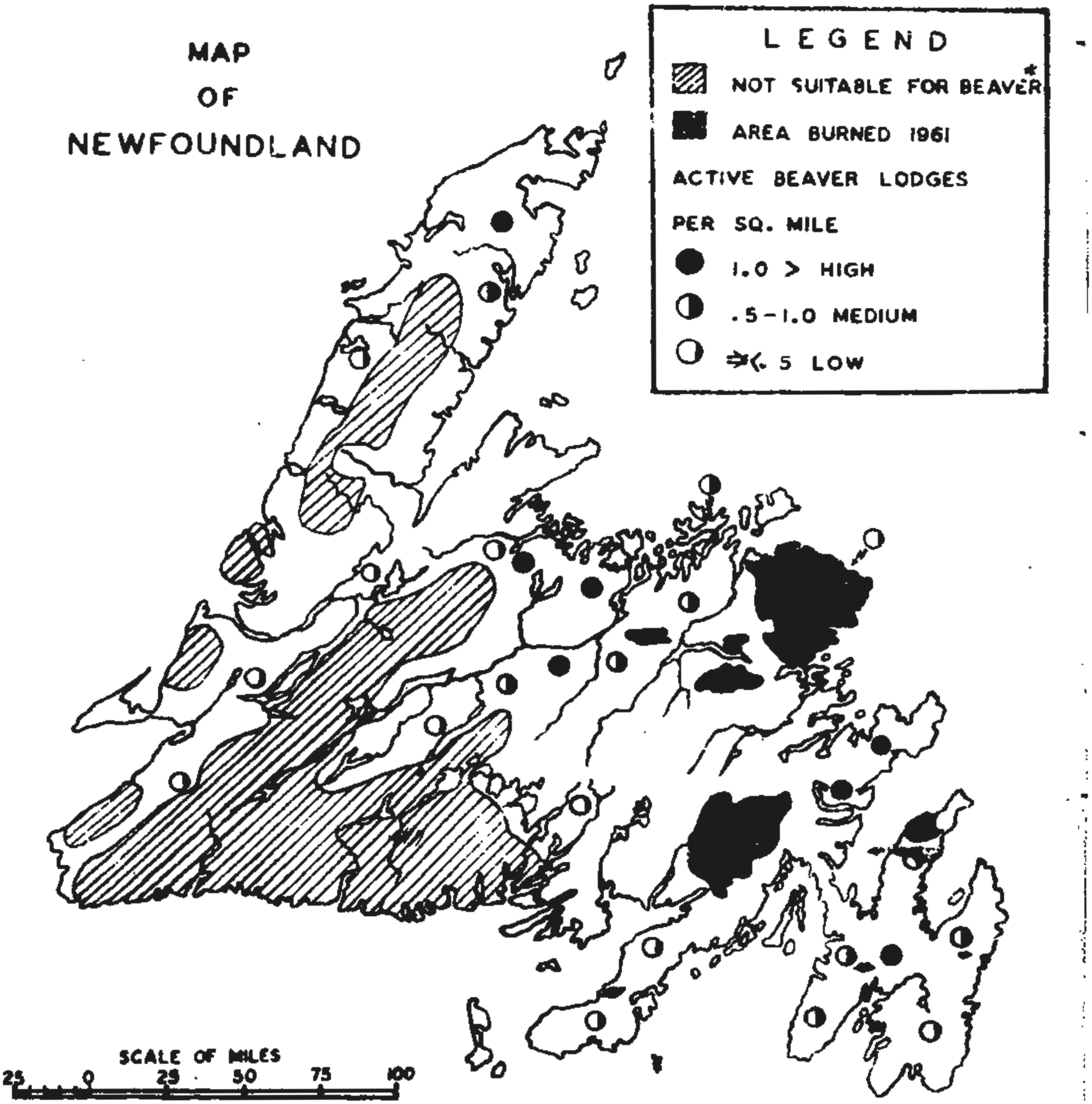


Fig. 5 - Active Winter Lodge Locations, Grand Falls Study Area 1958-1963.



*Barrens, rock and complete lack of food

Fig. 6 - After Bergerud, 1962. Carrying Capacity of Beaver Habitat in Newfoundland.

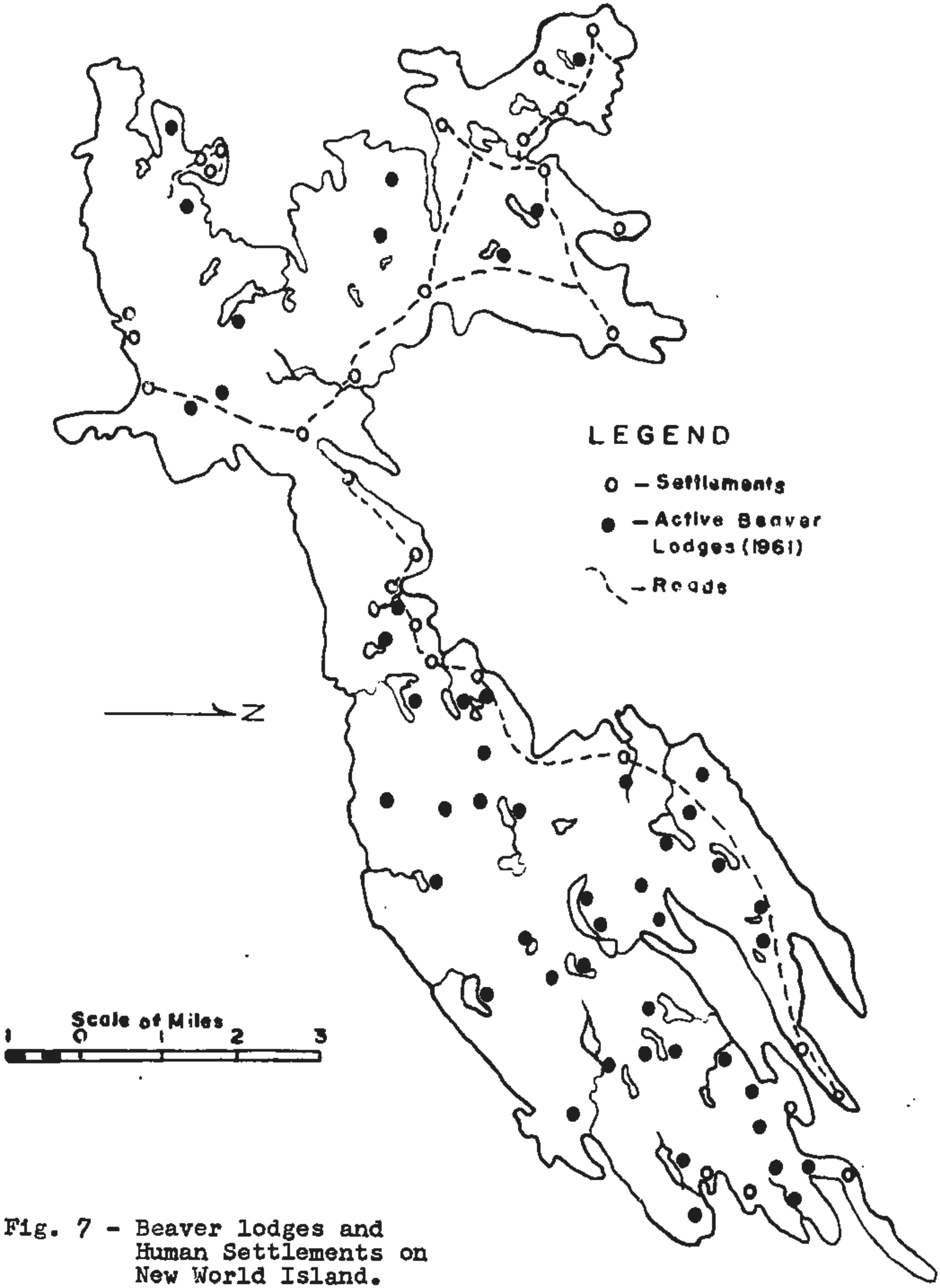


Fig. 7 - Beaver lodges and Human Settlements on New World Island.

DISCUSSION

(A) Habitat Relationships

Influence of Topography, Water Type and Availability

Topography determines the type and availability of water for beaver colonization. The two study areas, for example, represent very different types of habitat. Topography may make streams and rivers uninhabitable because of excessive gradients. Rutherford (1955) suggests that streams with gradients up to 8 per cent may be colonized in more mountainous areas. Retezer (1956) found that 68 per cent of the beavers in the Rocky Mountains of Colorado are located on streams of gradient less than 6 per cent, that 28 per cent had colonized streams with gradients 7 - 12 per cent, and that 4 per cent were on streams with gradients 13 - 15 per cent. No beavers were found where gradients exceeded 15 per cent. Hodgdon and Hunt (1955) found that in Maine few beavers colonized streams with gradient greater than 2 per cent. In West Virginia, Swank (1949) found the greatest concentrations of beavers in "gently sloping" streams and minor concentrations in "precipitous" stream sections.

In the Grand Falls study area the stream gradients range from less than 1 per cent to 4 per cent. The average gradient is 1 per cent. The steepest section of each stream is the last downstream mile before it enters the Exploits River.

No beaver colonies are found in this last mile of 4 per cent gradient. The headwaters and the middle sections of the streams have gradients ranging from 1 - 3 per cent. Here are contained 67 per cent of the beaver colonies in the study area (Table 1).

On New World Island the longest stream is 1.5 miles long. The majority of streams are short, .25 to .5 mile, usually flowing directly from one of the small ponds into the ocean. There is no regular pattern of drainage. Because the streams are short and have a steep gradient they are normally not colonized by beavers.

Four colonies (8 per cent) are located on the four longest streams of New World Island. These streams have a gradient of 2 per cent. The gradient of the other streams is 5 per cent. This is beginning to be a prohibitive gradient, and is definitely so when food is not abundant. The streams of New World Island must be classified as unsuitable for beaver habitat.

Considering the entire beaver range in North America, it is apparent that beavers occupy sites where topographic development and stream gradients range from very low to steep. In low or flat areas, topography probably exerts a minor influence after determining the water type. But in hilly or mountainous country, the steepness of the slope will determine the suitability of the site for beaver occupancy.

In addition to excessive stream gradient, two other prominent features of terrain affecting beavers are (1) the steepness of the upland slopes adjoining the stream, and (2) width of stream valley. Narrow valleys are often severly affected by flooding, whereas in wider valleys the flood water spreads and little damage results. This is important to the permanence of beaver lodges and dams.

Also, wider valleys have large areas favourable for the growth of alder, willow, aspen and harbaceous foods generally. Narrow valleys do not permit extended growth of these food species because drainage creates dry soil unfavourable to them. Narrow valleys usually indicate youth and consequently close crowding of the conifer forest since hardwoods are normally only present after disruption of the forests.

Retzer (1956) found that 64 per cent of the beavers in the Rocky Mountains of Colorado were in valleys of width greater than 150 feet. The final mile of the streams in the Grand Falls study area exhibits the narrow-valley factor. The forests are dense spruce and balsam fir with very few hardwoods. The valley widths at stream level are approximately 60 feet. In addition to being narrower and steeper, the valleys have a dampness that must be due to the close crowding forest preventing sunlight penetration. This dampness may also be a deterring factor to colonization.

Mud is in short supply in these narrow valleys, due in part to the forest cover preventing erosion of the stream slopes. Beavers must have mud for building. They are unable to create sediments themselves. In even their most intensive cutting and dragging operations, I observed very little bare surface soil. Commercial logging often creates bare soil. Beaver dams control the movement of sediments downstream. Silt settles in front of the dam and is used by the beaver. Some finds its way over or through the dam and continues downstream. The farther downstream from the headwaters the less silt will be available to beavers unless local erosion creates a supply. The upper reaches of the streams of the study area are of low gradient and are seldom subjected to flooding. Glacial till, in the form of thinly forested stream banks and barren ridges, is subjected to sufficient erosion from natural forces to provide ample supplies of silt. Little of this silt reaches the lower sections of the streams.

Narrow valleys mean steep upland or valley slopes. As it nears maturity, a stream widens its valley. The slopes near the stream are considerably lowered. But further back from the stream, sections of the old slopes may remain quite unchanged. Thus, when a stream is otherwise suitable, these steep upland slopes may have a restraining influence on beaver colonization.

