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A LAND CAPABILITY

CLASSIFICATION SYSTEM

FOR BEAVER

bу

Brian Slough

B.Sc., University of British Columbia, 1974

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the Department

of

Biological Sciences

C BRIAN SLOUGH 1976

SIMON FRASER UNIVERSITY

July 1976

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APPROVAL

Name:

BRIAN GRANT SLOUGH

Degree:

Master of Science

Title of Thesis:

A land capability classification system for Beaver.

Examining Committee:

Chairman: Dr. J. S. Barlow

Dr. R.M. Sadleir Supervisor

Dr. R.C. Brooke

Dr. C. Crampton

Dr. M. McClaren

Dr. G.H. Geen External Examiner

Date approved 28/1/76

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ABSTRACT

Beaver (Castor canadensis Kuhl) habitat factors and beaver colony site density were sampled on 136 lakes (about 1140 shoreline miles) and 45 stream sections (90 stream miles) in the northern interior of British Columbia. The quantified beaver habitat components were then related to beaver colony site density by multiple regression analyses.

On the basis of the results of the analyses, a land capability classification system for beaver was developed. The regression equations are also useful as models of beaver-habitat relationships and can be used for beaver inventory by prediction of colony site density.

Conservation of existing aspen stands, common throughout the beavers range in North America, is considered the most powerful management tool for the maintenance of high beaver populations.

Evidence is presented which shows that alder, commonly found in beaver food caches, is more important as a construction material (used to submerge more preferred foods) than as a food species.

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INTRODUCTION

The exploitation of natural resources in wildland areas has resulted in conflicts of interest between land uses, necessitating multiple land use planning. The Canada Land Inventory (C.L.I.) was established in 1961 to assess the land resources and capabilities for various uses including wildlife, agriculture, forestry and recreation. Such an inventory should reflect the inherent capacity of the land to provide the physical and biological environmental requirements for these several uses. Biophysical land classification projects were initiated by the C.L.I. to "differentiate and classify ecologically significant segments of the land surface, rapidly and at a smallscale (reconnaissance survey); it is to satisfy the need for an initial overview and inventory of forest land and associated wildland resources. This inventory will serve as the ecological basis for land use planning" (National Committee on Forest Land, 1969, p. 2). Land capability classification involves assigning capability classes, which reflect the ability of the land to provide the needs of a specific use, and capability subclasses, which specify the biophysical limitations

on the production of the resource. In this way the resources of an area can be assessed and related to the land and other resources. Wildlife classification systems have been devised for economically important species, such as ungulates and waterfowl. These classification systems are being refined and new species are being added. The next priority of the C.L.I. is fur-bearers, in particular beaver, which contribute to a significant portion of the economy of wildlands. The purpose of this study was to develop a land capability classification system for the beaver (Castor canadensis Kuhl).

Beavers are highly appropriate for use in developing a land capability methodology. Suitable habitat is sought out and exploited by beavers to an extent that allows one to conclude that unexploited habitat is unsuitable. Beavers are not cryptic in habitat use, making suitable habitat easily observable. Thus, the species requirements which are lacking in unsuitable habitat and are present in suitable habitat are determinable.

Efficient habitat exploitation by beaver is achieved primarily through the extensive dispersal characteristics of the species.

Young beavers leave their parent colony at one to three years of age in search of new habitat (Bradt, 1938; Novakowski, 1965;

Gunson, 1970; Boyce, 1974). This emigration occurs before new kits are born in the spring (Bradt, 1938). The dispersal age depends primarily on the quality of the habitat (Gunson, 1970) and the degree of habitat saturation (Boyce, 1974), with beavers remaining in the colony longer in saturated, high quality habitat. It is not known whether beavers are driven out by the adults (Bradt, 1938)

Emigration of young beavers may involve movements over considerable distances, both over land and via waterways (Leege, 1968). Distances travelled average about 5-10 stream miles (Denney, 1952; Hodgdon and Hunt, 1953; Beer, 1955; Hibbard, 1958; Berghofer, 1961; Leege, 1968), but distances up to 148 stream miles (67 airline miles) have been recorded (Hibbard, 1958). The demonstrated mobility of beavers should allow all suitable habitats to be explored. Since habitat selection is based on instinctive and habitual preferences of an animal, rather than being a trial of new situations (Miller, 1942), it can be assumed that only suitable habitat will be selected. Beavers may very well be the wildlife species most suited to land capability classification.

Adult beavers are non-migratory, occupying a set home range and territory (defended against conspecies) (Townsend, 1953; Aleksiuk, 1968). The location of the territory is evidenced by signs of beaver activity such as dams, lodges, dens, felled trees, and food caches. Territorial boundaries are marked with "scent mounds" which act to reduce the need for active territorial defence.

The nature of the habitat itself explains why beavers exploit their habitat through migration of the young and subsequent territoriality of the adults. Beavers are associated with subclimax plant communities (discussed in a later section). These are either edaphic climax communities (often pulse-stabilized) on the shores of lakes and streams (some alluvial soils along watercourses

preclude the growth of climax conifer species), or are temporary communities which follow fire (and in some cases are initiated by windthrow, insect outbreak, and logging (Lawrence, 1964)). There is a selective advantage for the young of beavers which are exploiting either type of community to disperse over large areas in search of new habitat. Exploitation of the former habitats is necessary for the long-term stability of beaver populations, while temporary habitat allows local population increments. Since the locations of temporary habitat are unknown to beaver, dispersal of the young is a way to locate and exploit them. Limitations imposed by the relative scarcity of permanent habitat favour territoriality of adults. Adaptations of moose (Alces alces andersoni Peterson), an ecologically similar species to beaver, to efficient habitat exploitation were discussed by Geist (1971, pp. 121-124).

To assess the present land capability to support beaver it is necessary to relate land use by beaver to measurable factors of its biophysical environment. These factors are the habitat requirements of the beaver. The habitat requirements are generally known and have been used in the past to assess beaver land capability (see Literature Review). The major difference between the land capability methodology developed in this thesis and other capability analyses is the quantification of the relationship between beavers and their environment. Multiple regression analysis was the technique used to maximize the objectivity of the classification system.

In addition to the development of a land capability methodology for beaver, this study provides:

- 1) a model of the relationship of beavers to their habitat
- 2) a means of beaver inventory
- 3) a basis for beaver management
- 4) a land capability methodology which may be applied to other wildlife species or resources.

LITERATURE REVIEW

A) Beaver Habitat Requirements

The habitat requirements of beaver are well documented in the literature. They are readily observable in the field and so have been recorded independently by numerous authors. Authorities will not be cited in the discussion of the environmental factors below except in the case of food requirements where definitive studies have been necessary.

Perhaps the most concise definition of the beaver biotope, given by Zharkov and Sokolov (1967), is a body of water with a stable water level and banks lined with deciduous trees and shrubs. Water is the prerequisite to beaver habitat. The water supply must be permanent and the depth must be sufficient to accommodate lodges and banks, dens, and allow free movement from the lodge to the food cache during the winter. The water level should preferably be stable. Bednarik (1971), summarizing 23 years of beaver study in Ohio, believed water level stability to be the most important factor determining sustained site habitation, with woody plant composition ranking next in importance. Seasonal water fluctuations,

including flash floods and droughts, are dampened by the damming of streams (including lake outlets), which allows beavers to effectively control the water level. Wave action should also be minimal so that lodges and food caches are not destroyed. Bank materials must be able to support dam and lodge construction. Finally, a suitable source of food and construction materials must be present and accessible. Accessibility depends on distance from shoreline and local topography. The food species should preferably be within 100 feet of the water. Hall (1960) found that 90% of all cutting was done within that distance although distances up to 650 feet (Bradt, 1938) have been reported. This distance is further limited by steep topography. Streams flowing in and out of lakes, and low marshy areas adjacent to the habitat encourage channeling and damming to make more food available.

Quantity as well as quality of food species will affect beaver habitat suitability. The distribution and abundance of food species are limited in turn by such factors as climate, elevation, soil types, aspect and the seral stage of community development (succession). Although beavers are known to sample almost any woody or herbaceous plant (Bradt, 1938), they show distinct preferences for a small number of such species. Denney (1952) reviewed the literature on beaver foods in North America and published a preference list. The four most preferred species that he reported are common in British Columbia. They are, in order of the beavers' preference:

- 1) Aspen (Populus tremuloides Michx.)
- 2) Willow (Salix L. spp.)
- 3) Cottonwood (P. balsamifera L. ssp. trichocarpa T. & G.)
- 4) Alder (Alnus Mill spp.)

America is well known. It is the tree most commonly felled for food and building material by beaver (Denney, 1952; Hall, 1960). The preference list must be determined by the relative palatability, or the benefit/cost ratio to the animal. An analysis of the chemical composition of woody species from Cowan et al. (1950) indicates that preference may be determined by two opposing factors; protein content and resinous fat content. The protein contents (% dry weight) (Cowan et al., 1950) of the major food species are:

1)	Aspen (bark)	12.66
	Aspen (stem)	7.10
2)	Willow (stem)	6.32
3)	Cottonwood (stem)	6.08
4)	Alder (stem)	9.95

Preference declines with decreasing protein concentration.

Although the more resinous species are high in protein concentration, they are "unpalatable." White birch (Betula papyrifera Marsh), resin birch (B. glandulosa Michx.), and conifers are other unpalatable and nonpreferred species.

¹Plant nomenclature is after Hitchcock and Cronquist (1973).

Utilization of aspen is directly proportional to availability, and the supply usually declines steadily to a complete loss under constant use (Hall, 1960). Size class utilization of aspen also depends on availability, except for the use of 2-inch trees which are preferred in the fall when dam and lodge construction are increased (Aldous, 1938; Hall, 1960). As the aspen is cut the land becomes occupied by either herbaceous vegetation, or by coniferous vegetation such as subalpine fir (Abies lasiocarpa Nutt.), spruce (Picéa A. Dietr. spp.), or lodgepole pine (Pinus contorta Dougl.).

Willow and alder can sustain beaver in the absence of aspen. Both are renewable resources within the life of a single beaver colony. The yield is sustained by block-cutting, or a shifting of the cutting site, to allow regrowth and regeneration of cut trees (Hall, 1960; Willow: Northcott, 1971; Alder: Bednarik, 1971). Severely overbrowsed sites may be abandoned to allow regrowth, but this vacancy is usually only temporary. Regrowth of alder is slightly slower than that of willow (Aleksiuk, 1970).

Cottonwood usually occurs with aspen and so is considered to be only of minor importance to the beaver.

Aquatic vegetation (mainly Nuphar J. E. Smith spp.) and terrestrial vegetation (mainly Ericaceae shrubs and herbaceous plants), where present, may be the most important summer foods of beaver (Northcott, 1971, 1972). It is doubtful that they impose any limitations on beaver numbers as woody species are also available at this time. During the winter only woody species are stored in any quantity, so it is their availability which ultimately determines the location and survival of

a given colony. Summer foods may act as a buffer to the exploitation of winter foods, and hence prolong the period that a site is able to support a colony. This effect has not been studied to date.

B) Previous Beaver Land Capability Classification Systems

The capability of various habitat types to support beaver depends on the ability of the environment to supply the requirements of the species. The early beaver land capability classification systems differentiated habitat types into primarily descriptive and arbitrary units. For example, Atwater (1940, p. 101) classified waterways on the basis of their general biophysical suitability for beaver:

"Class 1--Most favourable location for beavers. Ample forage of preferred types; room for expansion; reliable water supply; topography favourable for dams, lodges, and feed production. Support at least 6 colonies/mile.

"Class 2--Favourable location for beavers. Same requirements as above but expansion limited by topography. Support at least 4 colonies/mile.

"Class 3--Fair location for beavers. Forage not so plentiful or made up to some extent of less desirable types. Room for expansion strictly limited. Water supply variable. Support at least 2 colonies/mile.

"Class 4--Marginal locations for beavers. Forage made up of less desirable types: alder, swamp birch, etc. Topography steep and rocky, water supply unreliable. Support only scattered beavers.

"Class 5--Unfavourable."