Steepness of slope exerts the strongest influence against colonization in the early years of a colony's existence when food is plentiful. These slopes are then avoided. I found no method to accurately determine the age of old beaver food trails. However, it was possible by observation to see the very old overgrown ones, the ones being currently used and those of intermediate age. It was readily apparent that the oldest trails were on the most level ground. The oldest trails of colony S (Fig. 4) in the Grand Falls study area were across a bog to the woods beyond. The slope of this trail was 4 degrees. The newest trail at colony S ascended a 50 degree ridge to secure six aspen of stump diameter two inches scattered along the top of the spruce slope.

Aspen was the only species for which such difficult climbs were made. Normally, slopes greater than 15 degrees are not ascended for any other species with the possible exception of alder. It appears that these unusually steep slopes are climbed only when food supplies are exhausted and unfavourable topography (New World Island) or a high density population (Grand Falls study area) interfers with free movement to a more favourable area.

Rocky streams were not colonized in either of the study areas. On New World Island the majority of the streams have channels that are raw and rocky, with no semblance of silting in even the more gentle sections.

Rutherford (1955) states that initial beaver occupancy of any area is largely or wholly governed by topography and forest fire. Topography does, indeed, determine the water type of an area available for beaver colonization. Two new colonies established in the Grand Falls study area during my investigations were on streams. The new colonies on New World Island were on ponds. This is an important consideration when it is realized that an area with inhabitable streams can support a larger population density than an area where streams are uninhabitable. In 1961 the mean number of beavers per square mile for the Grand Falls study area was 5.5; for New World Island 3.2. The importance of topography to carrying capacity is thus obvious.

My studies show that stream sections in which the gradient exceeds 3 per cent are not normally colonized. All other factors of terrain will be overcome in times of necessity. For example, the willingness to climb steeper slopes when food is in short supply. If colonization does occur on steeper streams, it would probably be for a limited number of years. I believe that areas of long time beaver occupancy would have a maximum stream gradient of 3 per cent in Newfoundland. The three main stream systems of the Grand Falls study area have a gradient less than 3 per cent.

These streams have been continuously occupied by beavers for at least 20 years. Granite and glacial till comprise the rock type of the area. These are very stable and suited to long-time occupancy. Soils from such unstable rocks as shale are subject to such severe erosion that beaver impoundments are short lived due to rapid deposition and filling of ponds.

Influence of Fluctuating Water Levels

An important factor influencing beaver habitat in Newfoundland is the rapidly fluctuating water levels in some areas as the result of logging operations. Fluctuating water levels have an affect on species composition of important terrestrial and aquatic vegetation. These effects will be discussed later. In this section the effects of fluctuating water levels as a possible deterrent to colonization will be considered.

Wherever beaver colonies are located, they are subjected to the natural spring and summer changes in water levels, and normally are not affected by them. In French Pond in the Grand Falls study area there is a drop in pond level of 2.5 feet from May to July every year. Greenwood's Brook, which flows out of French Pond, is difficult to cross in early June because of the volume of water. In late July it is possible to cross without difficulty. French Pond has supported beaver colonies since 1938. The four colonies of Greenwood's Brook have been there almost as long. The normal sequence of flooding and run-off does not interfere with beaver activity. Water levels have started to drop by the time the kits are due towards the end of May. Under normal circumstances there would be no danger to kit survival.

The other two major stream systems as well as the lakes and ponds in this study area are subjected to similar natural rise and fall of water level. An increasing population in the area up to 1960 (Table 23) indicates no adverse affects of the normal fluctuation; it is a characteristic of beaver habitat.

Two logging river systems in central Newfoundland were surveyed by light aircraft and canoe to determine the extent of beaver colonization (Table 2). The Rattling Brook system is approximately 50 miles long. Two lodges were found in the main river. These lodges were in two short side arms of the river. A dam was built across the mouth of each arm sealing it off from the river. The arms did not then experience the fluctuations of the main river. No lodges appeared in the main river channel. Thirty-one lodges were recorded in the small brooks and ponds that drain into the main river. Twenty-six of these were within .25 miles and 5 within .5 miles of the river. No lodges were recorded from the .5 to .75 mile strip on each side. Beyond this distance

I felt the areas were no longer under control of the river and these were not surveyed.

None of the streams containing the 26 lodges are used to regulate the level of Rattling Brook. Four of the larger streams flowing into Rattling Brook are feeder streams for the river. Each feeder stream contains an A.N.D. company dam and gate structure to control the flow of water for the driving of pulp logs to the mill.

These dams can raise the level of the lake behind them from four to five feet. In July the gate in one of the dams was closed and in one week the water had risen 2.5 feet. When the gate was opened this head of water ran for 12 hours, and flooded the stream to the main river for this entire period.

The Noel Paul River system is in a generally low density beaver area. However, a similar pattern of beaver distribution is evident. Only one lodge occurs in the 60 miles of the main river. This lodge, as for Rattling Brook, is in a side arm of the river. Five lodges were located within .25 miles of the river, four on streams and one on a pond. One lodge was located on a stream within .5 miles of the river. No lodges were observed in the .5 and .75 mile strip. No lodges were found on the feeder streams.

In the course of ground investigations of the feeder streams of Rattling Brook I located a very old and collapsed beaver lodge which was not visible from the air. The superintendent for this area of the logging division told me that beavers were found on the lake and stream before its use as a feeder stream. Since the logging dam had been built, there had been no further evidence of beavers. He stated that this had been the case for all the areas under his control.

Apart from the actual effect of water level fluctuation on vegetation and kit survival and general inconvenience to beavers, there is the actual mechanical damage inflicted to dam, lodges and the animals themselves by the logs being propelled downstream by the driving current. It is apparent that beavers do not colonize logging systems. Which of these two factors involved is the deterring one is not certain. It is probably that both are responsible. I would suggest, however, that kit mortality and vegetation destruction is the stronger factor. Beaver lodges and dams receive considerable damage from humans and large mammals such as moose. Such damage is usually tolerated by the beaver.

While beavers do not colonize logging rivers, it appears that they may travel them in search of streams and ponds favourable for colonization. This is probably the explanation for the decreasing number of lodges at greater distances from the river.

The literature contains very little reference to the effects on beaver of abnormal fluctuating water levels. Rawley (1954) includes fluctuation as one of the characteristics determining his four habitat class types in Utah. His class I (productive) and Class 2 (moderately productive) habitat types have little or moderate fluctuation. Class 3 (fairly productive) and Class 4 (marginally productive) have much and great fluctuation respectively. If this fluctuation is of the natural or human-induced type is not clear.

Tappe (1942) states that sudden fluctuations in water levels are tolerated by beavers in California. Tappe is referring to sudden natural irregular floods such as caused by heavy rain storms and associated run-off. He does not consider the type of logging river system fluctuations dealt with here. I have already stated that natural fluctuation is a characteristic of beaver habitat.

<u>Effects of Fire and Logging on Forest Succession</u>

Beavers are adapted to early stages of forest succession where hardwoods are present. When a forest is maintained in the constant cover of climax tree species, beaver populations will be greatly reduced. In Newfoundland, the major stable forest types are black spruce, balsam fir, dwarf shrub bogs and alder swamps, (Damman, 1961). Only one stable forest type is suitable for beaver, the alder swamp. Unless the stability of the other forest types is interrupted by fire or logging (which cause an abrupt change) or by such natural processes as fertility and moisture (which cause a gradual change) beavers will not colonize them. Fire and logging releases the hardwoods that may have always existed there as suppressed species or permits the introduction of hardwoods from a nearby source. In any event, the fast growing hardwoods sprout up quickly. For a number of years, until overtaken and suppressed again by the conifers, the area becomes an excellent beaver area.

Tables 3 and 4 summarize the following discussion of forest types.

Balsam Fir Forests

Balsam fir forests are most severly changed by fire. Solid stands of white birch, black spruce, aspen or mixed birch and pincherry are commonly found after fire. Most of the hardwoods in the Grand Falls study area are from the forest fire which swept the area in 1922. Many of the black spruce stands also originated at this time. If the fire is in the autumn, a balsam fir seed supply may be available and regeneration of balsam fir results. This rarely happens, (Damman, 1961).

The nearness and composition of a black spruce seed source to the fir forest after a fire determines succession. If black spruce is rare and birch seed more plentiful, then birch succession results. Trembling aspen stands are rare in Newfoundland. They develop only after fire and have only been found on the sites of Rubus-fir, Hylocomium-fir forests and Lycopodium-alder swamps, (Damman, 1961). Aspen stands never cover very large areas.

After logging there is normally regeneration of the original forest with an increased representation of birch if a birch source is available.

Balsam fir forests are killed after approximately one year of beaver flooding (Table 17). These forests require 20 to 30 years to regenerate after removal of the beaver dams.

Beavers selectively cut the hardwoods from a balsam fir forest and thus release the conifers which then eventually crowd out the remaining beaver foods, the remaining hardwoods.

Black Spruce Forests

Mature and near mature black spruce forests can perpetuate themselves after fire. This has been the pattern in the northern section of the Grand Falls study area. Only when the soil is exceptionally poor or rich will other types regenerate. Also, if the stands are young when burned, and are not bearing seed, the black spruce forest cannot reproduce itself.

Repeated fires will eventually reduce almost any forest into waste land, especially if the site is poor.

After logging the forest regenerates to a type similar to the original. If the site is wet it regenerates to birch. This has happened over large areas of Rattling Brook logging area.

When the soil is favourable, there is slow regeneration of black spruce forests after logging.

Most black spruce are killed after one year of flooding. Twenty to thirty years are required for the forest to re-establish after the removal of the dams.

As with all conifers, when hardwoods are selectively cut by beavers from a spruce forest, the remaining hardwoods are forced out.

Hardwoods Forests

Even repeated fires cannot normally destroy birch forests from rich sites since the seeds can be transported over long distances. Fire favours hardwood forests. Any favourable site may be occupied if seeds are available. The few aspen stands in Newfoundland have resulted from fires.

Balsam fir will regenerate after logging if seeds are available. If no balsam fir, birch will re-occupy the site. Birch is rarely found in undisturbed forests. It can only survive as a dominate. For 6 years after logging, growth rate of birch is equal to that of spruce or fir. After that, browsing by moose may keep it at an average height of 2.5 feet. This has happened in the Noel Paul River area. It may even be completely eliminated from successfully rejuvenated birch stands. Minimum age for seed production from birch is 25 years.

Aspen and birch normally do not survive more than one year of flooding. Other hardwoods, such as maple, may survive for two years. When the water is removed, hardwoods require approximately 10 to 15 years to re-establish.

If aspen is present, beavers utilize it faster than it can regenerate, thus destroying it completely. As had happened in the Grand Falls study area, birch normally replaces the aspen until it is suppressed by spruce or fir.

If no aspen is present in the hardwoods forest, the forest is more stable and can withstand the invasion of the conifers for several decades since beaver utilization of hardwoods other than aspen is light and consequently the conifers are not released as early.

Hardwoods - Conifers

Hardwoods normally re-establish after fire. This is the pattern south of Lewisporte following a small fire in 1954. However, conifers also began regeneration at the same time and will surpass the hardwoods in a shorter time (15 to 20 years) than would normally have been the case if the forest had originally been mostly hardwoods.

The hardwoods may become dominant after logging if the site is rich enough. Otherwise the original forest returns.

Hardwoods will dominate for a time after removal of the flooding waters. Then the original forest will re-establish.

By selectively cutting the hardwoods, beavers hasten the complete invasion of the conifers.

Alder Swamps

Alder swamps are common in all forest types in Newfoundland. Fire favours alder growth and expansion since it makes more moisture available and clears more space for alder invasion. Most favourable for alder swamp expansion is repeated fires and subsequent long regeneration periods. Fire rarely affects alder swamps because of the wet nature of their environments. In addition to alder, willow and dogwood thrive under such conditions making such sites very dependable beaver areas.

As after fire, alder expands its range tremendously after logging. It often results in elimination of scattered conifers because of the rapidity with which a dense alder canopy is established.

Alder can withstand up to 5 years of flooding but the majority of alder stems die in 2 or 3 years. Flooding by beavers probably causes more damage to alder sites than any other factor.

With removal of the dams, alder regeneration is immediate if sufficient plants survived. If 100 per cent alder deaths occur, alder regeneration must wait for grasses and sedges to re-establish first, a period of approximately five years. (Knudsen, 1962).

Beaver cutting normally has no destroying effect on alder swamps since sprouting is usually greater than cut-back.

Colony Abandonment

The two major causes of colony abandonment are probably lack of food and competition for food. Harassment by predators or man may occasionally result in abandonment.

Lack of Food

In the course of this study, I examined 54 beaver colonies (44 active and 10 inactive) to determine the presence or absence of aspen, birch, alder and aquatic vegetation in these colonies. Thirty of these colonies were within the study areas, the remaining 24 were in various parts of Newfoundland. Of the 10 inactive colonies:

- 1 had no food
- 9 had no aspen; 1 had scattered aspen
- 3 had no birch; 7 had birch
- 9 had poor alder; 1 had abundant alder
- 3 had good aquatic vegetation; 7 had poor aquatic vegetation.

For the 44 active colonies:

- 30 had no aspen; 12 scattered aspen; 2 had relatively good aspen.
- 12 had no birch; 32 had birch
- 42 had good alder growth; 2 had poor alder growth
- 30 had abundant aquatic vegetation; 14 had poor aquatic vegetation.

The terms 'good', 'fair', in the above listing are not in any sense definite terms but they are relative within the 54 colonies and I think they suffice to indicate the relative quantity of food available.

Birch appears in 7 of the inactive colonies. It would not appear that this species is important in holding the colony to its territory. Alder, I think, is a key species. Nine of the ten inactive colonies had very poor alder growth because of moose browsing or flooding death. Forty-two of the 44 active colonies contained abundant alder. Aquatic vegetation may not be the important colony holding species that alder is, but such aquatics as the water lilies, I think, are more important than is normally believed. In the Tobiatic Game Sanctuary in Nova Scotia, colonies of beavers exist almost entirely on aquatic plants in the absence of hardwoods, (Van Nostrand, 1962). These beavers do not construct winter browse piles, but leave the lodge throughout the winter to dig for aquatic roots on the pond bottom. This same practice may be occurring in parts of Newfoundland, particularly the Avalon Peninsula.

Tables 5 and 9 list the data for a more detailed study of 5 active and 2 abandoned colonies in the Grand Falls study area.

Two of the abandoned colonies, J and T, (Fig. 4), have food supplies considerably less than is available to the active colonies. Lack of food is almost certainly the cause of abandonment. A third abandoned colony, Colony A, contains more abundant food supplies than most of the active colonies. Lack of food could not have been the reason for its abandonment.

This withdrawal without apparent reason has been recorded by many investigators. Hodgdon and Hunt (1955), in their Maine study, state that beavers sometimes leave their site before the food supply is depleted.

It appears that alder (and willow, where it occurs) and perhaps aquatic vegetation for pond colonies, are the key species in holding a beaver colony to its territory when all other food species are depleted. This is what my studies indicate for Newfoundland. Other investigators have found similar conditions. Neff (1957) states that food shortage is a primary cause of colony abandonment in Colorado. In one of the areas of his investigations, several colonies were subsisting on little more than willow. These colonies were trapped out by poachers. There was no attempt by other colonies to invade this area. Neff points to lack of willow and other food as the reason. Retezer (1956) in his study of Rocky Mountains beaver habitat, found that of 74 abandoned colonies, 18 had no food, 9 had some aspen plus other food, 38 had no aspen, 9 had abundant willow. For 130 active colonies, 63 had no aspen. Alder and willow was the main remaining food for the active colonies. Knudsen (1962) reports for beaver in Wisconsin that "birch is only used after preferred species are all gone", and that beavers will abandon the colony when all other species are depleted in spite of good birch stands remaining.

When colonies are finally abandoned because of lack of food, or when new sites are colonized by two-year olds in the normal sequence of events, what food species are essential in the selection of the site for the new colony? During my investigations on the Grand Falls study area, two new colonies were established. The site chosen for new colony M lacked aspen entirely, birch was available to a limited degree, but alder was abundant. New Colony Y_1 fared a little better; alder was abundant, birch was available together with a small stand of aspen. The colony site selected by 5 beavers which were released on a small island in Notre Dame Bay was a tiny stream with a rich supply of alder and little else. These beavers had travelled approximately 1 mile across the island from the bog where they had been released. The bog was chosen because it had a small stream flowing out of it and scattered birch was available around the edge of the bog. The alder growth around the bog was not plentiful.

It would appear from these observations that alder may be the major influence in colony establishment just as it appears to be the key species in colony abandonment.

It is probable that topography and density are also factors in abandonment. On New World Island where topography is rough and irregular and where few streams offer pathways of movement, very little colony abandonment occurs. The isolated colonies remain stationary; travelling is difficult and even if it were not, more favourable areas do not exist. In the Grand Falls area, travelling is facilitated by three stream systems and movement occurs more readily.

Competition for Food

In Newfoundland the beaver has three potential food competitors, the moose, muskrat, and the snowshoe hare. The snowshoe hare is the least important of these since its food is limited to terrestrial plants, and its population status is never too strong, even during cyclic peaks.

Table 6 shows the competition by moose and muskrat on beaver food. Moose utilize, at least to some extent, the same terrestrial species that are most important to beaver; alder, willow, white birch, aspen and viburnum. (See also Table 9). Birch is the preferred moose species and is used throughout the year. Aspen is the preferred beaver species but birch is relatively well utilized, being represented at 5.7 per cent of the cut in the Grand Falls area and 4.6 per cent on New World Island, (Tables 9 and 10).

It was apparent from the investigations of colony abandonment that birch is an expendable species to beaver. It would therefore be expected that moose browsing on birch would not affect beavers to the extent of causing colony abandonment. A very high moose density was established in the Miguel Mountain area following the regeneration of birch after a forest fire some 20 years ago. Intense moose browsing has kept the birch at an average height of 10.5 inches. Manuel (1963) states that the age of these trees is 11 to 13 years. Two beaver colonies have established in the area. They utilize the abundant stands of alder (which are not moose browsed) and neglect the birch.

Moose browsing of aspen is probably moderate but it may have an important application. In one small aspen grove of 55 trees in the Grand Falls area, 6 aspen had been felled by beaver and not utilized (Table 7). Three of these had caught in nearby trees and were unavailable. The other three were on the ground. They had been moderately peeled by moose and were not touched by beavers. Several other stumps showed fresher cuttings than the fallen trees. I interpreted this as meaning that beavers had not made use of the aspen after moose had partially used it. In the same stand 5 other aspen had been peeled by moose and were not cut by beavers but were standing in the midst of what appeared to be stumps cut more recently than the peeling.

I did not observe this possible avoidance by beaver of moose-peeled aspen anywhere else. No pieces were found in a brief search I conducted around the dam and lodge of the colony. Barking by beavers would have removed all evidence of moose peeling. On the basis of such limited evidence I cannot say if such a relationship between moose and beaver exist in aspen utilization. The success of beaver in Newfoundland in the comparative absence of aspen would make the moose peeling factor unimportant. It is almost certainly not a cause of colony abandonment.

If moose browsing of a beaver food is a cause of abandonment, that food species is alder. It has been established that alder is the key species in abandonment, and probably also in re-establishment. It was, therefore, necessary to determine the intensity of moose browsing on alder at active and abandoned colonies.

Two abandoned and five active colonies in the Grand Falls area were selected for the study. (Table 8 contains the data). Moose browsing occurred on 88.2 per cent of the alder and 100 per cent of the willow stems available at the inactive colonies. For the active colonies, 23.9 per cent of the alder and 32.4 per cent of the willow stems had been browsed. (*Alnus rugosa* was untouched by moose.) The intensity of browsing on the other species may be read from the table. The greater intensity of browsing at the inactive colonies is evident. The effect of browsing by snowshoe hare is almost negligible.

These two inactive colonies were situated on two ponds in the middle of a long, wide valley. Areas of Barrens and bog alternated along the floor of the valley. Much moose sign was evident and well-worn paths indicated it to be a much travelled moose route. The alder was kept at half its normal height, averaging 2 feet. Such stunted alder would not be valuable to beavers either as building material or food; especially the latter since they had been stripped of all tender shoots.

The intensity of moose browsing on alder necessary to cause movement is uncertain. It would depend on the availability of other plant species as an alternate food and building material. In colonies T and J (inactive) no aspen was available, birch was present in small quantities and aquatic vegetation was meager. These and other species were also moose-browsed, especially a stand of Viburnum trilobum in colony T.

The muskrat is not a competitor for the terrestrial food of beavers. Only 4 of the 25 terrestrial species are used by muskrat (Table 6). On the aquatic food species of beavers, muskrat utilization is 100 per cent and moose utilization is 78 per cent. This would be very serious competition on a food resource were it not for two things; (1) I believe from observations that beaver use of aquatic vegetation, exclusive of the water lilies, is limited. The use is chiefly for nest lining and is probably quickly substituted by terrestrial grasses, uprooted aquatic grasses themselves or chips of aspen. (2) The parts of the water lilies eaten by moose and muskrat are not the same parts utilized by beavers. Beavers prefer the fleshy root or rhizome. Moose and muskrat eat the leaves and stalks. This may have one deterring effect, removal of the leaves and stalks may prevent the beaver from locating the plants.

I believe that a relatively well-supplied beaver colony will not be adversely affected by competition for aquatic food. I think it is probable that absence of aquatic vegetation is much more important. When a beaver colony is subsisting on a meagre alder supply, presence or absence of aquatics may well decide the fate of the colony. The abundance of water lilies in the two Miguel Mountain colonies may be almost as important a factor as the lush alder growth.

Effects of Harassment by Predators and Man

It is uncertain to what extent beavers fall prey to other animals in Newfoundland. I have made only one observation of a death which may have been a predatory kill. I recovered parts of the jaws and some other bones of a beaver at the base of a tree in a food trail in the Grand Falls study area. The bones had a covering of lichen growth on them indicating an age of at least two years. The bones were 300 feet from the water and measurements of teeth width (.25 inch wide) indicated the animal was probably a yearling.

Otter, Lutra canadensis degener Bangs, fox, Vulpes fulva deletrix Bangs, mink, Mustela vision Schreber, black bear, Ursus americanus hamiltoni Cameron, lynx, Lynx canadensis subsolanus Bangs, goshawk, Accipiter gentilis atricapillus (Wilson), bald eagle, Haliaeetus leucocephalus washingtonii (Audubon), horned owl, Bubo virginianus heterocnemis (Oberholser) are possible predators on beaver. Hodgdon and Hunt (1955) report in their Maine study that:

> "The beaver is not preyed upon by other animals to any extent. Its defense mechanisms are excellent. By remaining in or near the water, it eludes most potential land predators and none of the aquatic animals prey upon beaver. Of the land predators, the bobcat apparently attempts to kill beavers. The Canada lynx would be in the same category as the bobcat, but the lynx is not numerous enough to be a factor in reducing beaver numbers."

These two investigators list bears, fishers, otters, mink and avian predators as possible natural enemies of beavers.

Lynx would probably be the most natural predator on all age classes of beaver than any of the other animals listed. Lynx scats were found in all beaver food trails of all colonies with the exception of two colonies that were less than two years old. It is probable that a lynx would use a food trail as a hunting ground for rabbits which are also attracted to beaver trails. It is also very possible that a lynx, encountering a beaver in a trail would attack it.

Saunders (1961) found 100 per cent occurrence of beaver hair in an unknown number of lynx scats collected from an area of central Newfoundland in 1958. He also found beaver hair in 2 of 5 lynx scats from the Grand Falls study area in 1959. But the presence of beaver hair or bone fragment in scats is not evidence for predation since lynx are known to kill and eat beavers in steel traps and to take beaver carcasses from trappers' camp doorways.

I think that in a marginal habitat, or where food is far from water, lynx would probably exert a certain amount of pressure on beaver colonies. Also, during a dry season when it is difficult to maintain water levels. But, because of the normally low numbers of lynx in Newfoundland and their involvement with the rabbit cycle, I do not consider that they are a predatory threat to Newfoundland beaver or a cause of colony abandonment.