Scheffer (1941, pp. 321-322) observed that beavers transplanted in Oregon would not settle in sites with the following characteristics:

- "1) Lack of shelter; open meadow without concealing shrubbery.
- 2) Stream banks too low or slope too steep; no place afforded for deep ponds that would not freeze solid in winter.
- 3) Elevation too great in regions of heavy snowfall.

 The maximum elevation in eastern Oregon for satisfactory planting of beavers is thought to be about 6,000 feet.
- $^{6}4)$ Streams too swift or subject to excessive flooding.
- 5) Lack of palatable foods; aspen or poplar. The presence of these species and the ability of willow and alder to regenerate determined the duration of permanency of the plantings."

Scheffer then grouped colonies in physically suitable sites in relation to their present food supply (pp. 322-323):

"Group 1--Colony in nearly pure stand of aspen, leading to speedy exhaustion of trees and emigration of beavers.

"Group 2--Colony in willow not producing foliage as fast as required leading gradually to depletion of food and emigration of beavers.

"Group 3--Colony in satisfactory balance with willow, producing foliage as fast as it is being cut.

"Group 4--Colony living at a subsistence level on mediocre food."

Retzer et al. (1956) ranked streams in the Colorado Rockies by valley grade, valley width, and substrate type. This was one of the first attempts made to quantify these kinds of habitat variables. Beaver preferences, as indicated by colony density, were for valley grades less than 6% and valley widths greater than 150 feet. Stable substrate types such as granite and schist were considered to be more suitable over the long term than shale or rhyolite. More recently Boyce (1974) quantitatively related beaver density to food supply.

In the U.S.S.R., beaver areas have been ranked according to water level stability, abundance of bank vegetation consisting of aspen or different species of willow, and the degree of exploitation by man (Zharkov, 1970).

Some authors have devised large-scale land classification systems for beaver based on the suitability of gross landscape features such as topography and parent materials, and the resultant characteristic types of lakes and streams (Thomasson, 1973; deBock et al., 1973; Traversy, 1974). Due to subjectivity, these classification systems lack the detail and accuracy required to assess the capability of a single lake or stream for beaver inventory or management purposes.

STUDY AREA

The study area was situated in the northern interior of British Columbia between 54°0' and 55°30' north latitude and 124°0' and 128°45' west longitude (Fig. 1). This area was chosen for several reasons, (1) it shows the highest annual beaver pelt returns in the province (B.C. Fish and Wildlife Branch-records), (2) the Environment and Land Use Committee Secretariat is involved in a multiple land use study in the area, (3) there is a good data base of topographic maps, forest cover maps and aerial photographs for the area, and (4) there is a diversity of climate, physiography and vegetation in the area, which provides a range of conditions sufficient to develop and test the capability analysis.

A) Physiography

Information on the physiography of the study area (see Fig. 1) has been adapted from Holland (1964). The main landforms include the Nechako Plateau of the south and east, the Skeena mountains of the northwest, and the Hazelton mountains of the west.

Most of the area under study is situated on the Nechako Plateau, which is the northernmost section of the Interior Plateau. This is an

area of low relief and gentle, rolling topography. The average elevation is about 4,000 feet above sea level. The last ice age left the bedrock of the Nechako Plateau covered almost completely with glacial drift. As the ice moved across the plateau numerous grooves and depressions were carved out. These are now occupied by lakes of all sizes, including many of the largest lakes in the province. The Skeena mountains extend from Telkwa on the east side of Bulkley River, northward beyond the boundary of the study area. Cirque and valley glaciers have had a major effect in shaping the mountains, leaving rugged peaks separated by wide valleys. The Skeena mountains rise abruptly above the plateau to elevations of 6,500 feet. The Hazelton mountains lie to the west of the Bulkley River.

Many high gradient streams typify the mountains of the study area. The mountains contain many small lakes; only a very few are large.

B) Climate

The climate of the study area is a continental type with long, cold winters and short, warm summers. The mean annual temperatures vary from 34.0°F. at Babine Lake to 39.8°F. at New Hazelton in the west where the maritime climatic influence of the Pacific Ocean becomes increasingly evident. Mean monthly temperatures vary from 5.1°F. - 14.3°F. in January to 55.2°F. - 59.4°F. in July at the same locations.

Precipitation is generally light (less than 20 inches per year), being slightly higher in the mountains of the west. From 25-50% of the total annual precipitation falls as snow, again depending on local topography and proximity to the Pacific Ocean. Temperature and precipitation data from selected climate stations in the area are summarized in Fig. 2. Climate data from all Atmospheric Environment Service (1973) weather stations in the area is given in Appendix A. Locations of the stations are given in Fig. 1.

The lakes in the study area are generally frozen over from October to May at higher elevations (3,500 + feet) and from November to late April--early May at lower elevations. Large lakes such as Babine Lake may remain open until December. Those streams that freeze (including shore ice) usually freeze later, and open up earlier, than the lakes (L. J. Cox, 1976, pers. comm.; see also Appendix B). Low water occurs during the freeze-up period. Runoff is at its peak by May in the tributaries, and by June in the major streams (Fig. 3). The Stuart River in the east does not peak until July due to the colder climate over most of its drainage area. The Stuart system also has a more stable discharge rate, being higher than that of the Bulkley in winter and lower in the summer, even though mean annual total discharges are almost equal. The seasons are probably more stable in the Stuart area in terms of both temperature and precipitation. Lake and Stream water data (Fig. 3 and Appendix B) are from annual reports of the Water Resources Branch (1970 to 1975 inclusive, 1974). The surface water stations are located on Fig. 1.

Regional Protection Officer, Fish and Wildlife Branch, Smithers.

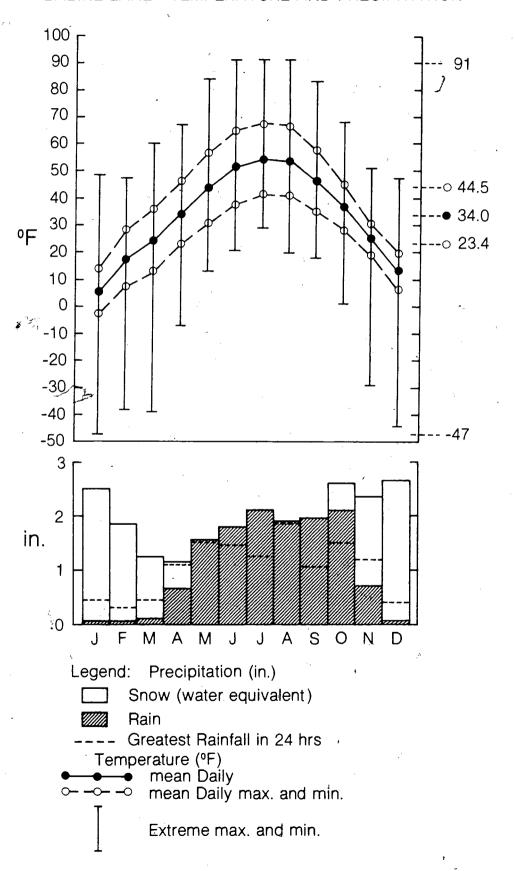
Fig. 2

Mean monthly and mean annual temperature and precipitation from selected weather stations in the study area.

- a) Babine Lake--Lowest mean annual temperature and highest mean annual precipitation of weather stations in the study area.
- b) New Hazelton--Highest mean annual temperature.

 Telkwa--Lowest mean annual precipitation.

BABINE LAKE—TEMPERATURE AND PRECIPITATION



b) NEW HAZELTON—TEMPERATURE TELEWA—PRECIPITATION

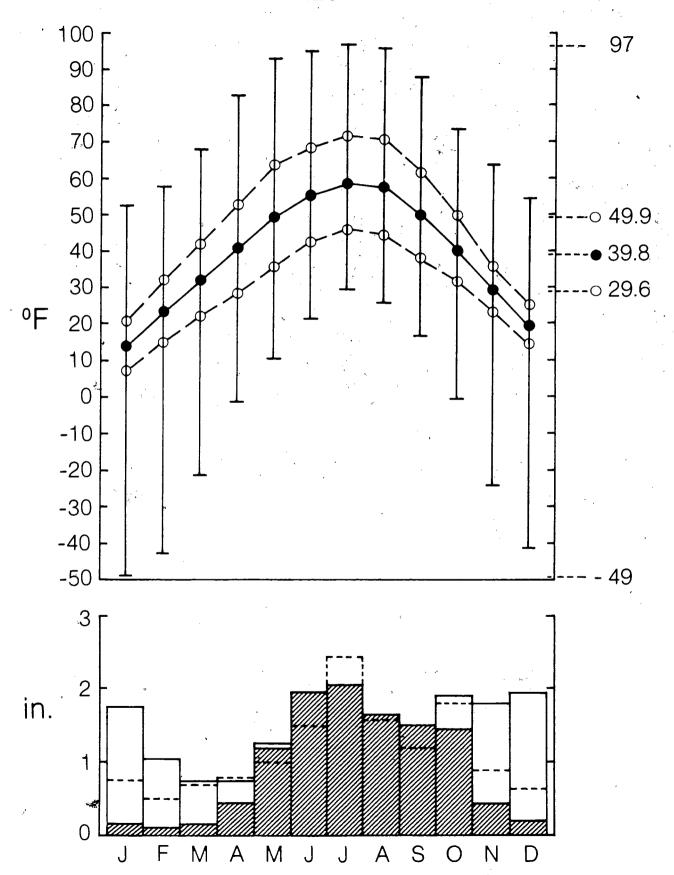
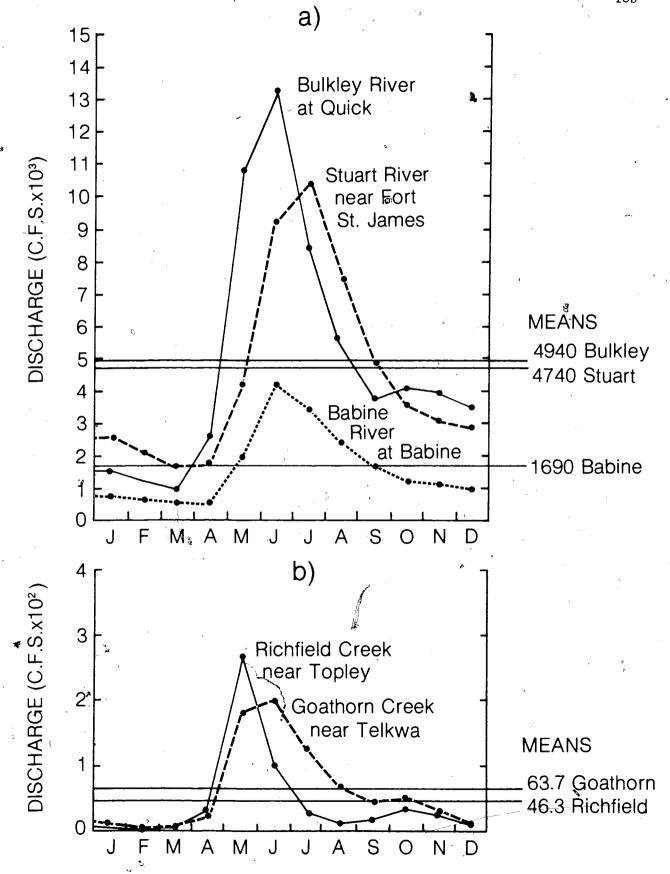
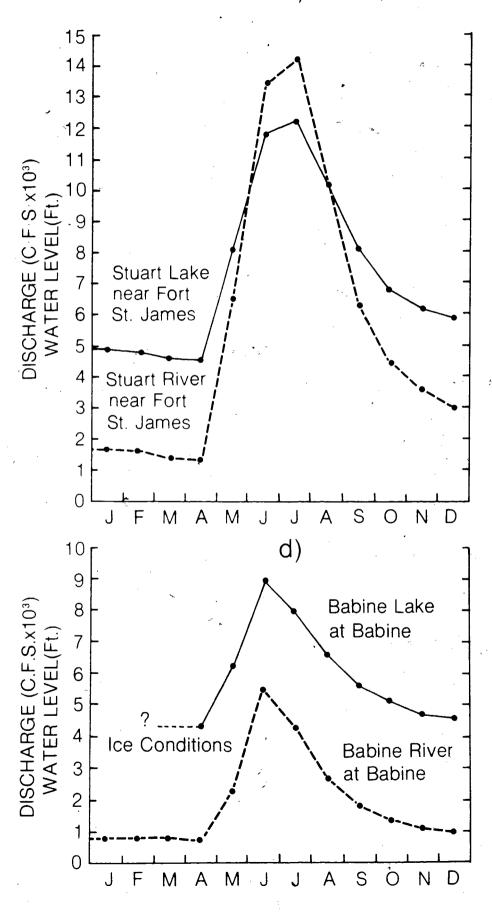


Fig. 3

Stream discharges and lake water levels from selected gauging stations in the study area.