During my study, observations of the other possible predators and their relation to beaver activity suggests no disharmony in the beaver colony. Otters were observed in two colonies on several occasions during both summers and no alarm was evident on the part of the beavers. The colonies remained occupied. Miller (1960) reports the occurrence of two adult otters in one of these same colonies in 1959. At the time of his observation there were four beavers, including one kit, present. The beavers were only 'slightly disturbed'. Semyonoff (1951) found no traces of otter predation in the Archangel province of Russia. Zhanoff (1951) reported no instance of predation in the Ob-River Basin of Russia. Hodgdon and Hunt (1955) reported an instance in which three beaver kits were live-trapped from a colony where otter sign was plentiful.

The black bear has been suggested by many investigators as a beaver predator of minor importance. These bears were numerous in the southern part of the Grand Falls area before and during Miller's study. The small number of fishing cabins in the area were regularly raided by the animals. There was no apparent effect on the beaver population which continued to increase until 1960 when there were 24 colonies in the study area. Several of the bears were shot and the others left the area so that there was no evidence of bears during my two summers in the area. The absence of bears did not cause an increase in beaver population. The number of colonies did, in fact, fall to 14 in 1962.

Tracks of mink and weasel, <u>Mustela erminea richarsonii</u> Bonaparte, were occasionally observed around the colonies without apparent effect on the colony.

It is probable that some or all of the predators mentioned occasionally take a beaver. In most cases the prey would be a kit. However, I do not think the pressure of predators is ever sufficient to cause abandonment of the colony by beavers.

Harassment by man is only a cause of colony abandonment where the interference is indirect, such as tree cutting or land clearing around the colony and pollution of streams. Man's natural curiosity leads him to break open lodges and dams and toss stones at the beavers. Such direct harassment as this seldom affects the beavers adversely. It is a common occurrence when large animals use the dams and lodges as bridges or resting places.

In the Grand Falls study area, four consecutive summers of live-trapping, tagging and release did not cause abandonment or in any apparent way adversely affect the animals. On New World Island, many lodges are located in roadside ponds within 100 feet of the highway across the Island (Fig. 7). The beavers habit of damming highroad culverts and drainage ditches is well-known. It is evident that beavers are very tolerant of man and his civilization, even to the extent of becoming a nuisance in some areas.

(B) VEGETATION STUDIES

Food Habits and Factors of Food Utilization

Numerous investigators have reported on the food habits of beavers and all agree that beavers will sample most any herbaceous or woody plant. It is also a matter of agreement that beavers show preference for a compartively small number of plants. Denny (1952) in a review of the literature up to 1950, reports that "Investigators concurred on the general list of plants taken for food by beaver, namely, in order of choice - aspen, willow, cottonwood, alder, maple and ash". Denny also states, "The preference for aspen where available, has been noted throughout the beaver range in North America.

Availability

This is probably the major factor in food utilization. But as important as availability is to the beaver, it is less important to it than perhaps to any other wild animal. The beaver's ability to cut its food, and the fact that this food is the bark of trees is unique in the animal world. The beaver lives on plant food but is actually unaffected by yearly variations of plant food-supply. As Elton (1927) says, "It lives on capital and not on income". Browse that is one inch too high for a deer is unavailable to it. There is no partial availability of a food species to beaver. A tree or a plant is completely available or it is not available at all.

The effect of availability is evident from Tables 9 and 10. A species which is not available cannot become a utilized food. Dogberry, for example, is not represented in the Grand Falls food list, but comprises 4.4 per cent of the total cut on New World Island.

There is also the factor of availability of numbers as well as availability of species. More alder is available in Grand Falls area than on New World Island and although much more alder is cut in Grand Falls, the percentage utilization is approximately the same in both areas - 82.8 per cent and 83.9 per cent respectively. This suggests that availability may not be a factor in alder utilization when preferred foods are not abundant. Colonies need a certain quantity of alder and they take this irrespective of the supply remaining. They do not take more because more is available, unless of course, no other food is present.

If more aspen (a preferred food) were available, less alder would be used. The Grand Falls beavers took 5.4 per cent more aspen than the New World Island animals, and cut 1.1 per cent less alder. It would therefore seem probable that the supply of aspen controls to some degree the cutting of both aspen and alder. As aspen supplies are depleted the cutting of alder increases. Hall (1960) found a similar pattern of alder and willow usage in his California study. He states that "There is no obvious relationship between supply of willow and the rate of use".

Alder is a tough, fast-growing species. It sprouts very rapidly and the sprouts are sizeable stems in 2 or 3 years. It can withstand heavy usage by beaver and still survive. A certain amount of die-back takes place in the alder patch even if no beaver are present. This is usually during winter. If beavers have access to alder in winter they may cause the die-back to exceed the rate of sprouting. This would soon deplete the supply. The supply would also be in danger if beavers cut heavily into one section of the alder stand for more than 2 or 3 years. The animals enjoy the tender shoots and the stand would not be able to maintain itself. Beavers usually shift their site of operation around the colony as alder becomes overbrowsed in one area. This allows time for rejuvenation. Investigators on the rate of rejuvenation estimate that from 20 to 40 per cent of the current year's growth can safely be cut by beavers without endangering the alder supply. This would seem sufficient to meet the alder requirements of beavers under normal circumstances. In Grand Falls, for example, 28.7 per cent of the alder has been cut. There would seem to be no danger there. On New World Island, 61.7 per cent of the alder has been utilized. Here utilization is probably sufficiently in excess of rejuvenation to eventually result in depletion of the alder supplies.

With the exception of alder (and willow, where this species is abundant) the utilization of all other tree species is probably determined by availability. Hodgdon and Hunt (1955) state that, "Other trees occur in the beaver's diet in relation to their availability". These authors quote Hazeltine (1950), "Availability had an effect on the choice of trees cut". My studies also show this. With the exception of alder and willow, utilization of other hardwoods was greater in the Grand Falls study area where availability was greater.

Of all the hardwoods utilized by beaver, aspen is the only one which appears to be a preferred food. The others are used to some extent for construction around the colony, but are probably only secondary or pastime foods. When one is not available, another will be readily substituted. Maple and viburnum were not represented in the food list of the colonies studied on New World Island, but dogberry filled the gap. These expendable substituted hardwoods would therefore normally always be available to beavers and will not be discussed further.

Aspen, however, has no substitute. Wherever it exists it is the favourite food of beaver. When it is abundant it is probably a major influence in determining the areas conolized by beavers. Hodgdon and Hunt (1955), report, "It appears that the presence of this tree has much to do with the distribution and location of beaver colonies". Nash (1951) states, "There is a definite relationship between the presence of aspen and the abundance of beavers". In Newfoundland, however, colonization usually proceeds without the influence of aspen.

In Newfoundland, aspen is the least abundant of all hardwoods. Utilization of this meagre resource is normally determined by availability. Beavers attempt to cut every aspen available, the greater the supply the more intense is the beavers' effort to use it. Under conditions such as this, the aspen cannot long survive. It is not a renewable resource in the sense that alder is renewable. Aspen sprouting and growth is much slower than alder and even large groves are soon depleted. Aspen requires disturbed forest conditions, such as caused by fire or logging, to gain a foothold amongst the conifers. Even with a headstart, aspen is soon dominated by the re-established conifers. As the beavers cut the aspen, they release the conifers which then completely re-invade the area. Thus, the "aspen consumption phase" (Hall, 1960) of a beaver colony is normally the early years of the colony. As Hall says, "Aspen and beaver in any combination, inevitably lead to relatively complete loss of aspen".

In the Grand Falls study area, I investigated 55 old cutting sites at 15 beaver colonies. (I define an old cutting site as one to which the food trail has not been maintained for several years). At every one of these old sites, every available aspen had been cut. The stumps ranged in diameter from 1 to 7 inches.

In the 23 current cutting sites of these same 15 colonies, very little aspen remained. In the colonies were it was available, it was being utilized in relation to availability and forest type.

When aspen is readily available, wastage is great. Swank (1949) quotes the figure of 64 per cent wastage of aspen in areas of high availability. Gibson (1957) suggests 10 per cent wastage on 1 - 4 inch diameter aspen, 50 - 64 per cent on larger aspen. This wastage is due to the trees growing close together, preventing trees cut by beavers from falling to the ground. Large size is a factor in wastage. Diameters under 4 inches are normally completely utilized. When larger trees are cut only the branches and top down to 4 inches were taken in the Grand Falls study area. I found 10 per cent wastage in aspen $<$ 4 inches in diameter, 40 per cent in larger aspen. When aspen becomes less abundant, beavers substitute other trees which usually grow less closely than aspen. Wastage is not as great and fewer trees are cut. Aspen availability effects the number of trees cut by the colony.

The following list illustrates the effect of availability on food habits:

Investigator	Area	1st	2nd	3rd	4th
Hodgdon & Hunt	Maine	aspen	alder	willow	birch
Swank	West Virginia	service berry	willow	cherry	witch hazel
Retzer	Colorado	aspen	willow	pine	alder
Bradt	Michigan	aspen	maple	willow	
Nash	Manitoba	aspen	willow	alder	birch
Northcott	G. Falls, Nfld.	alder	aspen	birch	viburnum
Northcott	N.W.Island, Nfld.	alder	birch	dogberry	willow
Semyonoff	Russia	willow			

Stocking, Forest Type and Diameter Preference

Forest type does effect utilization of tree species other than alder as shown in Table 11. This table was compiled from the same data used for Table 9.

In old cutting sites that were formerly closed canopy aspen, closed canopy birch or mixed hardwoods forest types, 100 per cent of the aspen had been cut. Stump diameters remaining were from 1 to 7 inches indicating complete utilization as the supply neared depletion. Current cutting of aspen shows 95 per cent of the cutting to be in the 1 to 4 inch diameter range class with the 2 and 3 inch diameter classes ranking most important. These represent 75 per cent of the aspen cut.

The 1, 2 and 3 inch diameter sizes represent the most utilized sizes of all trees taken by beaver. (The six 4 inch cherry trees taken in the Grand Falls area is an exception due to non-availability.) In the Grand Falls area 97.8 per cent of the trees cut are in these three diameter classes. On New World Island it is 99.8 per cent. Much greater availability of smaller diameter classes permits the almost total restriction to these classes. The predominance of these small diameter classes in the Grand Falls area is due to the youth of the forest. Selective cutting of the larger trees for firewood by the settlers of New World Island has left a predominance of smaller trees there.

In existing areas of closed canopy aspen, 45 per cent of the aspen has been taken. The diameter size cut is a factor of availability. This is especially true for the first and second year's cutting at a new aspen site. Colony Y_1 in the Grand Falls area cut 19 aspen during its first fall.

The cutting was a fine example of the effects of availability on cutting (Table 13).

The small number of birch and other hardwoods which may be found in an area of closed canopy aspen are ignored by beavers.

In areas of closed canopy birch, a small representation of aspen may be found. At the time of my studies 85 per cent of this had been cut. Similarly, 83 per cent of the aspen had been removed from existing areas of mixed hardwoods. These percentage figures represent the cutting up to the year of my studies. An investigation 5 years earlier or later would yield lower and higher figures respectively. However, taken together, it would appear that since the percentages represent approximately the same number of years of beaver cutting in each case, the aspen in less crowded growing conditions is taken first. The occasional aspen from a hardwoods-conifer forest are completely removed in one or two years.

Birch is normally secured from areas of closed canopy birch near the water. Should any other forest type containing sufficient birch be nearer water, birch requirement will be obtained here. Birch is not a ferreted-out species as is aspen, as little work as possible is expended on securing it. However, the largest tree I recorded cut by beavers was a 23 inch birch which overhung a stream in the Grand Falls area.

Other hardwoods are normally taken from hardwood-conifers forest types. The small number of conifers utilized by beavers are also taken from here.

Distance from Water and Slope of Ground

When considering these two factors of tree cutting, it appears that distances from water and slope of ground which are prohibitive to the cutting of other tree species are not prohibitive to the securing of aspen. I have found that beavers will travel much longer distances and climb much steeper slopes for aspen than for any other tree species. (Table 12). I recorded one distance of 652 feet from water to a small aspen grove where several aspen had been cut. Miller (1963) discovered a single aspen stump cut at a distance of 793 feet from the water. He also reports one colony in the Grand Falls area which preferred to swim 600 feet across the Exploits River and into the woods on the other side rather than cut the birch which was abundant on the shores of their pond.