- a) Mean monthly discharges (in cubic feet per second, C.F.S.) of the major rivers. Means to 1973.
- b) Mean monthly discharges of two tributary streams of the Bulkley River. Means to 1973.
- c) Comparison of daily water level of Stuart Lake with daily discharge of Stuart River. On 15th day of month, 1974.
- d) Comparison of daily water level of Babine Lake with daily discharge of Babine River. On 15th day of month, 1974.





C) Vegetation

Five biogeoclimatic zones (after Krajina, 1969) are represented in the study area. These are, in increasing rank of area covered:

- 1) Coastal Western Hemlock (CWH)
- 2) Alpine Tundra (AT)
- 3) Engelmann Spruce--Subalpine Fir (ESSF)
- 4) Cariboo Aspen--Lodgepole Pine--Douglas Fir (CALPDF)
- 5) Sub-Boreal Spruce (SBS)

The CWH zone is found in the extreme northwest corner of the study area. The climatic climax tree species of this zone is western hemlock (Tsuga heterophylla Sarg.), while western redcedar (Thuja plicata Donn.) prevails on moister sites. The CWH zone occurs from valley bottoms to about 3,500' from 550 N. Lat. northwest along the Bulkley River. Shrubs such as willows, red osier dogwood (Cornus stolonifera Michx.), and hazel (Corylus cornuta Marsh) are abundant as pioneer species on moist and fine textured soils. Some of the coarser textured soils have regeneration of trembling aspen following disturbance. Cottonwood is common along streams on deep alluvial soils.

The AT zone generally occurs above 5,500 feet. It is characterized by an absence of all major tree species. Some shrubs such as low growing willows and many alpine herbaceous plants are adapted to the extreme environmental conditions of this zone. At the lower elevations of the AT zone, subalpine fir and resin birch may occur in krummholz form. This zone is of little importance to beaver as sufficient food is lacking.

The ESSF zone extends from the AT zone (about 5,500 feet elevation) down to 3,500 feet where it mixes with either CWH, CALPDF, or SBS. In this ESSF zone Engelmann spruce (Picea engelmannii Parry.) dominates on wetter sites while subalpine fir dominates on drier sites. Subalpine fir is also prevalent following fires. Lodgepole pine and resin birch are frequently found in the ESSF zone. Alders commonly form thickets along streams and lakes.

From Smithers, southwest along the Bulkley River and to the east of Burns Lake, the CALPDF zone occurs below 3,500 feet. forest climax species in this zone is typically white spruce (P. glauca Voss). Between 3,000 and 3,500 feet this is often mixed with Engelmann spruce--subalpine fir. Hybrids between the spruces are common. Douglas-fir (Pseudotsuga menziesii Franco) regenerates under a canopy of trembling aspen in isolated areas to the southeast. Lodgepole pine is usually the pioneer species following light fire disturbances, but trembling aspen is prevalent on areas repeatedly burned and disturbed. Trembling aspen is presently the most common species of the CALPDF zone within the study area. Alders and willows are common along the banks of lake's and streams. Alders favour regularly disturbed banks with rich, rocky and moist soil. Willows and cottonwood are found on sandbars and other well-drained soils, but they also thrive in marshy areas at or below the water level. They are able to withstand flooding and silting. These characteristics separate their habitat from that of alder.

The SBS zone occupies most of the study area and is found east and north of the CALPDF zone at altitudes below the ESSF zone (3500

mariana B.S.P.) occurring on poorly drained sites and subalpine fir on areas which have been affected by recent forest fires. Fires are common in this zone, and aspen and lodgepole pine are the common colonizers. Douglas-fir occurs with resin birch on nutritionally rich sites. Willows and alders typically line banks of streams and lakes.

METHODS

A) Description of Data Collected

In order to assess habitat suitability for wildlife species it is necessary to measure the intensity of land use by the species in various habitat types. In wildlife capability classifications (e.g. Blower, 1974) the intensity of land use has typically been measured by the current species population density on a given area. For population levels to be representative of habitat quality one critical assumption must be met; that is that the land is at its species carrying capacity. Natural and human-induced population fluctuations deny the fulfillment of this assumption for most species. This effect is augmented in species which are slow to disperse to new or vacant habitats. In addition, population census methods are often inaccurate. Beavers, although efficient habitat users through juvenile dispersal (see Introduction, p. 2), have unstable population levels and are difficult to enumerate.

Beavers' populations fluctuate yearly depending on the natural demographic characteristics of the population, a function of the number of animals in a colony at any given time, and trapping intensity.

The beaver colony is a social organization with distinct characteristics which exploits the environment as a unit. Bradt (1938, p. 145) defined the colony as "a group of beavers occupying a pond or stretch of stream in common, utilizing a common food supply and maintaining a common dam or dams. They may or may not be living in the same lodge or burrows. Beavers appear to maintain a system of territorial rights, and there is no evidence of overlapping in the colonies." The colony size ranges from a single animal to a complete family unit consisting of two adults, kits, and yearlings. Novakowski (1965) and Boyce (1974) have noted 2-year old groups present in some colonies in northern Canada and Alaska. In most areas, two-year olds leave the colony before the new kits are born (Bradt, 1938). Since the litter size varies from 1 to 9 kits or higher (mean litter size is 3.70 (Henry and Bookhout, 1969)) the number of individuals in a colony is highly variable.

Beaver populations are difficult to census, even though census techniques have been refined over the years. The following techniques have been tried and found unreliable:

- 1. The average number of beavers/colony is highly variable (Townsend, 1953). This method is used, however, in the U.S.S.R. for censusing large areas (Zharkov, 1963).
- 2. The number of lodges is not related to colony size (Bradt, 1938). Colonies of all sizes usually have only one or two lodges or bank dens.

- 3. The number and size of dams depends more on the local conditions of topography, stream flow, water depth and stream width than on the number of beavers. Bradt (1938) found no correlation between the number of dams maintained by a colony and the number of animals in the colony.
- 4. The area (Hammond, 1943) or volume (Pearson, 1958) of the food cache show no relationship to colony size. The size of the cache is a function of water depth, size of trees used, and colony size.
- 5. The caloric content of the food cache varies with the age composition and size of the colony. Adult animals may be able to live below the basal energy requirements thus making the caloric content of the cache unrelated to the individual energy requirements of beaver (Novakowski, 1967).

Therefore, the beaver colony, irrespective of size, represents the best unit of land use by the beaver. The density of beaver colony sites was used, in the land classification system presented in this thesis, to indicate beaver habitat suitability. Field observations of land use from the ground consisted of an enumeration of all colony sites on lakes and on stream sections. The primary indicator of land use was the presence of lodges and bank dens. Some colony sites, however, were inferred from the presence of dams and by the sequence of active and inactive dams on streams.

According to Townsend (1953, p. 477), "colonies cannot be limited arbitrarily by the grouping of beaver structures . . . , where they are are often continuous over wide areas." During low population densities the territorial boundaries of one colony may include lodges and dams which would normally be in the territories of other colonies (now vacant). This creates a difficulty in delineating colony limits where the lodges are close together. Therefore, the "number of colony sites" is defined in this study as "an estimation of the number of colonies a body of water could support if all the present lodges (including bank dens) were occupied, with each lodge representing a potential colony site." This number of lodges was determined by direct observation. Many colonies build satellite bank dens for use as safety retreats while away from the main lodge. These are usually just simple holes in a bank and are easily distinguishable from dens used as residences by the absence of typical lodge construction (used to protect the entrances). Only dens which were obvious beaver residences were enumerated. It was also noted that some colonies built "twin lodges" or two lodges of identicle size and construction, usually less than 25 feet apart, and often with a single food cache between them. "Twin lodges" were considered as a single colony site only.

The definition of colony sites depends on three critical assumptions. First, it is assumed that all suitable sites have at some time been exploited (or are currently occupied) by beaver and that evidence of their use still remains. This assumption is satisfied by the dispersal and habitat utilization characteristics of the beaver as described in the Introduction. The second assumption is that successive colonies occupying a single site will repair old lodges if possible rather than construct new lodges or dens. This

assumption was verified by the repeated field observation of the reoccupation of old lodges and the extreme rarity of construction of completely new lodges. The third assumption is that the number of colony sites is directly related to the colony carrying capacity. This assumption will be dealt with in the Disscussion. Their dispersal characteristics (e.g., see Leege, 1968) allow beavers to find all suitable colony sites. The frequency of recolonization of old sites which are still suitable, and colonization of newly acquired habitat (due to succession and physical changes in the environment) is most likely high enough to assure that signs of all potential colony sites are present. Since habitat selection is primarily instinctive, successive colonies should choose the same locations for lodge construction. Therefore, they should re-occupy old lodges or build new lodges in the same location if the old lodges have degenerated beyond repair.

Colonies utilizing both a lake and a stream were included in the estimate of both lake sites and stream sites regardless of lodge location.

As there are differences between lakes and streams, the land capability classification methodology was determined seperately for each. The definitions of "lake" and "stream" as used in this thesis are (National Committee on Forest Land, 1969, p. 28):

Lake: "Continuous uninterrupted expanses of permanent or intermittent standing surface waters of various depths that lack any continuous directional flow . . . "

Stream: "Surface water with a significant and discernible flow in a definite direction, following a gradient, and usually confined to a defined bed or course."

The specific environmental variables used in the analysis were selected on the basis of their importance as habitat requirements for the beaver as described in the Literature Review. A description of the biophysical variables and their methods of measurement are given below.

Lake Variables

- 1. The physical habitat was quantified by measuring lake area and lake perimeter. Stability of a lake in terms of wave action and destructiveness is dependent on the reticulation of the shoreline and was indexed by calculation of an area/perimeter ratio. Perimeters (in miles) were measured with a "map measurer" from government aerial photographs (scales: 40 and 80 chain; dates given in Appendix C). Areas (in acres) were measured from the air photographs with dot counters. For lakes with areas less than 50 acres a dot counter was used which measures accurately to ± 1 acre. Lakes with areas greater than 50 acres were measured with a dot counter accurate to ± 5 acres on 40 chain air photographs and ± 20 acres on 80 chain photographs. Areas of islands were not included in lake areas and island perimeters were included in lake perimeter.
- 2. Water level stability was indexed by the following characteristics of the lake outlet:

¹The "map measurer" is used to trace the perimeter with a small wheel which shows the distance measured on a calibrated scale. The scale is calibrated to measure distances accurately to 1/4 mile and 1/2 mile on 40 chain and 80 chain air photographs respectively with measurements of smaller lakes being less precise.

Water Level Stability Index	Description
1	The outlet is not regulated. There is no evidence of past or present damming at the outlet. The outlet is usually too wide or fast flowing to allow damming.
2	The outlet is regulated between spring floods. Dams are constructed at the outlet but are usually washed out or destroyed by spring floods. Such spring washouts are evident only until repairs are made, usually in the late summer prior to the winter food storage activities.
3	The outlet is regulated. The dam(s) shows no

The water level stability index was determined from ground field observations only. Three classes were chosen because of the ease of definition of the two extremes (1&3). All intermediate conditions were then referred to the middle class.

evidence of damage by fluctuating water levels,

even when the colony site is abandoned.

by taking measurements (in miles) with a "map measurer", of perimeters of lake shores which are lined (within 100 feet of water) with important forest types, from British Columbia Forest Service forest cover maps.

The species chosen for analysis were the four most preferred species from Denney (1952): aspen, willow, cottonwood and alder. The amount of shoreline covered by at least 10% gross volume (the minimum amount classified by the Forest Service) of the above species was measured. The maps are scaled at 1.5 inches to 1 mile. The map measurer is accurate to 1/3 of a mile.

The reliability of the forest cover maps was checked during the summer field season of 1975. The classifications of aspen and cottonwood stands were found to be extremely accurate. Areas of alder and willow

abundance correlated well with the types termed "non-productive brush" and "swamp" respectively. It was found, however, that "swamp" was often misclassified as "non-productive brush." These two variables were separated and combined in the analysis to test for similarities and differences between them. "Swamp" is also commonly associated with abundances of the aquatic vegetation which provide summer food and possibly buffer the exploitation of winter foods. The forest cover maps are updated by the Forest Service about every 10 years, so inaccuracies due to natural succession are rare.

Elevation (in hundreds of feet) was also included in the analysis of lakes to test primarily the harsher climate at high elevations which might limit beaver habitat quality. Unfortunately, food species are also limited here, making the effects hard to separate.

A special food species variable was created (for aspen on lakes) by giving major stands (more than 20% gross volume) twice the weighting given minor stands (10-20% gross volume). The purpose was to test if the Forest Service classifications could be used as a more sensitive indicator of food abundance and hence of beaver abundance.

2) Stream Variables

1. The amount of aquatic habitat surveyed in a sample unit was quantified as stream section length (in miles). This measurement is analogous to lake perimeter, and was measured in the same way using a map measurer and air photos. Stream sections are of uniform gradient as described below.

2. Environmental stability was quantified by 3 parameters: stream gradient, flow rate, and stream width. Gradient of the stream sections was calculated from 1:50,000 federal topographic maps by measuring the stream distance between 100 foot contour lines and dividing by a scalar. For example, a 1% gradient is represented by 100 foot contour lines which are 1-2/3 inches apart. The gradients were then classed as follows:

Gradient Class	Actual Gradient
1	0-1%
2	>1-2%
3	>2-3%
4	>3-6%
5	>6% + 4

Stream sections which originally were comprised of more than one gradient class were divided so that each section was characterized by only one gradient class.

Flow rate was indexed from subjective field observations as follows:

Flow	rate index		Descriptio
g	1		slow
	2	A	medium
	. 3		fast

Stream width is the average width of the stream section (in **feet) as estimated in the field.

3. The amount of food was assessed in basically the same way for streams as for lakes. The length of stream in the sample section which was lined on either shore by the food species was recorded.

Cottonwood was not included due to its infrequent occurrence in a statistically small sample of streams. Non-productive brush and swamp were combined for the same reason.

Field work was done from May to August in both 1974 and 1975 and in October, 1974. All lakes and streams were surveyed either by foot or, if navigable, by boat.

Data used in the lake and stream analyses are summarized in Appendix C and the sample locations are shown in Fig. 1.

River drainage. This area consisted of many small lakes (Table 1) and, though the lake sizes were representative for the immediate area, they were not representative of lakes of British Columbia in general or even of the northern interior. In 1975, the study area was extended to include large lakes of the Babine, Stuart, and Endako River drainages. The complete sample of lakes includes all sizes up to Babine Lake, the second largest natural lake in British Columbia. The purpose of the field work in October, 1974, was to check some of the colony site counts, made the previous, summer, for accuracy. It also provided an opportunity to study food cache contents in relation to the available food supply.

Streams were also sampled in 1975 with the object of obtaining a representative sample. Since the major determinant of stream morphology is topography, with stream gradient being the major factor involved, the sample of streams included a range of stream gradients (Table 1). Beavers are most likely to be found on low gradient streams. Thus it was necessary to bias the sample towards

Table 1.--Distribution of lake sizes and stream gradients sampled

a) Lake size classes

Lake Area Class	Number	Sampled	ू [®] ⊹ Total
	1974	1975	
1-10 acres	14,	19	33
11-100 acres	16	22	38
101-1,000 acres	24	20	44
1,001 ⁺ acres	2	19	21
Total	× 56	80	136

b) Stream gradient classes

* *	Stream Gradient Index		Number Sampled
	1		27
	2		9
	3		4
	4		3
· •	5	`	2
,	Total	·	45

low gradient streams to obtain adequate variability in the other factors which determine beaver habitat suitability (for example, the abundance of food species). The stream sample included 45 separate stream sections of approximately 90 miles total length.

B) Analyses Used

In order to relate the distribution and abundance of beaver colony sites to the environment in an objective, meaningful way a valid statistical technique must be used. The technique should not only describe the relationship of colonial sites to individual environmental parameters, but also to a combination of these parameters allowing for interactions. The technique should also provide a means for predicting the location of colonies if the necessary environmental parameters are known. Such a technique is multiple regression analysis.

The use of regression analysis reduces subjectivity in habitat assessment and subsequent land capability classification. The significance of the habitat variables as indicators of land capability is tested with robust statistical tests (F- and t- tests). Despite gaining objectivity with a classification developed from regression analysis, it does not demand a greater input of time and effort than do the standard subjective methods such as the land capability classification methodology for wildlife developed by the Canada Land Inventory (Perret, 1969).

Multiple Regression Analysis

The following description of multiple regression analysis is adopted from Ezekiel and Fox (1959) and Draper and Smith (1966).

Multiple regression analysis allows one to study the linear relationship between a set of independent variables and a number of dependent variables while taking into account the interrelationships among the independent variables. The basic concept of multiple regression is to produce a linear combination of independent variables which will correlate as highly as possible with the dependent variable. This linear combination can then be used to "predict" values of the dependent variable. The difference between the value of the dependent variable and the value predicted by the linear combination of the independent variables is known as the residual. The regression equation is written as follows:

Equation 1.
$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_k X_k$$

where Y is the dependent variable, the X's are the independent variables, the β 's are the regression coefficients, and β_0 is a constant.

The predicting equation, which estimates the terms of Equation 1, is:

Equation 2.
$$\hat{Y} = b_0 + b_1 X_1 + b_2 X_2 + \dots + b_k X_k + r$$

where r is the residual or error of estimation.

Many of the properties of multiple regression may be understood by considering the residual. The residual has mean zero, and the sum of the squared residuals is the smallest possible for any linear combination of the given independent variables. In other words the "sum of squares" is lowest for the b's of the regression equation.

In this sense the regression equation provides an optimum prediction of the dependent variable.

Stepwise regression is a variation of multiple regression which provides a means of choosing independent variables which will provide the best prediction possible with the fewest independent variables. Stepwise regression adds (i.e., "forward stepwise") or subtracts (i.e., "backward stepwise" or "elimination") one independent variable at a time. If adding, one adds the best predictor in conjunction with the variables already added, if subtracting one subtracts the worst possible predictor in conjunction with the remaining variables.

Elimination was chosen for the present analysis because it starts out with all the variables in the equation and drops those that do not act well with the rest. Forward stepwise regression begins with no equation rather than with a "total interaction" equation, thereby possibly ignoring some significant interactions.

The data was analysed using a general purpose multiple regression programme entitled "REGRO7" (J. S. Lewis, Statistics Canada) in an IBM 370/155 computer.

The analytic measures which are used in the Results and Discussion sections are described below.

Prior to the elimination analysis itself, a correlation matrix is calculated. The correlation matrix gives the degree to which the variables, including the dependent variable, are associated in all

possible pair-combinations. The correlations between the dependent and independent variables should theoretically be poor as the dependent variable is assumed to vary randomly with the independent variables. High correlations between any two independent variables are also considered to be deleterious, as only one of the two will probably be retained as a significant predictor with the other only providing redundant information.

The correlation matrix may also be used to construct a "causal model" which reflects the total process in effect in addition to the simple bivariate relationships given by the correlation coefficients. For this purpose, partial correlation coefficients are calculated from the correlation coefficients using normalized regression coefficients (i.e., allowance is made for the effect of the other variables in the regression equation).

The overall significance and linearity of the regression equation is determined by an analysis-of-variance test. The resultant "regression F" is then compared with a tabular F-value at the desired level of significance. "Partial F-values" test the linearity of the individual variables in the regression model.

The precision of the estimated regression is given by the coefficient of multiple determination, R^2 . This value converted to a percentage ($R^2 \times 100\%$) gives the percent variation in the dependent variable which has been explained by the independent variables.

The "b's" of the regression equation help provide an understanding of the relation of each independent variable to the dependent variable. The direction (positive or negative) of this relationship is obtained primarily from the regression coefficients. It is worthwhile to test for independence of the b's, that is, to see if the true values, or β 's, are equal to zero (H_0: $\beta=0$). For this purpose either the partial F-values described earlier or null t-values can be used. Both are given in the results. The statistic "t" can also be used to test the hypothesis that β is equal to any other than zero, and it can also be used for finding the confidence interval of β .

Confidence limits for estimates, $\overset{\boldsymbol{\lambda}}{\mathbf{Y}}$, were calculated using the equation

$$\frac{1}{Y} \pm t \times \sqrt{\text{variance of Y}}$$

The computation method is given in Reese (1964, p. 74).

Although the regressand is a discrete variable the estimate, Y, will be taken from the set of real numbers. The estimate should not be rounded off to the nearest integer value as the equation is not intended to estimate integer values. This problem can be alleviated by accepting all integer values which fall within the confidence limits as possible estimates.

In performing the regression analysis it was assumed that the errors, $(Y_i - \overset{\wedge}{Y_i})$ were independent, have zero mean, have a constant variance and follow a normal distribution (necessary for making F-tests). The validity of these assumptions was tested by assessing plots of the data. The errors were plotted 1) in a frequency plot, 2) against the fitted value $\overset{\wedge}{Y_i}$, and 3) against the independent variables.

Other assumptions were also made about the analysis. First, it was assumed that X-values are measured with no error. The fulfillment of this assumption is unlikely. It was also assumed that the dependent variables were distributed normally about the regression surface. If this is not the case a transformation or weighting procedure is recommended. It is impossible to plot the distribution of the independent variables about the regression surface in multiple regression analysis. Plots of individual independent variables, however, show a non-homogeneous variance of Y in many cases (Appendix D).

It's probable that the latter and other assumptions were not adhered to. To test the consequences of this an independent check was made on the validity of the regression model for lakes. The sample size for stream data was not large enough to allow a valid check to be made. Before the analysis was carried out a random sample of 34 lakes (Appendix C2) was removed from the total sample of 136. Then the predicting equation (given in the Results) was used to predict the number of colony sites on the independent sample lakes. The actual values for the dependent variable were then regressed on the predicted values.