Other investigators have found a similar pattern in cutting. Bradt (1947) reported that beavers do not ordinarily travel more than 200 feet over land to cut trees but he found aspen trees cut as much as 650 feet from the pond. Hodgdon and Hunt (1955) state that between 200 and 300 feet is the distance normally travelled by beaver for food but for preferred foods they will go farther; their maximum recorded distance was 467 feet from the water.

I found that most of the other tree cutting was done less than 150 feet from the water. The maximum distance recorded for birch was 135 feet. This was a single tree of stump diameter one inch and was directly in the food trail. Alder and willow distance is 140 feet. All other cutting, with the exception of cherry, was within 100 feet of water.

The distances from water suggested by other investigators as the normal foraging distance for beavers are:

Investigator	Area	Distance
Lawrence	Michigan	330 feet
Bradt	Michigan	200 feet
Hodgdon & Hunt	Maine	300 feet
Nash	Manitoba	100 feet
Hall	California	100 feet
Swank	West Virginia	260 feet

At colony J, a small grove of aspen was located 1,100 feet from the colony. Eight hundred feet of this distance was across an open bog. There was no way of knowing if the beavers were aware of this aspen before the colony was abandoned. It seems probable that they would have located it in view of the remarkable ferreting out sometimes observed for single aspen in deep woods. Assuming the location of the aspen was known, the 1,100 feet must have been a prohibitive distance since no traces of beaver cutting was evident. The prohibiting factor may have been the 800 feet of coverless terrain to be traversed. Beavers would have been extremely vunerable crossing this section.

The absence of even moderate stands of aspen in the study areas made it impossible to obtain any significant relationship between the distance from the water and the diameter size or number of aspen cut. The limited quantity of aspen had been practically all utilized at the time of my study. But from the data of the two colonies where aspen was available and from general observations of cutting prior to my study, certain generalizations are apparent. Apart from the selection of small diameter size during the early years of a colony, aspen cutting is probably random and without pattern most of the time. In the colony with the aspen grove where no cutting was done, widely scattered single aspen were cut from dense spruce forests and dragged to the pond over a distance of some 200 feet farther than the aspen grove in which cutting had been abandoned. In following food trails, I have often observed small aspen standing near the water and much further inland, stumps where larger aspen had been felled. Such unpredictable cutting patterns as these suggest that beavers cut aspen where they please, with little regard for plan. A more organized pattern of cutting may exist where aspen is abundant. Investigators in areas of abundant aspen do suggest such a pattern of more trees cut nearer the water.

On New World Island, I recorded a food trail leading up a 75 degree slope to the top of a ridge 320 feet from the pond. Two aspen of one inch stump diameter had been taken. In the Grand Falls study area, glaciation has resulted in a number of very rocky, step-like slopes from certain sections of Greenwood's Brook. Beavers from the colony traversed this difficult stair-like slope to secure four aspen from the top.

Alder is sometimes obtained from slopes requiring a 40 degree climb from the water. This maximum figure was also observed on New World Island. Normally such climbs are unnecessary because of the abundance of alder around the shores of the colony.

All other tree species, including birch and other hardwoods, are taken at the easiest point in the colony.

Food Habits

Summer Foods

At the beginning of my first summer's study (1961), I painted all existing stumps in three cutting areas, each less than one acre in extent. I visited these areas regularly during the summer to record and paint new stumps. Trees were cut at only two of these colonies. At colony A a summer cutting of twelve aspen and one birch was recorded (Table 13). At the second site, Colony Y_1, 19 aspen had been cut during the fall. No cutting was done at the third site, but individual scattered aspen were taken at greater distances from the water during the fall.

Limited tree cutting is done during the summer. Alder is taken regularly, but in small quantity and is probably used mainly for dam repairs. An occasional hardwood, including aspen and birch, is cut near the water. The cutting of twelve aspen at colony A appears to be exceptional. I did not observe anything else similar to this during my study. The two beavers at colony A did not winter there in 1961. They abandoned the colony sometime during the late summer. There may be a relationship between the cutting of the 12 aspen and abandonment of the colony.

On numerous occasions during the summer I observed beavers wandering around in the alders and shrubbery at the side of the pond or stream. They would snip off the top of a blueberry bush or sheep laurel or some other shrub, and eat the tips and the leaves.

Probably the most important summer food is aquatic vegetation, water lilies ranking first among these. The lilies will be discussed more fully later. I was unable to devise a method to accurately determine the summer foods utilized by beavers. Terrestrial shrubs could have been quantatively studied but without a similar investigation of aquatic vegetation such study would not be of very great significance. I was not successful in finding a small pond on which I could manipulate the water level, including draining and refilling. Such a set up as this would have permitted griding the pond bottom and recording (with the pond dry) the removal of pond vegetation by beavers from a system of sample plots.

Since it is necessary to have some knowledge of the summer foods used by beavers, I consider a rough indication better than no information at all. I was able to establish roughly the number and quantity of summer foods used by counting the number of beaver-chewed pieces of each terrestrial and aquatic species found floating the waters of the colony (Table 14). It would seem probable that the more is cut, the more is wasted. The table is an averaging of the material seen in the water during six visits. For example, in 6 visits to Grand Falls colonies, I observed 6 pieces of water lily root, i.e. one piece at each visit. On New World Island, three pieces of lily root were observed on each visit. Two pieces were found for each visit to Avalon Peninsula colonies. This would indicate a greater use of water lilies on New

World Island than in the Grand Falls area, with the Avalon Peninsula occupying an intermediate position.

The water lily ranks the most important summer food of beavers in the three areas investigated. Aquatic vegetation generally would appear to serve as the bulk of the beavers' summer food. Alder is the terrestrial plant species cut more often than any other. The importance of alder as a building material suggests that while it ranks number one of terrestrial plants cut, its utilization as a summer food is much less. The shrubs in general, including a predominance of Ericaceae plants, probably are the most important terrestrial summer food. They rank closely behind alder and their importance as a building material is normally much less than alder, (Table 24).

Availability permitted the limited appearance of aspen and birch as summer foods in Grand Falls. These species did not appear at all on New World Island, and on the Avalon Peninsula no aspen was recorded but one occurrence of birch observed. The reluctance of beavers to cut any tree larger than an alder during the summer is clear. This is due to a number of things; the unpleasantness of cutting and hauling in the heat, increased vunerability as water areas diminish in size, or perhaps an understandable preference for aquatic vegetation in season.

I did not undertake a large scale study of food preference shown by captive beaver. But while engaged in the trap-transfer programme during the study, I did record the food habits of some of the beavers. In order of preference, the tree species were Populus tremuloides, Myrica Gale, Rhododendron canadense, Vaccinium angustifolium, Alnus crispa and A. rugosa, Viburnum cassinoides, and Betula papyrifera. No aquatic vegetation was offered.

Nash, in a similar general study of food habits of captive beaver in Manitoba, lists aspen, willow, alder and birch as the order of preference. My results are similar to Nash's, but both suffer from failure to include the aquatic vegetation. I do believe, as already stated, that aquatic vegetation is the basis of the summer diet, and that the water lily ranks number one in this.

In an attempt to learn something of the food potential of the water lily, I carried out studies of these plants in the Great Rattling Brook area of central Newfoundland. Thirty complete yellow water lily plants and root systems were dug from the bottom. These plants were all from water less than four feet deep. The roots were so firmly rooted into the bottom that great care was required in releasing them, and I could devise no workable method to obtain them from water deeper than four feet.

Two species of yellow water lily were identified, *Nuphar microphyllum* and *Nuphar variegatum*. Table 15 contains the size and weight data.

Nuphar variegatum grew on muddier, boggier bottoms and produced the largest and fleshiest roots, up to 4 inches in diameter. The stems which support the leaves do not sprout all along the root, but only from nodes spaced at various intervals along the root. There was always a forking of the root at the node, resulting in a root system containing up to 5 branches. The longest internodal distance was 14 inches, the shortest was 4 inches. The longest overall root system was 27 inches. I could find no relationship between size or number of leaves on the surface and size of root beneath. From 6 to 14 stalks may sprout from a node irrespective of the diameter or length of the root. Each stalk supported a single leaf. The leaves varied from 2 to 10 inches in length.

Nuphar microphyllum grew where there was a higher percentage of sand in the soil and produced smaller, much harder roots. These roots were never more than 2 inches in diameter and were not fleshy. The leaves were just as numerous as for the other species but were smaller, ranging from 1 to 4 inches in length. The stalks supporting the leaves were thinner and string-like in appearance and were redder in colour. The length of the overall root system is similar to that of N. variegatum.

The lilies grow even on those parts of the bottom which are quite rocky. If there is soil enough the roots lie between the rocks and are very difficult to reach. Roots in this position would be inaccessible to beaver and thus unavailable as food. Twelve of the 30 plants secured for the study were so masked by rocks of various sizes as to be unavailable to beaver. This represents 40 per cent of the plants secured. These plants were chosen at random from a 2 mile section of Rocky Pond and included 1.75 miles of pond shore and .25 miles along the brook flowing out of the pond. It is not possible from this limited study to say that only 60 per cent of the water lilies are available to beaver. The availability figure will vary in relation to the geology of the bottom. But the point revealed by the study is that a mass of bobbing water lily leaves on the surface of a pond does not indicate a limitless food resource beneath.

I did not observe lilies growing in water over a depth of 6 feet. The roots appear to grow from one end and die back at the other, thus creeping along the bottom. This is how I interpreted the observation that the root was usually in process of decay at one end but was always vigorous at the other end. The roots appear to grow roughly parallel to the shoreline and are always in the same depth of water. If the roots were perpendicular to the shore the plant could grow into deeper water if the level of the pond began a gradual drop.

I also found that both species of lily grow in the tide free bends of the streams. The species present depending on the sandiness of the soil, N. microphyllum predominating. Here also there was a general growth pattern of the root parallel to the riverbank. In the sandy and pebbly sections of the stream, the roots are not as deep into the bottom as the normal two inches.

Beavers probably do not utilize the leaves and stalks of the water lily to any great extent. Moose nibble and eat the leaves and stalks, as also do muskrat. I have observed these two animals feeding on these parts of the plants, but I have never observed beavers doing so.

In the Grand Falls area I observed the tracks of a beaver in the mud surrounding Seacat Pond. The pond had been abandoned by beavers many years ago judging by the caved-in and grassy condition of the old lodge. By following the tracks, I determined that the animal had come from a colony on Greenwood's Brook, a quarter of a mile distance overland. Aquatic vegetation in this colony was not abundant, while in Seacat Pond there was a denser growth of water lilies than in any other pond of the study area. Beaver tracks were observed on two other occasions around the pond. The movement data of these two sets of tracks was not determined. Print measurement of the three tracks indicated that at least two animals were responsible for the tracks. I suggest that these observations indicate a desire by beavers of nearby colonies to feed on this aquatic vegetation.

Winter Foods

The plant species appearing in the winter browse piles of the two study areas (Table 16) probably represents the typical Newfoundland beaver colony's winter food. By comparing this with Tables 9 and 10, it is obvious that availability determines the browse pile composition. Alder represents the largest volume of material (60 per cent in Grand Falls and 70 per cent on New World Island). Birch is next in importance, followed by aspen and other hardwoods and a small representation of shrubs. Conifers are sometimes included but a summer checking of the remains of browse piles reveals that the sections of conifers are seldom browsed in any way. The remains of winter browse piles consists mainly of alder with this trace of conifers.

Effects of Flooding on Vegetation

The beaver is unique among most animals in that it creates its own living space or niche. But in doing this it also creates the conditions which can destroy its food. Water which is so laboriously hoarded, will kill most of the vegetation which it floods. Table 17 contains data for the time required to water-kill the more common plant and tree species.

When a beaver dam is errected, the most conspicuous change occurring in the environment is the killing of trees by the impounded water. Most herbaceous material is killed in 1 or 2 years. Many alder and willow plants are killed in 2 years but some survive for as long as 5 years.

Wilde (1950) and his co-workers investigated the changes produced in soil fertility by impounded water. The two principal processes taking place in flooded soil are de-oxidation and hydrolysis. Deoxidation causes the soil to be saturated with toxic gases including hydrogen sulfide. This gas reacts with the iron compounds of the soil and enriches the soil in soluble ferrous iron. The accumulation of ferrous iron ties up the phosphorus of the soil in an insoluble form. The end result is a soil stripped of its available nutrients (mainly phosphorus) and enriched in growth-inhibiting substances (gases). These toxic substances injure the plant roots and useful soil microorganisms such as the symbiotic mycorrhizal fungi on which depends the successful growth of trees and plants. The absence of mycorrhizal fungi may be the major factor retarding the re-invasion of trees into such soil. Successful tree and plant growth is only attained when the soil has been re-vitalized by natural forces such as water fun-off and the normal living processes of birds and animals.

When water is impounded behind the dam there is a rise of the ground water level in the soils adjacent to the pond. This decreases the tree growth by partly drowning the roots systems or by decreasing the amount of air in the soil.

When the dam is removed, the change of ground water level causes greater damage than flooding. This is because the rapid change in ground water level creates the danger of drought injury which normally decreases the growth rate of forest stands adjacent to the pond.

Plant succession on drained flowages is briefly as follows: following removal of the dam there is an invasion by grasses and related marsh plants. This vegetative cover obstructs the regeneration of forest trees. Willow, alder, dogwood and other moisture-loving plants come next. It may take several decades for the original hardwood or conifer forest to re-establish. The length of time and the pattern of re-invasion is determined by the type of soil. On coarse, sandy soils hardwoods usually re-establish in a few years. On fine,silty soils the grasses may resist the re-invasion of forests for 10 to 20 years. (Wilde, 1950).

Because of the key importance of alder to the success of beaver colonization, a close look at the flooding survival of this plant seems indicated.

In the Grand Falls study area, colonies Y_1 and M were 2 and 3 years old respectively in 1962. The colony territories were increased in size by flooding each year of my study (Table 21). There was no apparent damage to the flooded alder. It sprouted just as vigorously as before flooding. Colony A was closely investigated because of it's unique position of being abandoned while still containing aspen. From what I could establish from Miller's studies, this colony was four or five years old at the time of abandonment. Alder stands around the periphery of the flowage appeared to be suffering no adverse effects from the flooding. But in the central part of the flowage, a small area of standing alder contained only dead stems. These alder had been flooded for a longer time, (5 years), to a greater depth, (3 feet), than the periphery alder. Part of the alder stand at colony M had been flooded by almost 3.5 feet of water for 2 years and survived. Other such observations as these during the study suggest that it is the duration of the flooding rather than the depth that effects the alder. Survival is not threatened until probably the fourth or fifth year. Payne (1961) found a similar survival pattern in his Nova Scotia studies. He states that "Where alder has survived in excess of four years, site, resistance of individual clumps, age of clumps or other factors, may have had an effect". He suggests that young stands of alder will survive more readily than older stands, but that older stands flooded for less than 3 years will survive. The development of adventitious water roots by the flooded alder may be a factor in its survival. Little data was collected on these roots during my study but the presence of such roots was noted upon occasion.

It appears that alder will survive sudden changes of water levels through drainage of flowages. During the first summer of the study, I removed two beavers which had established the summer before on a stream adjacent to a logging road in central Newfoundland. Their dam had caused sufficient flooding to eventually become a threat to the road. I destroyed the dam after removal of the beavers. The following summer I re-visited the drained flowage. There was no apparent damage to the alder resulting from the sudden drop in water level after 2 years of flooding. Similar removal of two beavers from a flooded drainage ditch at the end of one of the runways of Gander airport caused no damage to alder stands flooded for one year.

I have no data for the length of time flooding, followed by rapid drainage will be damaging to alder. Payne states that alders flooded for 4 or more years will be effected by sudden drop of water levels. He further states that a gradual drop in water level will effect alder flooded for a shorter time than 4 years.

Generally then, it appears that alder can withstand flooding for up to 3 years. Depending upon the age and condition of the stand, some may perish in 2 years while others survive for 5. Depth of water is not as important a factor as duration of flooding.

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(C) POPULATION STUDIES

Population Dynamics

Most species of wild animals exhibit some form of territoralism; they select and defend an area against competing members of the same species. In some cases the territory only serves in time of mating, sometimes only for feeding. Sometimes it may serve both purposes, temporarily or permanently. Defence of the territory is sometimes conducted by the male, in other species the female is the home defender.

For the beaver, the colony territory means permanence. It lives there. Feeding, mating and raising of young all take place within the territory. The colony is a social grouping and defence of the territory is normally the responsibility of the group.

The territories of beaver colonies vary greatly in size. This variation is apparent even in land areas of physical similarity. The number of beavers per colony is normally not unduly variable. In the Grand Falls study area, colonies of 4, 5, 6, and 7 animals represent 83 per cent of all colonies. The mean colony size is 4.6 beavers. Figures for representative sections of the rest of Newfoundland give a mean colony size of 5.1 beavers (Bergerud, 1961). Litter size of Newfoundland beavers compared to other regions of North America are:

Region	Total Litters Recorded	Average Litter Size	Extreme Litter Size	Source
North Dakota	16	4.2	2-6	Hammond
Michigan	65	3.7	1-8	Brandt
Washington	115	3.6	1-8	Provost
Alaska	11	2.8	2-4	Hakola
California	14	2.7		Grinnell, et al
Newfoundland	81	2.5	1-5	Miller

Normally, then, a beaver colony is not too variable in numbers of animals. Many large territories together in an area results in a low density beaver population. Small territories give a high density. This is a problem of concern to the wildlife manager since the beaver is a valuable fur resource.

Inter-Specific Conflict

The moose and the muskrat are the two competitors for beaver food. Heavy competition by these species could cause an expansion of colony territory to annex food supplies.

Harrassment by natural predators or by man may cause the beaver much concern and keep him near the water. Under these circumstances it is not possible to travel long distances overland for food. Expansion of the territory along the water front to new areas of food adjacent to the water takes place.

Another possible effect of harrassment would be to limit the colony to a small portion of the pond or lake in the hope of escaping the predator. This is only conjecture. I believe that harrassment has little to do in determining the size of the colony territory. My observations in the study area indicate no adverse effects of normal harrassment on the beaver colony. On reviewing Miller's trapping and tagging data, I found that this disruption of the life of the colonies in no instance caused the abandonment of any colony or resulted in change of territory size.

Intra-Specific Conflict

The degree of tolerance of one beaver colony for another is a factor in determining territory size. Water is the paramount thing in a beaver's existance. Invasion of the home waters by an outside beaver is not tolerated. Territories do not overlap. There is always a water and land neutral zone between colonies. More emphasis is placed on the water distance. This is shown by measurements made in the Grand Falls study area (Table 20). The average water distance between colonies is 674 yards. The variation is from 2 to 1,276 yards. The average land distance separating colonies is 184 yards. The variation is 0 to 528 yards. These measurements have more meaning when applied to stream colonies since pond colonies are already naturally separated. However, in the Grand Falls area, the ponds are so close together in such gentle topography, that the neutral zone readily applies.

On New World Island the rough face of the land creates a natural neutral zone and makes it unnecessary for the beavers to enforce one. The exception to this is the establishment of 2 colonies on the largest lake on the island. The colonies are located one at either end of the lake. The shape of the lake hides the colonies from each other. Otherwise, the situation would probably be intolerable. This is a variation of the well-known edge effect.

French Pond in the Grand Falls area is of comparable size with this lake on New World Island. Yet, only one colony is found on French Pond. The pond is regular in shape and the establishment of another colony would be quickly obvious to the present colony.

In the natural course of territory expansion, a stream colony must usually expand upstream or downstream. The only alternative is the annexing of a pond adjacent to the stream. Consequently, new stream sections are annexed a little at a time because the new territory may bring the colony within the aggression zone of the next colony along the stream. Thus, stream colonies are normally smaller than pond colonies because of the pressures inherent in the method of expansion. Pond colonies in an area of numerous ponds such as the Grand Falls area have almost no interference in expansion. If another pond is needed and is available, it will be annexed if not already occupied, (in which case the colony must look elsewhere). The territory grows in pond-sized chunks and is normally larger than a stream colony.

A combination of stream and pond or ponds give the advantages of both to the colony. Ten of the 16 colonies investigated in the Grand Falls area contained 2 or more ponds plus the stream section (Table 18).

In the Grand Falls area, all the ponds near enough for annexation by the present colonies have already been added to the various territories, and in all but two cases sections of stream are available for expansion. On New World Island, only 3 of the 10 colonies investigated had water available for expansion. In all 3 cases, these were stream sections.

From the foregoing, it is apparent that stream colonies are normally smaller in size than pond colonies. This is important in considering the population density of the areas.

Age of the Colony

New colonies began with a newly-mated pair. Two animals need little food and the territory is usually small. The two youngest colonies in the Grand Falls area are the smallest in size. (Table 18). Colony M was developed in 1960. It was 110 yards long the first year (Table 21). In 1961 it had grown to 147 yards and in 1962 it was 195 yards long. The colony was established on a small stream. Colony

Y_1 became established on a larger stream in 1961. It was 160 yards long this first year. At the end of 1962 it had grown to 250 yards.

This is typical of the trend of expansion. When a colony is established no more territory is annexed than is needed to meet the needs of the colony. Both colony M and Y_1 had approximately .5 miles of stream available at both ends of the location site at the time of establishment, but only the needed amount of territory was claimed.

As kits are born and food supplies used, expansion takes place.

The oldest colony in the Grand Falls area is Colony S. It is 2,200 yards long, including the lake and stream sections at each end. The original site of colonization was the lake. As the population of the colony increased beyond the food supporting capacity of the lake, the stream sections were annexed. The colony upstream from Colony S is the new colony Y_1. There are 420 yards of stream separating the two colonies. The second year expansion of Colony Y_1 was upstream away from Colony S.

The es tablishment of this new colony Y_1 between the two existing stream colonies illustrates how the slow rate of expansion of stream colonies creates the conditions for a larger beaver population than is generally found in an area where pond colonies predominate.

Movement

Movement of beavers is probably of three types:

- natural emigration of sub-adults (two-year olds)
- emigration of adult males who have lost their mate.
- movement of individuals or the entire colony within the colony territory or outside.

The first two are part of the well-known pattern of the beaver's way of life. Since this paper is mainly an investigation of the factors influencing carrying capacity, these types of movement are of no concern. The third type of movement will be briefly considered since it may be related to carrying capacity.

As has already been stated, the topography of New World Island has created what may be considered as isolated colonies. Beavers remain in these colonies until forced to move through lack of food or other such ultimate cause.

In the Grand Falls area much movement takes place between the ponds of the multi-pond colonies or between the stream and ponds of a stream-pond combination colony. Table 22 indicates the movement data of the 14 tagged beaver trapped from the area in 1962. Only 3 of these animals had never been recaptured away from the site of original capture.

These were 3 females. Of the remaining 11 beavers, 5 moved outside the colony territory as well as within it, and 6 showed movement only within the territory.

When considering the over-wintering sites of the colonies, there appears to be reluctance to occupy the same pond for several successive winters. Since 1958 , only 2 colonies, N and S, have over-wintered in the same site three winters in a row, (Fig. 5). It appears that deep water conditions are preferred during the summer, especially if it is a dry summer, since a natural lake provides better water conditions than the streams. Fourteen of the 17 different capture sites of Table 22 are the larger bodies of water in the colonies concerned. This represents 82 per cent re-capture in deeper water. Perhaps aquatic vegetation also influences the choice of the larger ponds in summer. For overwintering, however, the streams are preferred. Since 1958 there have been a total of 84 lodges in which beavers overwintered. Of these, 61 or 73 per cent of the lodges were on the streams in smaller stream ponds of the colony territories.

Looking again at Figure 5, it is apparent that a general movement trend is taking place away from the marginal habitat at the southern end of the study area to the more favourable Greenwood's Brook drainage system.

The southern part of the study area is now poor beaver habitat. More forest fires have ravaged this section than elsewhere in the area. Consequently, soils here are poor in the nutrients required for successful invasion of forests, permitting instead only a lichen woodland to develop. Fewer ponds and streams are found in the southern part. The pressure of moose competition has already been discussed for the 2 abandoned colonies in this area. It is probable that the carrying capacity of the study area had been lowered to a point where movement for food became necessary. It would be expected that the earliest movement in such a case would be from the areas of marginal habitat to areas of available food. This is apparently the pattern.