The variables used in the regression analyses are listed in Table 2. Most of the independent variables were related to the dependent variable in a non-linear way, making linear transformations necessary. The type of transformations used were determined by running a regression analysis with all the parent independent variables, the X's, and all their common transformations (square, square root, inverse, and common log). Inverse and common log

Table 2.--Variables used in the analysis

	Description	colony sites		length	of length	of length	Ģ	idth	of width	of width	- -	gradient		flow rate	
ons	Desc	Number of co	Length	Square of le	Square root of length	Common log of length	Width	Square of width	Inverse of v	Common log of width	Gradient	44	Flow rate	Inverse of	
b) Stream sections	Variable Code	COLS	$^{ m L}_{ m S}$	rs_{S}	LSR_S	$_{ m LL_S}$	Ws	WSS	WIS	$\mathtt{WL}_\mathbf{S}$	$G_{\mathbf{S}}$	GIS	Fs	FIS	
· -	Description	Number of colony sites	Elevation	Inverse of elevation	Perimeter	Square of perimeter	Area	Square root of area	Area/perimeter ratio	Square of ratio	Water level stability	Length of aspen shoreline	Square root of TAL	Length of cottonwood shoreline	
a) Lakes	Variable Code	COLSL	B L	$\mathbf{T}_{\mathbf{I}\mathbf{S}}$	$^{ m L}$	$^{ m T}_{ m Sd}$	$^{ m A}_{ m L}$	$ASR_{\mathbf{L}}$	$^{ m R}_{ m L}$	$ ext{RS}_{ ext{L}}$	T _M	$TA_{ m L}$	$\mathtt{TASR}_{\mathbf{L}}$	$^{ m C}$	

$^{ m N}$	Length of non-productive brush shoreline	<u>.</u>	ASS	•	Square of A_{S}
. S	Length of swamp shoreline		NSS		Length of non-productive brush & swamp shoreline
$^{7}\mathrm{sn}$, Length of non-productive brush and swamp shoreline	ક	SSSN		Square of NS _S
${ t NSSR}_{ m L}$.Square root of $\operatorname{NS}_{\mathbf{L}}$	•			
$\mathtt{TARANK}_{\mathbf{L}}^{\mathbf{l}}$	Weighted aspen variable			٠	-
$\mathtt{TARANKSR}_{\mathbf{L}}^{\ 1}$	$\mathbb{R}^{n \times n}$ Square root of TARANK $_{\mathbf{L}}^{1}$				

Table 2--Continued

lSpecial variables weed in separate analysis.

transformations could be applied only to those variables with non-zero values--all except forest cover variables. All those transformations which improved the regression by increasing the coefficient of multiple determination, \mathbb{R}^2 , beyond the increase attributed to the parent variable were included. Improvements could have been due either to an individual effect or to a combined effect if the functional relationship of independent to dependent variable was complex (e.g., $\mathbb{Y} = \mathbb{A} + \mathbb{$

The regression technique was used in other ways to aid in interpretation of the data. The aspen variables, ${\rm TA_L}$ and ${\rm TASR_L}$ were replaced by the weighted variables ${\rm TARANK_L}$ and ${\rm TARANKSR_L}$ (p. 30) to test for sensitivity of the forest cover maps as indicators of food abundance. The relative importance of habitat factors may differ within different physical types of lakes and streams as it does between lakes and streams. The sample of streams was not large enough to test for such effects but lakes were grouped into two size classes, lakes with areas less than and greater than 100 acres, giving sample sizes of 52 and 50 respectively. These selected samples were tested with the aspen variables and with weighted aspen variables substituted for the aspen variables. Unless indicated the same variables (Table 2) were used in all the regression runs.

Beyond the biological interpretation of the relationship between beavers and their environment is the application of this knowledge to beaver management. Practical use of the regression model was assessed

for two purposes: 1) beaver inventory, and 2) beaver land capability classification. The estimates of colony sites obtained using the model were compared to ground and aerial inventory counts for a sample of 6 stream sections totalling 11.5 miles of heavily used beaver habitat.

Land capability was assessed by converting the number of beaver tolony sites to capability classes (each class consisting of a range of sites, for example; Class 3: 2-4 sites per stream mile). The biophysical limitations were described for each class. This is similar to the method described for ungulates by the British Columbia E.L.U.C. Secretariat (Blower, 1973). The study area was then mapped to illustrate the land capability classification system.

CHAPTER 5

RESULTS

A) Simple Regressions and Correlations

Of the lake variables given in Table 2a and described in the Methods section, only EI_L was not significantly correlated with COLS_L (P>0.05)¹, the number of beaver colony sites on lakes (Table 3a). The parent variable, E_L , was, however, significantly correlated with COLS_L . The significant correlations were squared (to give the coefficients of determination, or r^2) and plotted in a histogram (Fig. 4a) to illustrate the relative abilities of individual variables to explain the total variation in the number of colony sites. The food variables, NS_L and TASR_L , were the most significant, each of which individually accounted for 71% of the variation in COLS_L . A physical variable, ASR_L , accounted for 60% of the variation. Most of the other variables were also highly correlated with COLS_L . Much less significant were W_L (16%) and E_L (6%).

Many of the stream variables (Table 2b) were not significantly correlated with ${\rm COLS}_{\rm S}$ (Table 3b). However, all variable families (including parent variable with transformations), with the exception of

 $^{^1}P\!\!\leq\!\!0.05$ is the level of significance used throughout the thesis.

Table 3.--Correlations (r) for all combinations of variables with regression constants (b_0) and coefficients (b_1) for simple regressions of COLS on each independent variable

	Regressions.	COLS _L) Coefficient b _j	-0.430	0.214	6.43E-4	0,169	8.26E-2	1.89E-4	-4.26	0,269	3,30	6.02	6.77	5.56	69.4	11.54	0,302	4.13	~ "	* * * * * * * * * * * * * * * * * * * *	Regressions	COLSS)	Coefficient	5	0.455	2.4bE 2	2.13	4.10 -2.66E.3	-1.55E"5	-6.83	0.587	-1.57	6.40	1.01	0,360	2.46E-2	2,88	0.691
/	Simple Rega	, (Y CA Constant Coa b ₀	- 7		86.7	1,96	0,102			4.23	1.13	2.99	3,79	3,43	2,47	-0,530	4.25	1.28					겉	0	2,33	2,95	7 88			3.86	2,49	5,98	-1.61	1 03	2,85	3.07	1,39	2.39
•		TARANK _L (-													06.																				•
		NSSR _L	-			-											.55	.68				1						2										
=		NST N													•	.90	19.	.72																				
		$^{\rm S}_{\rm L}$.81	. 16	.75	74.			-	1	NSS	,														16.
		$_{\rm N}^{\rm T}$.31	8.	. 70	.23	•43					ASS														,15 ⁷	
		CSR_L											36	.62	.61	¥.	. 90	88					Y S.													\$. 24 ³	• 13 [^]
		7					4	,				- 89	18	.57	47	.42	• 95	• 78					FIS												₹01°	01 ^{\(\)}	¥.	. 14
		TASR _L									7.0	68	45	.72	.71	.67	;	;				ı	ខ្ម					*	÷					90	<u> </u>	01	34	√/T:-
	_	$_{ m IA_L}$								0	9	06	. 22	.74	. 59	. 54	;	:				į	GI S				٤						ć	 7.87	.27	.20×	.43	√97°
	Correlations (r)	r r							ć	67*-	22	.32	-,32	-,23	34.	-, 28	-,29	77		,	Correlations, (r)		သိ				1	• યા	3.					7,77	- 22 Y	.16	-,35	~77.°-
	orrelat	RS_L						5	æ	79.	. 07	55.	88.	8	.75	99.	\$.	• 76			orrelat	;	MLS.	•	1							87	١٠.	 	53	67.	30,	, zo.
	O	$^{\aleph}_{\mathrm{L}}$		-				.92	-,51	3 8	3.5	5, 29	643	69.	69.	8	.61	80			64	;	MIS								-,81	. 54	51	. 22%	- 217	20^{λ}	29	٠ TQ.
	-	ASR	<i>,</i> #				·89	88.	47	86.6		80	.37	83	.74	69.	68*	*					SSM							27×	69*	- :20 y		, co	.76	• 65	.227	·19^
		$\mathbf{A_L}$.93	.70	.79	29	26.		. 82	. 20	98.	• 65	.57	96.	.87			,	> .	S						.97	14	.82	28 ^λ	15.		.75	.67	. 23×	٠ <u>۲</u> α>
		$^{\mathrm{T}}_{\mathrm{Sd}}$			5	.77.	.45	67	20	. 97	. 8	3 6	γ11.	9.	47	.42	.97	. 78	٠			;	LLS	,				79.	.62	-, 52	. 65	-,35	14.		.75	.62	15:	, ,
ή, 		a l		į	59.	.93	. 68	69.	- 36	66.	60	89	.27	78	65	. 59	.78	.91				. !	LSRS				90	.72	.72	15	• 62	-,30	ر درور	. 06A	۷01.	.77	97.	5
		$\mathbf{EI}_{\mathbf{L}}$		٠14	12^	,12	$^{\cdot}$ 16 $^{\wedge}$,16 ^λ	00.	•16^	7,7	. 26	147	7,71	17	.15 ^λ	116	.27					r_s		• •-	Ċ	٠.	. 73	.72	.24 ^{\(\gamma\)}	.53	۰- 19 ^۷	ξς. (62)	, CO	.95	.97	. 22 ^{\(\)}	, Δ1.
	•	$\mathbf{E}_{\mathbf{L}}$	96 -	-116	-•12^ -•14	γ61	20	٠.19	450	-,18^	ر ا ا	28	γ ₂ -12	-16	-, 20	-,20	18	-,31		8			LS	_	;	٠, د د د	88	7.5	9/.	-,32	. 59	-,25√	67.		76.	8	 	Ç
		7 s $_{1}$ ∞	24 19 ³																	Section	٠	-	SÇTOO														69.	
a) Lakes	. 	BLES	E_L 8.1.			ASR														b) Stream Sections			VARIABLES	-			•										NSS	

P>0.05, v 100° (lakes) and v 43 (stream sect

aplots are given in Appendix D.

 A_S and AS_S , did have at least one member which was significantly correlated with $COLS_S$. The histogram of significant r^2 -values (Fig. 4a) shows the food variable NS_S to have the greatest independent effect on variability in the number of colony sites on stream sections (48%). Other variables showed much weaker correlations.

Correlations only indicate relationships of individual variables to the suitability of sites for beaver habitation and do not provide a total model relating the quantified components of beaver habitat. Thus the discussion of the importance of individual variables should be based on the models of variables interacting to determine site suitability. The models are derived from the elimination analyses.

B) Elimination Analyses and Final Models

The regressions of the numbers of beaver colony sites on environmental variables were significant at each step for both lakes and stream sections (Tables 4a and b, regression F-values). The initial R^2 -values were 0.9332 and 0.8386 respectively.

As all individual variables were not significant in the early steps of elimination (Tables 4a and b, partial F-values), the models of interacting beaver habitat variables were taken from the first steps which contained only significant variables. These are Step 10 for lakes and Step 9 for stream sections. The following predicting equations, or models in the form of Equation 2 (p. 35), were constructed from the regression coefficients of the variables present at these steps (Appendix E).

. Table 4. -- Statistics from elimination analyses

4

a) Lakes							,		<i>:</i> .							
Step	1	2	9	4	ب	9	^	ထ	6	10	:	12	13	17	15	16
Variable	-						Partial	F-values						t,		
E1L EL	0.17	0.25	116		1 1	1 1	: :	; ; ;	·	1 : :	1 1 3	:		1 1	1 1	HÌ
r, TA,	0.92	1.08	1.24	1.00	l _. ;	; ;	: :	:	. :	:	: :	: :	: ;	: :	: :	1
NSSRL	1.84	1.79	1.70	2.02	2.74	;	;	:	1	;	! !	;	;	:	:	;
S _L CSR,	3.24	3.67	2.26 3.48	3.66	3.04	2.02	2,01	: :	1 1		: :	14	: :	: :	i †	; ;
ن ان	4.72 h	5.24 >	5.05	4.65 ^λ	3.67	2.80	2,78	0.76		;	:	;	:	}. -	1	;
L PS.	2.0/ 10.97 ^{\(\)}	2.11 11.01 ^X	1.95 11.02	3.69 11.33	3.45 11.70\	9.38^{λ}		10.31	10.47 λ	√.88.6 9.88.		: :	: :	: :	: :	: :
ه ۲۲ م	8.75 ⁷	9.38 ²	9.22 ⁴ م 75.1	9.32 ^λ 8.64 λ	8.33 ^{\(\)} 0.77 \(\)	8.76 ^A	•	γ11,71 γ.00 9.00	11,35 ⁴ 8,28 ³	11.73 ³ ,	79.6	76.0	; ;	; ;	: :	;
ASRL	10.34 7	11.457	11,457	16.97	19.01	16.35 ×	18.77 \	18.15 \	17.74 7	23.09 X	15.27	5.542	7.23 X	()	1	:
$^{ m KS}_{ m L}$ $^{ m N}_{ m L}$ $^{ m TASR}_{ m L}$	18.55% 69.66% 7.00 ⁄	19.61 70.67 7.56 ⁷	19.69 71.50 9.76	19.56 79.84 \ 9.75 \	19.98 7 78.21 7 12.26 7	17.99 80.68 10.92 \tag{7}	21.98 105.53 ^λ 10.52 ^λ		$^{20.52}_{111.36}^{20}_{\lambda}$ $^{16.60}_{\lambda}$	21.34? 126.06λ 16.74λ			12.1/ 210.28 ^λ 22.02 ^λ	4.66° 191.49 [\] 217.93 [\]	180,43 ^λ 327,70 ^λ	245.09 Å
Regression F ^b (v ₁ , v ₂)	74,21 (16,85)	79.91 (15,86)	86.35 (14,87)	93.13 (13,88)	100.81 (12,89)	107.65	118.80 (10,91)	130.35	146.93 (8,93)	168,07	177.81 (6,95)	193.38 (5,96)	241.63	300.65	432.64 (2,99)	245.09
(with ranked aspen) ^C	75.46	81,22	87.81	94.48	102.28	109,50	121.15	131.19	147.62	169.34	180.23	194.02	240.34	297.21	418.40	246.46
Error Stand, Dev.	2,63	2.62	2.61	2.61	2,61	2,63	2,63	2.64	2.64	2,64	2,76	2.88	2.88	2.97	3,03	5.06
(with ranked aspen) ^c	2,61	2,60	2.59	2,59	2.59	2,61	2,60	2.63	2.63	2.63	2.74	2,88	2.89	2.99	3.07	5.05
R ²	0.9332	0.9331	0.9329	0.9322	0,9315	0.9294	0,9289	0.9273	0.9267	0.9260	0.9182	0.9097	0.9088	0.9020	0.8973	0.7102
(with ranked aspen) ^C	0.9342	0.9341	0.9339	0.9331	0.9324	0.9305	0.9301	0.9277	0.9270	0.9265	0.9192	0.9100	0.9084	0.9010	0.8942	0.7114
λ №0.05									-							

 a NS $_{
m L}$ was not included in the analysis because of perfect collinearity with other regressors.

b All regression F's significant (PC0.05).