Stability of a Population

Newfoundland has only small and isolated birch forests. Aspen is found in very few areas and then only in small pockets usually less than an acre in extent. Consequently, beaver populations that rely on aspen and birch are not stable over a long period because of the animals' tendency to utilize completely the small quantities of these species available.

On New World Island, aspen is rare and birch not very abundant. The population here is very stable. This stability is due mainly to unfavourable topography. But some movement does occur, the natural dispersal of sub-adults. I believe that if better food resources were available, there would be more movement of the type described for the Grand Falls area. However, the general lack of preferred food plus unfavourable topography creates a very stable population.

In the Grand Falls area some aspen is available and birch and other hardwoods generally fairly abundant. Beavers become accustomed to having these species in their diet and will undoubtedly search for them. I believe these same animals eventually become adjusted to living on alder and other less preferred food species after a number of years of fruitless searching for aspen. But while the movement in search of food continues, an unstable population results. For this reason, the Grand Falls beaver population is less stable than the New World Island population. (The ratio of inactive to active lodges is a measure of the difference in stability of the populations in the two areas.)

Generally speaking, Newfoundland lacks the food species of beavers which make for unstability of population. Except for the few isolated areas where aspen is available, a small but more stable population is characteristic of the Province.

The intense glaciation which Newfoundland has under gone has created numerous lakes of glacial origin. These lakes are very permanent and stable. Such lakes were formed when large blocks of ice melted, leaving holes or "kettles" in the plain of the moraine. Kettles are of many sizes and shapes and when they are deep enough for bottoms to be below the water table, permanent lakes result. Much of Newfoundland is thus stable beaver habitat, (Fig. 6).

(D) CARRYING CAPACITY

Factors Affecting Territory Size

Topography, Water Type and Availability

Topography determines the type and condition of water available to beavers (Table 1). On New World Island the topography is one of numerous small hills, small ponds bogs. There are very few miles of suitable stream. On New World Island 92 per cent of the beaver colonies are in ponds and lakes. These are more or less isolated colonies whose size is determined by the size of the pond and the border of forest surrounding it. Such colonies cannot normally be expanded. When food supplies are exhausted, the colony must move.

The size of 10 New World Island colonies is shown in Table 19. The colony size is the pond size. The largest lake on the island is approximately 1 mile long and this lake supports 2 colonies, 1 at each end. Other than this, it is 1 colony per pond.

Stream colonies are very expandable. In the Grand Falls area, where 67 per cent of the colonies are stream colonies, the largest stream colony is 1,848 yards long and the smallest 110 yards long. The largest colony in this study area was a lake colony 2,200 yards long.

Because of a less severe topography in the Grand Falls area, easy movement between ponds is possible. Consequently, 2 or more ponds are usually included in the colony territory. Table 18 gives the description of 16 colonies investigated in the Grand Falls area. There were a total of 26 colonies in this study area. Eight of these were pond colonies. Of there 8, only 2 contained a single pond in its territory. A favourite type of colony appears to be one that includes 1 or more small ponds and a section of stream. This is only possible when topography permits it.

Bogs may also be colonized if they are wet enough. There are approximately 4 square miles of bog in the Grand Falls area. Two colonies are found on bogs there. One of these occupies a small natural bog pond and a stream section in the middle of the large bog and perhaps may be equally considered a stream colony as I have done. The other is a true bog colony, apparently having excavated a circular miniature pond some 20 feet in diameter in the centre of the bog. The lodge stands near the centre of the excavation. Canals are easily constructed in such terrain and four of them radiate from the centre and across the bog to the upland slopes 150 feet away where alder, birch, and scattered aspen are found as well as good conifer growth. Alder is also available on most of the drier hummocks of the bog. The surface of the bog is covered by approximately 1 foot of water resulting from the damming of the small brook trickling out of the bog. The excavated centre of the bog contains approximately 4.5 feet of water.

On New World Island there are approximately 15 square miles of bog. No bog colonies are found there. I believe this is because of the drier nature of the bog. The forest cover of the island has been two-thirds devastated by local citizens. This, plus the fact of irregular topography and fast flowing streams, allows the bogs to become quite dry. Isolated bogs are found surrounded by hills with sufficient forest cover to keep the bogs wet all year round. But these bogs have no streams draining from them. A moving trickle of water through the bog is a requirement for beaver colonization. I believe that bogs are seldom colonized from choice but only from necessity.

During this investigation I covered much of Newfoundland in light aircraft. On the longer straight line flights, I sometimes recorded the occurrences of beaver lodges below and the type of water on which they were located. These observations were limited to the ¼ mile strip beneath the aircraft. At distances further from the flight line, pond or lake lodges would easily have been missed whereas stream colonies would have been **plainly** indicated by the usual area of dead vegetation resulting from the flooding. The locations of the 126 lodges observed on these flights outside the study area were:

Stream		Pond		Lake	
No.	%	No.	%	No.	%
84	67	22	17	20	16

No attempt was made to introduce availability of water type into the consideration of these locations. The typical Newfoundland terrain is so studded with ponds and lakes that availability of all water types may be considered equally good. As the table indicates, and as also shown by Table I, a preference for streams as colony sites is indicated.

Food Supply

The type and quantity of available food is one of the most important factors in determining the size of colony territory. Aspen is generally acknowledged as the preferred beaver food. Aspen trees grow very close together and are capable of supporting from 1,500 to 3,000 2-inch diameter trees per acre, (Bradt, 1947). Using Bradt's widely quoted estimates for beaver cutting, 216 aspen trees per beaver per year, an acre of aspen would last the average Michigan beaver colony of 5 animals for 1 - 2.5 years. Stocking studies of the few aspen groves available in my study areas indicate that, if an acre of aspen could be found in Newfoundland, it would contain approximately 1,600 trees. (Table 25). This could support the average Newfoundland colony, 5.1 animals, for several years even using Bradt's very high figure. I consider Nash's (1951) figures of 130 aspen cut per year per colony for Manitoba to be a more reasonable figure and more applicable to Newfoundland beaver. The only quantity data I have for aspen cutting has already been referred to, 2 beavers cut 19 aspen in 1 year. This is an isolated case but if considered in terms of cutting per colony, it would mean 42 aspen per colony per year. This approaches Nash's lowest yearly cut of 49 aspen by 1 colony for 1 year.

Whichever utilization figures are used, it is seen that an acre of aspen will support a beaver colony for several years. A small colony territory will suffice, just large enough to include the aspen stand and alders for building. Preferred foods permit smaller colonies

Unfortunately, this ideal condition does not exist in Newfoundland. If aspen is available to the colony it is as individual trees scattered among the conifers or as small and quickly depleted stands. Consequently, these colony territories must be larger to include the same quantity of food. As habitat conditions move towards the marginal, as far as food is concerned, larger and larger areas must be added to the territories to obtain the required food. Where topography prevents expansion, abandonment of colony results.

On New World Island, food is not a factor in territory size because topography demands that pond size be equal to territory size. In the Grand Falls area, expansion of colony territory to annex new food supplies is a common occurrence. The network of streams and ponds here makes it possible to add a further section of stream or another pond to the territory by simply occupying it and building a lodge near the new food supply. On New World Island a pond remains active longer than it will in the Grand Falls area because on the island abandonment rather than expansion is the rule when food supplies are depleted.

Considered in its broadest aspects, carrying capacity for beaver is a matter of available food and available water.

For the wildlife manager, the knowledge of carrying capacity is an urgent need. Decisions affecting the opening and closing of seasons are based not only on present populations, but on future populations. Animal populations display a typical pattern of growth. This pattern is commonly referred to as a sigmoid or S-shaped curve. Populations show a slow initial increase followed by a rapid rise, and finally a levelling off as carrying capacity is reached. The curve level at which the population becomes stabilized is known as the upper asymptote. Fluctuations around this asymptote constitute the minor annual variation of a normal population.

Throughout North America, investigators report that colonies living on aspen have larger populations than colonies living on other foods. Hay (1958) reports 7.8 animals per colony in Colorado where aspen is available, 5.1 animals per colony where it is not. Nash (1951) states, "The limiting factor to beaver densities is the abundance of <u>Populus tremuloides</u>", (aspen). Bradt's (1947) studies in Michigan indicate that colonies of 12 animals are possible where aspen is available.

Newfoundland, being almost without aspen, has a population per colony of 4.6 beaver. This is a lower per colony average than recorded for elsewhere in North America. Some other averages are:

Colorado	6.4
Maine	5.2
Michigan	5.1
West Virginia	5.3

Lack of preferred food is probably the limiting factor in the size of Newfoundland beaver populations.

Beaver populations adjust their number to keep them in balance with a food supply that is continually changing. These adjusting mechanisms have been operating in the population of the Grand Falls study area (Table 23). In 1958, there were 20 active lodges in the 15 square miles study area. All trapping was prohibited. In 1959, there were 23 colonies. In 1960, the population reached its greatest numbers when 24 colonies wintered there. The downward trend began in 1961 with 18 colonies and continued in 1962 when 14 active colonies remained. During the early years there were an average of 4.4 beavers per colony. In 1962, the figure had declined to 2.2 beavers per colony. Only three females were pregnant in 1962. It is almost certain that the dwindling food supplies had adversely affected the reproductive rate and caused a movement out of the area.

After the trapping out of the study area in 1962, 12 colonies moved in and established there in 1963. I would estimate that 12 to 16 colonies represents the carrying capacity of this area. This is approximately one active colony per square mile. If considered only in terms of stream miles, it is approximately one colony per stream mile. Although the water types are excellent for beaver, the low concentration of food prevents greater density. Hodgdon & Hunt (1955) determined that 8 colonies per stream mile were possible for 100 per cent food availability. Rawley (1954) estimates 5.7 colonies per stream mile in the best beaver areas of Utah. Newfoundland will never support such beaver densities.

A final necessity in determining carrying capacity from food supplies is the distance from water beyond which food is no longer considered available. The averages distances suggested for other areas of North America have already been reported. My studies indicate that 300 feet is a maximum unless aspen is present, in which case aspen within 600 feet and other food within 300 feet represents the available food supplies.

In Newfoundland, as elsewhere in North America, small streams and pond-stream combinations s upport the larges t beaver populations. The Grand Falls area is such an area. When the population reached 24 colonies in 1960, it represented 1.6 colonies per square mile. This population exceeded the carrying capacity of the area since during the next two years there were two successive drops in the population resulting in 0.9 colonies per square mile in 1962. I estimate this to be near the upper asymptote of the population curve. One colony per square mile probably represents the carrying capacity of the area and it will be interesting to view the re-colonization of the area following the trapping out of 1962.

On New World Island the 0.7 colonies per square mile represents an increasing population which may eventually reach one colony per square mile. Even unlimited food supplies could not establish a density much greater than this because of unfavourable topography.

Carrying Capacity Index

The Grand Falls study area represents the most productive type of Newfoundland beaver habitat. The water is excellent and the food typical of wilderness areas throughout the Province. The carrying capacity here represents a high on the index system, $>$ 1 active lodge/square mile.

New World Island has comparable food supplies but the water conditions for beaver must be classed as moderate.

The carrying capacity index for this region (.7 active lodges/square mile) would be medium.

Areas where both water and food are questionable would become low carrying capacity areas. A carrying capacity index of $<$ .5 active lodges/square mile may be assigned to these areas.

Tentatively then, three density classes may be assigned to Newfoundland beaver habitat. (Fig. 6):

1. Low - $<$ .5 active lodges per square mile
2. Medium - .5 to 1 active lodge per square mile
3. High - $>$ 1 active lodge per square mile

The status of the population within any area is indicated by the number of inactive lodges per active lodge. The declining Grand Falls population in 1961 shows 4.3 inactive lodges per active lodge (18: 77). Before reaching its upper asymptote (while still increasing) the Grand Falls population had $>$ 3 inactive lodges per active lodge. The increasing New World Island population shows 0.8 inactive per active lodge. I suggest that a population with 1 - 3 inactive lodges per active lodge is relatively stable.

Summarizing these status classes:

(1) 1 inactive lodge per active lodge, a young and increasing population. Below carrying capacity.

(2) 1 - 3 inactive lodges per active lodge - a stable population. A balance between carrying capacity and population.

(3) > 3 inactive lodges per active lodge - a declining population. Above carrying capacity. (Or an over-harvested population.)

By combining the two indicies the wildlife manager can gain much information. For example, a high density beaver area may show evidence of being over-harvested. Or a low potential density area may require additional harvesting to keep the population within the limits of the carrying capacity.

Denney (1952) in a summary of North American beaver management, suggests that large land areas such as provinces or states show a general trend of habitat in relation to beaver. He categorizes these trends as (1) improving, (2) static, (3) deteriorating. His conditions are:

Improving - reversion of agriculture land to forest, above average rainfall, pulpwood cutting (which permits hardwood growth).

Static - Unchanging

Deteriorating - agriculture increasing, land reclamation, little average rainfall.

Mainly on the basis of pulpwood cutting, he considers Newfoundland to be improving beaver habitat. His investigations were in 1947-48. Because of continuing pulpwood operations and also because of the numerous forest fires which ravaged large areas of our province in the last few years (Fig. 6), I believe Newfoundland may still be classed as improving habitat.

The following three habitat classes for beaver in Newfoundland are proposed:

Class 1 - Productive - alder with or without aspen or birch; other hardwoods; streams and ponds with stream gradient 1 - 3 per cent; dependable water supply; 1 colony per square mile.

Class 2 - Moderately Productive - alder and some hardwoods in moderate supply; larger ponds and/or streams with gradient $<$ 3 per cent; water supply dependable; .5 - 1 colonies per square mile.

Class 3 - <u>Marginally Productive</u> - alder in limited supply, no hardwoods; large lakes or stream gradient > 3 per cent; water supply not dependable (e.g. fluctuating); less than .5 colonies per square mile.

Table 24

Material used in lodge and dam construction in Grand Falls study area and on New World Island.

Area	Alder	Birch	Aspen	Spruce	Other	No. of lodges and dams
Grand Falls	54%	16%	10%	3%	17%	15
New World Island	83%	8%	4%	1%	4%	10

Table 25

Stocking and Growth of Aspen and Birch
in Grand Falls study area

Forest Type	D.B.H.							
	1	2	3	4	5	6	7	8
Closed canopy aspen								
Aspen								
Stems/acre	370	330	330	100	330	70	30	30
Mean age		28		38	39		46	
Mean Ht. (ft.)		20		39	33		47	
Sample size (plots)								
Sample size (trees)								
Birch								
Stems/acre	70		30					
Mean age	35		27					
Mean Ht.	32		29					
Sample size (plots)								
Sample size (trees)								
Closed canopy birch								
Aspen								
Stems/acre	15	15	7	7				7
Mean age		25		35				
Mean Ht.		25		33				
Sample size (plots)								
Sample size (trees)								
Birch								
Stems/acre	192	357	300	346	223	165	92	46
Mean age	15	36	30	35	41	36	50	
Mean Ht.	14	36	28	36	41	40	35	
Sample size (plots)								
Sample size (trees)								
Scattered Birch & Aspen								
Aspen								
Stems/acre	30	30	20	30				
Mean age		25		35				
Mean Ht.		16		34				
Birch								
Stems/acre	100	200	200	170	70			
Mean age	16	35	23	35	39			
Mean Ht.	14	32	25	32	39			

All plots 1/100 of an acre

CONCLUSIONS

Topography determines the availability of water for beaver colonization. Streams with gradient less than 3 per cent are the most favourable areas for long time beaver occupancy. Such habitat supports higher beaver densities than any other type in Newfoundland. Ponds are colonized readily, lakes fairly readily and bogs only out of necessity.

Abnormal fluctuations of water levels as a result of logging operations precludes beaver colonization in such rivers. Beavers will, however, travel these rivers and colonize their tributaries.

Logging and forest fires are beneficial to beavers since these create the conditions necessary for an invasion of hardwoods. Aspen in particular, and hardwoods generally, are the preferred beaver foods. These are not abundant in Newfoundland and alder is the most important plant species to beavers, both as a food and as a building material. Aquatic vegetation, particularly the water lilies, is the major constituent of the beavers' summer diet. Tree species, except alder and aspen, are represented in the beavers' diet according to availability. More than 90 per cent of the trees cut are in the 1 - 3 inch diameter class. Distances up to 600 feet are travelled to obtain aspen, but 300 feet from water is the maximum distance for all other tree species.

Most species of vegetation flooded by beaver are killed in 1 or 2 years. Alder may survive for 5 years.

Predation, or harrassment by man, does not normally adversely affect beaver populations in Newfoundland. These seldom cause colony abandonment. Colony abandonment is most often due to lack of food. It may also result from severe moose competition for alder. Moose and muskrat competition for other beaver foods, including aquatic vegetation, has no serious effect on the welfare of the colony.

Most summer movement by beavers, other than the normal emigration of 2-year olds, probably represents a search for food. Other movement results from the apparent reluctance of the beaver to spend more than 2 or 3 consecutive winters in the same lodge. Winter lodge locations are normally in the stream sections of the territory. The deeper water areas of the territory are preferred in summer.

Factors determining territory size of the beaver colony are: water type (stream colonies are smaller), food abundance (preferred foods permit smaller colonies), intra-specific conflict (always a neutral zone between colonies), and age of colony (young colonies are smaller). These factors combine to determine population density of any area. The maximum carrying capacity of the Newfoundland beaver habitat is probably 1 active lodge per square mile. Less than 1 inactive lodge per active lodge indicates a population below carrying capacity. More than 3 inactive lodges per active lodge indicates a population above carrying capacity. Beavers apparently adjust their numbers to keep in balance with a continually changing food supply.

LITERATURE CITED

Bangs, O., 1913. The land mammals of Newfoundland. Bull. of the Museum of Comparative Zoology. Harvard College. LIV(18): 509-516.

Bergerud, A.T., 1961. Beaver management report. Wildlife Div., Nfld. Dept. of Mines, Agric. & Resources, 40 pp.

______ 1962. Newfoundland Wildlife Management Annual Report. Wildlife Div., Nfld. Dept. of Mines, Agric. & Resources, 83 pp.

Bradt, G.W., 1947. Michigan beaver management. Game Div., Michigan Dept. of Cons., 56 pp.

Cameron, A.W., 1958. Mammals of the islands in the Gulf of St. Lawrence. Nat. Mus. of Can., Bull. No. 154, 165 pp.

Damman, A.W.H., 1961. Some forest types of Central Newfoundland and their relationship to environmental factors. Can. Dept. Northern Affairs & Nat. Res., 99 pp.

Denney, R.N., 1952. A summary of North American beaver management, 1946-1948. Colorado Game and Fish Dept. current report 28.

Elton, C., 1927. Animal Ecology. Sidwick and Jackson, Ltd., London, xx + 204 pp.

Fassett, N.C., 1940. A manual of aquatic plants. McGraw-Hill Book Co. Inc., New York. vii + 382 pp.

Gibson, G.G., 1957. A study of beaver colonies in Southern Algonquin Park, Ontario, with particular reference to the available food. M.Sc. thesis, Univ. of Toronto. 86 pp.

Gray's Manual of Botany, 1908. A handbook of the flowering plants and ferns of the central and northeastern United States and adjacent Canada. 7th edition. Robinson, B.L. and M.L. Fernald, editors. American Book Company, New York. 926 pp.

Grinnell, J., Dixon, J.S., & Linsdale, J.M., 1937. Fur-bearing mammals of California. Univ. of Calif. Press, Berkeley. 2: 629-727 (Quoted from Miller, 1960.)

Hakala, J.B., 1952. The life history and general ecology of the beaver (Castor canadensis kuhl) in interior Alaska. M.Sc. thesis, Univ. of Alaska. 181 pp. (Quoted from Miller, 1960.)

Hall, J.G., 1960. Willow and aspen in the ecology of beaver on Sagehen Creek, California. Ecology, 41(3): 484-494.

Hammond, M.C., 1943. Beaver on the Lower Souris Refuge. J. Wildl. Mgmt. 7(3): 316-321.

Hay, K.G., 1958. Beaver census methods in the Rocky Mountains region. J. Wildl. Mgmt. 22(4): 395-402.

Hodgdon, K.W. and Hunt, J.H., 1955. Beaver management in Maine. State of Maine Dept. of Inland Fisheries and Game, Game Div. Bull. No. 3. 102 pp.

Knudsen, Q.J., 1962. Relationships of beaver to forests, trout and wildlife in Wisconsin. Tech. Bull. No. 25. Wisconsin Cons. Dept., Madison, Wisconsin.

Lawrence, W.H., 1952. Evidence of the age of beaver ponds. J. Wildl. Mgmt. 16(1): 69-78.

Manuel, F., 1962. Personal communication.

Miller, D., 1960. Beaver research in Newfoundland. Unpubl. report, Dept. Mines, Agric. & Res. 209 pp.

Nash, J.B., 1951. An investigation of some problems of ecology of the beaver, Castor canadensis canadensis Kuhl, in Northern Manitoba. M.Sc. thesis, Univ. of Manitoba. 64 pp.

Neff, D.J., 1957. Ecological effects of beaver habitat abandonment in the Colorado Rockies. J. Wildl. Mgmg. 21(1): 80-84.

Payne, F.J., 1961. Effects of beaver flooding of alder woodcock habitat on the Moosehorn National Wildlife Refuge. M.Sc. thesis, Univ. of Maine. 76 pp.

Peters, H.S., and Burleigh, T.D., 1951. The Birds of Newfoundland. Dept. of Nat. Res., Province of Nfld. xix + 431 pp.

Provost, E.E., 1958. Studies on reproduction and population dynamics in beaver. Ph.D. thesis, State College of Washington. (Quoted from Miller, 1960).

Rawley, E.V., 1954. Utah beaver transplanting manual. Utah State Dept. of Fish and Game, Dept. of Interior Bull. No. 12. 15 pp.

Retzer, J.L., Swope, H.M., Remington, J.D., and Rutherford, W.H.R. 1956. Suitability of physical factors for beaver management in the Rocky Mountains of Colorado. State of Colorado Dept. of Game and Fish Tech. Bull. No. 2. 32 pp.

Rouleau, E., 1956. Studies of the vascular flora of the Province of Newfoundland (Canada). Pts. 1, 2 and 3. Contributions de l'Institut botanique de l'Universite de Montreal. No. 69. 106 pp.

Rutherford, W.H., 1955. Wildlife and environmental relationships of beavers in Colorado forests. J. of Forestry. 53(11): 803-806.

Saunders, J.K., Jr., 1961. The biology of the Newfoundland lynx, Lynx canadensis subsolanus Bangs. Ph.D. thesis, Cornell Univ. 109 pp.

Semyonoff, B.T., 1951. The river beaver in Archangel Province. Translations of Russian Game Reports. Vol. 1, Beaver, Beaver, 1951-1955. Can. Dept. of Northern Affairs and Nat. Res. pp. 5 - 45.

Shaw, A.M., Drummond, W.M., and Murray, P.J., 1956. Report of the Newfoundland Royal Commission on Agriculture. (Quoted from Miller, 1960.)

Swank, W.G., 1949. Beaver ecology and management in West Virginia. Cons. Comm. of West Virginia. 65 pp.

Tappe, D.T., 1942. The status of beavers in California. Div. of Fish and Game, Game Bull. No. 3. 59 pp.

van Nostrand, F.C., 1962. Personal communication. (July).

Wilde, S.A., Youngberg, C.T., and Hovind, J.H. 1950. Changes in composition of ground water, soil fertility and forest growth produced by the construction and removal of beaver dams. J. Wildl. Mgmt. 14(2): 123-128.

Wildlife Investigational Techniques, Mosby, H.S. (editor), 1963. (Second edition). The Wildlife Society. xxiv + 418 pp.

Williams, H., 1963. Twillingate map-area, Newfoundland. (2 E/10). Report and map. Geol. Survey of Can., Dept. Mines and Tech. Surveys. Paper 63-36. 30 pp.

Zhanoff, A.P., 1951. Acclimatization of the beaver in the Ob River Basin. Translations of Russian Game Reports. Vol. 1. Beaver, 1951-1955. Can. Dept. of Northern Affairs and Nat. Res. pp. 46-59.