CTARANK, and TARANKSR, replace TAL and TASR,. Elimination aequence the same except where statistics have been deleted,

	,	16		;	;	;	;	;	. ;	;	i	;	;	;	;	;	;	,	28.24 ^{\(\)}		28.24 (1,43)		2.95	0.3964
- ;	,	15		:	:	:	:	;	;	;	:	:	;	:	1	;	;	13.23^{λ}	23.62 ^{\(\)} .		24.76 (2,42)		2.61 (2.95	0.5411 0.3964
		71		;	:	;		;	1 (;	;	;	;	;	1	1	° √€9°9	18.38 ^{\(\chi\)}	29°86		20.93 (3,41)		2.45	0,6049
		13	•	-	;	;	1	:	,	;	:	;	;	:	;	17.48^{λ}	26.47×	20.13^{λ}	26.98 ^λ		26.38		2.07	0.7251
		12		ŧ.	• ;	;	!	:	:	:	:	:	1	:	0.31	3,33	26,32 ^λ	19.80^{λ}	24.87		(5,39)	-	2.09	0.7273
		11		!	;	;	;	;	ľ	:	1	;	1	2,03	2.31	3,60	28.95 ^{\(\gamma\)}	22.24 $^{\lambda}$	16.60 ^λ		18.13 (6,38)		2.06	0.7411
		01		-; !	;	;	;	;	;		;	;	. √8. √8.	9.34 ^{\(\gamma\)}	8.18	γ09°6.	40.25 ^{\(\)}	20,57 √	22.75 ^{\(\)}	4	(7,37)		1.91	0.7825
	2	6,	8	;	;	1	;	:	;	;	1	4.14 ^{\(\rapprox\)}	9.32λ	12.74 $^{\lambda}$	10.61	11.93^{λ}	47.71 ^{\(\)}	18.34 ^{\(\)}	28;81 ^{\(\chi\)}		18,56 (8,36)		1.84	0.8049
		∞	al F-values	;	;	:	!	:	1	;	2,27	2,45	10.53^{λ}	11.62^{λ}	11.20^{λ}	12.03λ	21.13^{λ}	21,107	28.72×	13	17,34 (9,35)	,	1.80	學 3 0.8168
- r ,	2		Partial	;	:	1	;	;	1	1,15	2,82	2,32	11.63^{λ}	12,82 ^{\(\)}	12.30^{λ}	13.19^{λ}	5.44X	22.05^{λ}	27.75	. ;	15.79		1.80	0.8228
		9		;	1	;	;	;	2,06	3,24	4.05	3,25	11.71^{λ}	14.28^{λ}	12.687	13.89^{λ}	7.18 ^{\(\)}	23.12^{λ}	29.34×	1	14,98 (11,33)		1.77	0,8332
		2	,	:	1	1	;	0.61	1,67	2,46	2,97	3,78	11.62 $^{\lambda}$	14,733	12.85 ^{\(\)}	14.147	6,31	22,57 ^{\(\chi\)}	29.53 ^λ	ŧ	13,63		1.78	0.8363
		7			ľ		0,0	0.83	1,23	2,01	2,42	2.07	10.74^{λ}	13.78	12.10 ^{\(\rapprox\)}	13.55^{λ}	5.42×	20.45	2.57	1	12,37		1.80	0.8384
		n		;	į,	0.02	0.41	0.23	1.16	1.89	2.26	1,53	9.98₹	13.03^{λ}	11.28	12,82 ^{\(\)}	5.07×	17.18 ³ .	1.85	l	(14,30)		, 1.83	0.8385
		7		;	0.01	0.02	0,40	0.21	0.80	1.53	1.78	1,49	6.60°	12.58 ³ .	10.90	12,417	4.30 ×	3.06	1.77	1	. 10,04 (15,29)	,	1.86	0.8386
Inved	tions	-		00.00	0.01	0.02	0.38	0.20	0.72	1.40	1.64	1,01	7.81^{λ}	3.90	8.13^{λ}	7,17	3,98	2.91	1.71		9.09 (16,28)		1.89	0.8386
Table 4Continued	b) Stream Sections	Step .	Variable	ASe	ີຮິ	بن ب	NSO	FIC	WIS	ີສ	- T-	ر ۷۰	LĽ	ૢ૾ૺઽ	LSKS	ر	WS	GIS.	NSSS	4	Regression F ^o (v ₁ , v ₂)	1 1 1	Stand. Dev.	R. ²

Step	-	,7	7	4	so.	9	7	œ	6	10	1	21	2	:	<u> </u>	
Variable							f				1	: ``	3	5	15	91
					-		Part	Fartial F-va lues	nes	0						
R.	0.12		:	;	:	;	;	:	;							•
$E1_{L}$	0.25	0.20	;	;	ł i	;	;	:	;		:	;	:	;	;	7
EL	0.20	0.21	00.0	;	;	;	;	;		;	١,	;	:	}	;	;
NSSR	. 0, 55	0,0	0.70	0.75	!	;	:	;	: :	! •	!	1	;	;	;	;
S	1.11	1.22	1.28	1,35	0.62	;	;		;	:	;	;	;	;	;	;
CSRL	1.05	1.08	0.93	1,05	0	7 78		:	;	;	;	;	;	;	;	;
PSL	0,40	0.79	0.75	0.87	200			:	:	:	;	;	;	:	;	
ູ່້	1.78	1,73	85.7	1, 7,		1.65	0.20	;	;	;	:	;	;	;	;	: :
Ţ,	1.34	1.35	8	22	1001	1.00	7.17	0.96	ŧ i	;	;	:	;	;		
Ψ ¹	3.49	4.28×	7 J.B.	7577	1.00 (ag /	1.86	1.56	2.13	1.19	;	;	;	;	;	; ;	: :
1 tr	3.03	3 5	300	4.40	, 00.	7.19	6,45	6.39	5.63^	γ 90°9	;	. ‡	;	;		;
ASR.	3 73	, , , , , , , , , , , , , , , , , , ,	ζος 3	2.02	2.40	5.73	3.58	3.70	2,78	6.97₹	1,06		;	: ;	١,	;
RS,	× 77.5	, ca 4	200	, 10°0	7,000	5.87	6.04^	6.13^{\wedge}	5.18^{λ}	8,91 ^{\(\)}	2,66	3.63	1	; ;	;	;
1	× × × ×	0.55		V19.	7.40	8.27	8, 33 ^{\(\)}	8.39	7.47	6.18^{λ}	4.32λ	5 857	2 82	•	:	:
	74.0	60.0	90.0	6.87	6,18	6.75 ^λ	7.18^{λ}	7,19	7.70 ⁷	786 Y	5 70).		70.7	, i	:	1
l E	6.11.	6. 19 ⁷	6.224	6.39 ^X	7.417.	39.81^{λ}	43.62V	46.37 ^{\(\)}	45.49A	56 137.	λς, ειι	4,73	19.5	3.78	;	į.
Jycyr	3.82	4.17	4.15 [^]	5.17	5. 12 ³ .	5.337	4.61 ⁷	7.52	6.593.	7 227	10 30	113.24	10/./4	101.27	92.24	;
										;		11,937	112,04	150,61^	141.50	91.66^{λ}
욘		29.52	32,35	.35.83	39.02	50 67	47.43	2								
(v_1, v_2)	(16,33)	(15,34)	(14,35)	(13, 36)	(12,37)	(11,33)	(10, 39)	(07.6)	04.0	54	70,64	84.44	100,27	127,69	179.05	91,66
							()	(01.0)	(74.6)	(7,47)	(6,43)	(5,44)	(4,45)	(3,46)	(2,47)	(1,48)
with ranked								•								
aspen) ^c	27.64	30.22	33,13	36,67	40.20	44.47	48,52	54.95	61,42	69.45	:	;		÷		, ,
															.	93.6/
Stand, Dev.	3.87	3.81	3.77	3.72	3.71	3,69	3,68	3,6%	3		ć					
								,	10.04	3.63	3.86	3.86	3.94	4.02	4.14	7.05
(vith ranked				,												
aspen)	3.82	3.77	3,73	3.68	3.66	3,63	3.64	3.60	3.61	3.62	!	:	;	;	;	7
2.5																
¥	0.9290	0.9287	0.9283	0.9283	0.9268	3,9255	0,9240	0.9236	0.9218	0.9195	0.9079	0.9056	0.8991	0.8928	0.8840	0.6563
(with ranked								-		,						·
aspen) ^C	0.9306	0.9302	0.9298	0,9298	0,9288	3.9279	0.9256	0.9252	0.9230	0,9205	:	;	;	-		
															;	0.6612

Table 4.--Continued

Nursable 1 2 3 4 5 6 7 6 9 10 11 12 13 14 15 16 17 18 18 18 18 18 18 18	d) Lakes with areas less than 100 acres ^a	h areas le	sss than l	00 acres ^a		,			•			ż					
0.13 0.26 0.27 0.25 0.27 0.25 0.27 0.25 0.27 0.25 0.25 0.25 0.25 0.25 0.25 0.25 0.25	Step	1	. 7	е	.7	ر د	9	7	œ	6	10	Ξ-	12	13.	 17	15	16
0.13 0.26 0.26 0.27 0.02 0.27 0.27 0.27 0.27 0.27 0.27	Variable			•		٠.	,	Parti		(7) 61						-	
0.18 0.26 0.27 0.27 0.27 0.28 0.28 0.28 0.28 0.28 0.28 0.28 0.28		,										,			~		31
0.55 0.55 0.75 0.75 0.75 0.75 0.75 0.75	TASK	0,13	, · · ·	:	¥	1 1	;	;	!	;	;		!	:	:	;	•
0.55 0.25 0.37 0.37 0.39 0.35 0.35 0.35 0.35 0.35 0.35 0.35 0.35		0.18	97.0	1 (+ 1	;	;	;	!	:	:	:	;	:	;	;	;
0.35 0.455 0.47 0.47 0.47 0.47 0.47 0.47 0.47 0.47	PSL	0.27	1 0.27	0.02	:	;	;	;	;	;	:	:	;	;	!	:	;
0.754 0.60 0.74 1.60 1.11 1.2 1.2 1.2 1.2 1.2 1.2 1.2 1.2 1.	۳,	0.56	0.55	0.37	0,53	!	;	;	;	;	;	;	;	:	;	;	1
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1.47 3.43 3.68 3.51 4.409 4.25 4.303 3.76 4.07 3.61 4.994	EIL	2.97	3.01	3,03	3.10	2.82	3,57	3.17	3,22	2.73	3.17	2.58	;	;	1	:	:
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4.527 4.567 4.407 4.607 4.817 4.117 4.817 4.447 5.797 1.122	CSRL	3.51	3.51	3.44	3,55	4.58^	4.254	3,35	3.26	4.03	3.76	₹017	3.61	√66 ° 7	;	:	:
0.88	ප්	4.52√	4.56 [^]	7/7.7	√09°7	5.80^	√8 ∀ *5	4.51^	4.3·1^	4.85^	4.61^	4.81^	√44°4	2,79^	1.22	;	ļ
\$\begin{array}{c c c c c c c c c c c c c c c c c c c		0.88	4.62 [^]	4.50√	4.60 ⁴	4.83×	4.46A	4.24×	4.93 ^{\(\)}	6.82√	6.6 3₹	7,183	8.17 √	9.63y	7.48×	6.41 λ	;
2.71 2.96 3.22 3.55 3.85 4.09 4.08 4.40 4.73 5.12 5.56 5.95 7.38 7.54 10.86 1 (16.35) (15.36) (14.37) (13.38) (11.40) (10.41) (9.42) (8.43) (7.44) (6.45) (5.46) (4.47) (3.48) (2.49) (11.40) (10.41) (9.42) (8.43) (7.44) (6.45) (5.46) (4.47) (3.48) (2.49) (11.40) (10.41) (9.42) (11.04) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (10.41) (₹ 0.75	0.89	1,89	1.92	10.37	9.80 ^{\(\right)}	7.64^	10.48≻	9.08^	8.66^	8.15 ^{\(\chi\)}	11.11^{λ}	10.76λ	7.74	8.53^{λ}	13.45^{λ}
2.48																	
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0.5532	- 1			0.720)	1210.0	0.00	0.4330	0.440	0.400	0.4403	0.44.00	0.3920	0.000	0.3204	0.3032	0.2120
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Table, 4. -- Continued

Fig. 4

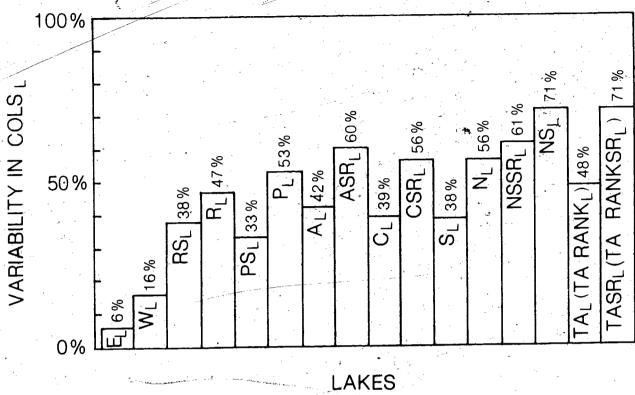
Percent variation in number of colony sites

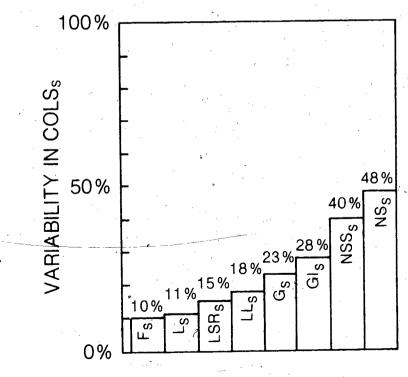
(COLS) accounted for by single variables

and groups of variables.

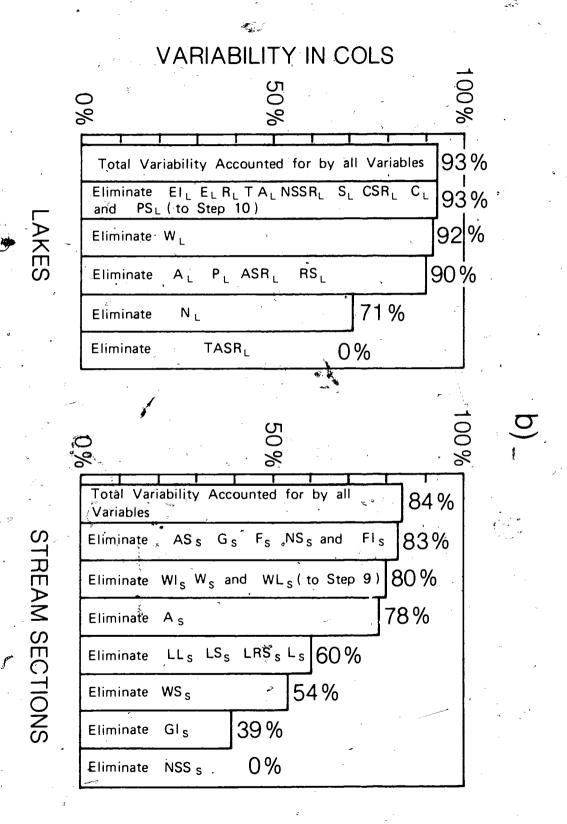
- a) Single variables from simple regressions (r significant, P≤0.05).
- b) Single variables and groups of variables from elimination analyses (all variables included).







STREAM SECTIONS



Equation 3.
$$\Upsilon$$
 (Lakes) = $^{-3.84} - 0.781(P_L) + 1.43E^{-3}(A_L) + 0.555(ASR_L)$
- $5.10E^{-4}(RS_L) + 1.24(W_L) + 1.79(TASR_L) + 6.32(N_L)$

Fig. 4b shows the relative abilities of variables in the models to explain the total variability in the number of colony sites between samples.

The significance of the lake variables in the model (those remaining at Step 10) is shown by the elimination sequence after Step 10:

,		$\frac{R^2}{}$	Difference
Step 10		0.9260	→ 0.0078
Step 11	$\mathtt{W}_{\mathtt{L}}$ eliminated	0.9182	0.0209
Steps 12-15	${f A}_L$, ${f P}_L$, ${f ASR}_L$ and ${f RS}_L$	0.8973	0.0207
, ES	eliminated	*,	0.1871
Step 16	${ t N}_{ extsf{L}}$ eliminated	0.7102	40.1071
en e	$TASR_{L}$ remaining		

Clearly the most significant lake variables were those quantifying food, N_L , and, in particular, $TASR_L$. Together these variables explained almost 90% of the total variability in $COLS_L$. The physical variables, A_L , P_L , ASR_L , and RS_L , explained an additional 2% of the variability while W_L explained less than 1%. The elevation, cottonwood and swamp variables had no significant effect at all.

The elimination sequence of stream variables after Step 9 is as follows:

* .:		$\frac{R^2}{R}$	Difference
Step 9		0.8049	0.0224
Step 10	A _S eliminated	0.7825	>0.0224
Steps 11-14	$ ext{LL}_{ ext{S}}$, $ ext{LSR}_{ ext{S}}$ and $ ext{L}_{ ext{S}}$		0.1776
and the second	eliminated	0.6049	
Step 15	WS _S eliminated	0.5411	0.0638
Step 16	${ m GI}_{ m S}$ eliminated	0.3964	→ 0 . 1447
	NSS _S remaining		The state of the s

Again a food variable, NSS_S, had the greatest effect on the number of colony sites (COLS_S), explaining about 40% of the total variability in COLS_S. Physical variables were much more important in the stream model than in the lake model. Together they accounted for almost 24% of the variability in COLS_S. On the other hand the aspen variables were less significant in the stream model (contributing 2%). The flow rate index variable family was completely eliminated before Step 9.

All variables contributed less in the models (Table 4 and Fig. 4b) than they did individually (Table 3 and Fig. 4a) as a result of correlations between the variables. Thus all variables provided some redundant information. The cottonwood variables, C_L and CSR_L , were so highly correlated with PS_L and TA_L (Table 3) that their individual significance was lost in the model of interactions. Similarly, S_L , which was dropped at Step 7, was highly correlated with N_L . Many variables

related through transformation were also redundant but some did provide additional information indicating a more complex functional relationship of the habitat factor to COLS (e.g. L_S and transformations). Lake elevation and stream flow rate were the only variables which had low correlations with other variables and which were also non-significant in the models.

C) Causal Models

As stated earlier, the correlation matrices can be used to construct causal models of the total processes underlying the regressions from which ecological inferences can be made. By considering the partial correlation coefficients from Step 10 of the lake analysis and Step 9 of the stream analysis (Appendix F), and correlation coefficients relating independent variables to the number of colony sites, the models in Fig. 5 were constructed. The models quantify the interactions of all components of the regression equations (Equations 3 and 4). The relative importance of variables in the causal models is similar to that derived from the sequences of elimination. In addition, it can be seen that most of the variables and variable families act independently. Also, a strong dependence of N_L on the physical lake characteristics, P_L, A_L, RS_L, and ASR_L, is shown. The effect of WS_S on COLS_S is indirect as it acts through an effect on the stream section length variables.

D) Other Elimination Runs

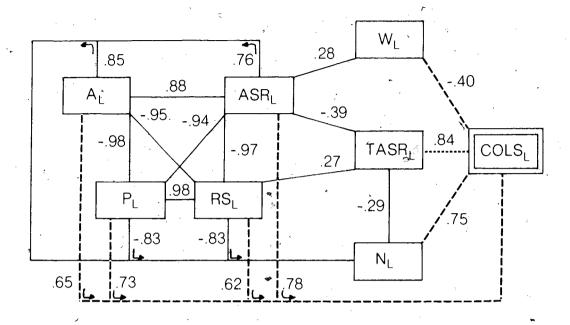
The weighted aspen variable, TARANK $_{\rm L}$, is a slightly more accurate measure of food abundance than TA $_{\rm L}$ (Table 4a). It increased the initial

Fig. 5 Causal models of relationships between variables

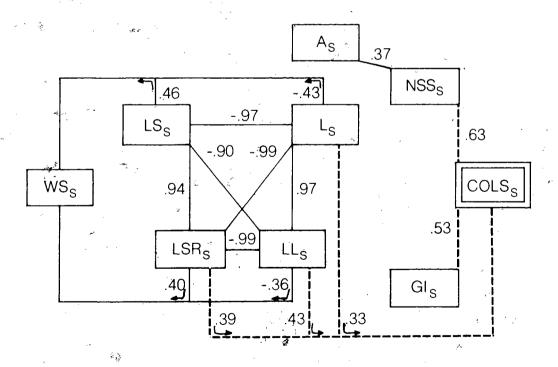
Lakes--Step 10, Equation 3

Stream sections--Step 9, Equation 4

LAKES (Step 10, Equation 3)



STREAM SECTIONS (Step 9, Equation 4)



 R^2 -value by 0.0010 over the value obtained using TA_L , while the Step $10\ R^2$ -value was increased by 0.0005. The contribution of $TARANK_L$ to an explanation of the variability in $COLS_L$ was about the same for lakes with areas greater than and less than 100 acres (Tables 4c and d). In all cases the effect is minimal so that the additional effort needed to measure and calculate this variable would not appear to be worthwhile.

The sequence of elimination was similar for lakes with areas greater than 100 acres and the complete lake sample 1 (Tables 4a and c). However, the Regression F- and R^2 -values were smaller and the standard deviations of the errors were larger, indicating that the complete model is a better predictor of the number of beaver colony sites on large lakes.

Lakes with areas less than 100 acres showed a vastly different elimination sequence from the complete sample (Tables 4a and d). Many of the differences are attributed to changes in positions of highly correlated variables. One notable change, however, is the increase in relative importance of ASRL for smaller lakes over both the complete lake sample and larger lakes. This may indicate a density-dependent effect on the number of colonies a suitable habitat can support which would be expected for a territorial species. Although the partial model for small lakes showed a decreased error standard deviation, the diminished Regression F- and R²-values show that this error is proportionally higher in relation to the actual variation in

¹The complete lake sample does not include the independent sample of lakes which was removed before the analyses.

 ${\tt COLS_L}$ than it was with the complete model. Therefore, the complete model, which explains more variability in ${\tt COLS_L}$, is both a superior model and a superior predictor than are either of the partial models.

E) Residual Analysis

The residuals, or errors $(Y_i - Y_i)$, of the analyses are listed in Appendix G. The frequency plots (Fig. 6a) show normality with mean zero in the case of both lake and stream section residuals. The plots against the estimates, Y_i (Fig. 6b), show approximate horizontal bands. However, the plots of the errors against the independent variables are difficult to characterize as horizontal bands as assumed (Appendix H). Many of the errors may be non-random because of natural biases in the habitat variables themselves. For example, the natural distribution of lake sizes is skewed to the left where it ends abruptly at zero, as there are no lakes of negative size. Many other factors also have non-normal frequency distributions.

The outliers, or samples with errors which are abnormally large relative to the others, are evident on the residual plots (Fig. 6b and Appendix H). They are valuable assets in the interpretation of the analyses as they may provide information which other points cannot, and hence merit further investigation.

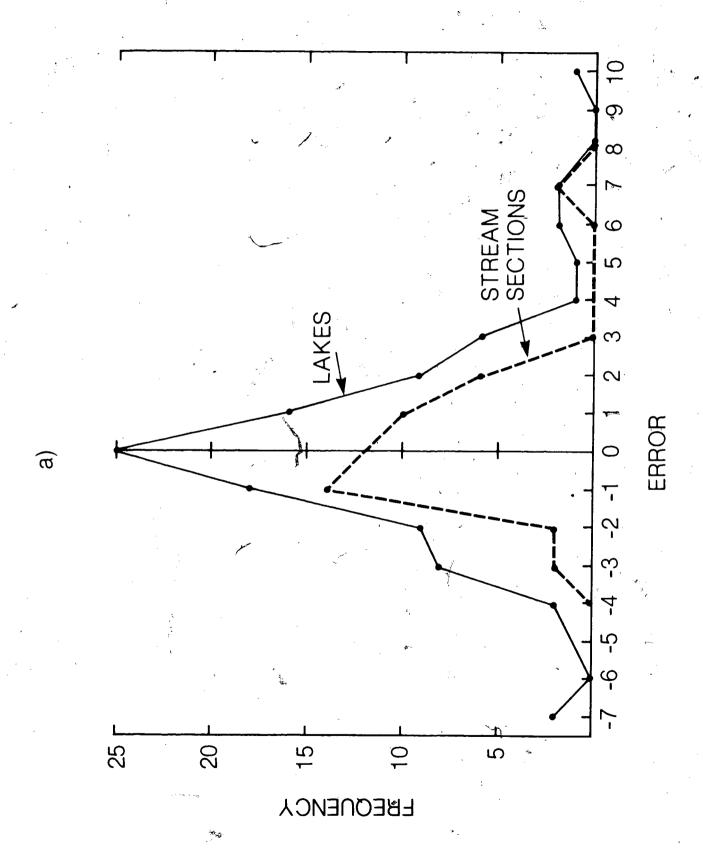
Outliers have been arbitrarily defined in this thesis as having standardized errors (Error ÷ Error Standard Deviation) greater than 2. The standardized errors are listed in Appendix G. The outliers are listed in Table 5.

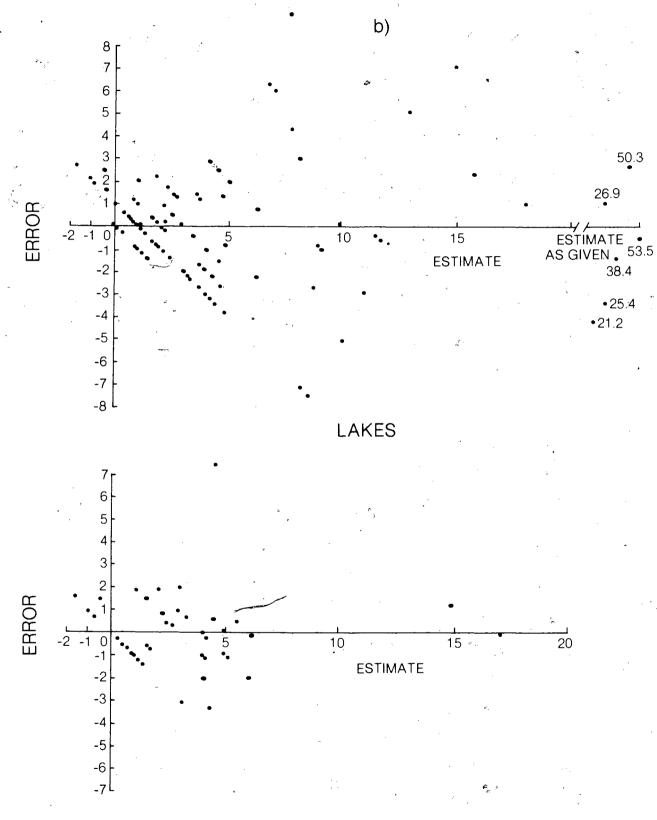
Fig. 6

Residual analysis.

- a) Frequency plots of residuals.
 Errors from Appendix G, rounded to
 nearest ±1.0.
- b) Residuals plotted against estimates.

 Errors and estimates from Appendix G.





STREAM SECTIONS

Table 5--Outliers in residual analysis

	• N	COLS	Estimate	Error	Standard Error	95% Confidence Interval of Estimate	
Elwin	T6	18	8,30	9.70	3.68	7-9	Ì
Tatin 2	S2	12	4.53	7.47		3-6	`
Swans	1.8	22	14.86	7.14	2.71	13-16	
Nakinilerak	134	13	6.47	6.53	2.48	2-9	
Parrot (S.E.)	L71	13	6.72	6.28	2.38	8-9	
Bay	, T. J.	13	7.04	96*5	2.26	8-9	
Nilkitwa	, į.		8.09	-7.09	-2.69	7-10	
Bulkley	L2	1	8,49	-7.49	-2.84	7-10	, -
Trembleur	133	13	26.20	-13.20	-5.00	22-31	÷
Decker	127	رن د	32.55	-23.55	-8,93	29-37	
,							ĺ

The four lakes with overestimates of colony sites (Bulkley, Decker, Trembleur, and Nilkitwa) have unique characteristics among the lakes in the analysis. Bulkley and Decker Lakes are both long and narrow with rail lines running along their entire north shores, making food trees inaccessible and the shoreline unsuitable for lodge construction. Burns Lake has similar characteristics but the suitable habitat is not uniformly distributed around the lake. Suitable habitats on this lake were concentrated on the convoluted south shore so the resulting estimate (50.31) was very close to the actual number of potential colony sites (53). The railway, therefore, destroyed proportionally less beaver habitat on Burns Lake than it did on Bulkley and Decker Lakes.

Trembleur Lake has a unique shoreline of steep, solid rock prohibiting lodge construction and food gathering. All but one of the 13 colony sites on this lake are situated at inflowing streams.

Nilkitwa Lake is also unique, being a fairly large lake with water no more than 10 feet deep in the centre. If lodges were constructed on the shoreline, winter ice would probably prevent access to the food cache in winter. There were no lodges constructed on the lake shore—one colony site made use of the lake at an inflowing stream. Other lakes, such as Ogston (L41), Mooseskin Johnny (I10) and Stern (I28), are also extremely shallow but errors of their estimates were low as the number of colony sites was limited by other factors which were measured (e.g. food species). In addition, their small sizes resulted in relatively low estimates with small standardized errors.

Additional information is provided by the lakes with underestimates. Four of these lakes, Day, Elwin, Swans, and Parrot (S.E.), have some recognizable similarities: 1) They are relatively small (A $_{\rm L}$ <1000 acres), 2) they have high perimeter/area ratios, and 3) a considerable proportion of their shorelines are lined with aspen. The interaction of these effects may be underestimated by the model.

Nakinilerak Lake was lined with more aspen than was indicated by the Forest Cover maps (field observation). Forest cover measurements for this lake were taken from "Interim Forest Cover" maps of the Babine Public Sustained Yield Unit (P.S.Y.U.) which covers Babine Lake and adjacent lakes north and east of the midsection of Babine Lake. These maps, dated pre-1960, are not as accurate as the more recent maps which cover all other P.S.Y.U.'s in the study area. The effect on the colony site estimates for other lakes in the Babine P.S.Y.U. was not as severe.

The single outlying stream section, Tatin 2, has no obvious characteristics which distinguish it from others. Either a combination of characteristics, a characteristic underrated by the model (e.g. aspen on shoreline), or an unmeasured characteristic was responsible for the underestimate.

F) Independent Test of Lake Model

The validity of the lake model was tested using Equation 3 (p. 52) and data from a sample of 34 randomly chosen lakes (Appendix C2).

¹More recent maps were not available at the time of the writing of this thesis.

Results of the regression of the actual numbers of potential colony sites, Y, on the numbers predicted by Equation 3, Y, are given in Table 6.

The lake model is apparently, therefore, a significant predictor of beaver habitat suitability. Violations of any of the assumptions mentioned in the previous section and in the Methods (Analyses Used) section, if existent, have had minimal effects on the validity of the model.

G) Beaver Inventory by Prediction

The models given in Equations 3 and 4 have valuable applications as aids in beaver inventory. Estimates may be made within any desired confidence interval. The 95% confidence limits for each lake (including the independent sample) and stream section are given in Appendix G. The possible estimates, integers within these limits, are also given. It should be noted that less precise confidence limits give narrower intervals.

The sample of 102 lakes had a total of 580 beaver colony sites. The sum of integers representing the lower and upper 95% confidence limits gave a 95% confidence interval of 502-676 colony sites. The interval for the 45 stream sections with 145 colony sites was 94-225. The 95% confidence interval for the 34 lakes which did not contribute to the lake model was 124-175, while the sum of colony sites was only 113. The three outliers in this small sample caused a net overestimate (sum of confidence limits of estimates less sum of actual colony sites) of 22-40 colony sites (Table 5: Decker, Trembleur, and Nakinilerak Lakes).

Table 6--Regression analysis of actual colony sites on predicted numbers of colonies

$$\lambda_F = 35.25 (1, 32)$$
.

 $\lambda r \doteq 0.7240$

Standard Error of Estimate = 2.31

	**	Standard Deviati	on
Mean Y	4.38	6.84	
Mean Y	3.22	3.29	
Constant (b ₀)	1.80	j	•
Coefficient (b ₁)	0.35	0.06	$^{\lambda}$ Null t = 5.94

λ_P<0.05

Results of the comparison of stream flight inventory and ground inventory with statistical prediction using the regression equation for streams (Equation 4) are tabulated in Table 7. The prediction method is far superior to aerial reconnaissance where ground inventory is not practical.

H) Beaver Land Capability Classification

Using the known density of beaver colonies on lakes and stream sections it is possible to distinguish beaver land capability classes arbitrarily (present capability). The classification units are individual lakes, and stream sections of uniform gradient and width, including land within an arbitrary distance of 100 feet of the shoreline (where most beaver cutting occurs). Five capability classes were distinguished as follows in Table 8.

The limiting subclasses to be used in the classification were derived from the analyses. Only significant biophysical factors were used. Special subclasses were derived from the inspection of outliers (residual analysis).

The capability map (Fig. 7) was constructed from the capability classes and sublcasses of Tables 8 and 9. Only the subclasses with major limiting effects on beaver productivity of the specific lake or stream section rated are given with the capability classes. The capability class thus reflects the degree of limitation imposed by the given subclasses.

Table 7--Comparison of stream flight, ground check, and prediction methods of beaver colony site inventory

	<u> </u>					
Stream	No.	Length (Miles)	Ground	Colonies Predicted	Flight	95% Confidence Interval for Predictions
Tchesinkut	S4	1.50	6	5.54	1	4-7
Tatin 1	S3	0.75	5 '	4.39	2	3-6
Tatin 2	S2	1.00	12	4.53	2	3-6
Duncan	S1	1.50	4	2.94	2	1-\$5
Sutherland	S44	1.75	4	4.25	0	3-5
Copper	S9	5.00	14	16.98		13-21
Totals		11.50	48	38.63	8	27-50

 $^{^{1}{\}rm Flown}$ with a deHaviland Beaver aircraft at about 500' (or less) above ground level at ground speed of 60-80 m.p.h.

Table 8--Beaver land capability classes

Class	Description	COLS _L per shoreline mi		COLS _L per stream mil	
1	No biophysical limitations affect beaver production	3+	\	6+	
2	Slight limitations	2-<3		4-<6	
. 3	Moderate limitations	1-<2	;	2-<4	ચ *
4	Severe limitations	<1	4	<2	
5	Limitations preclude beaver production	0		0	

Table 9--Beaver land capability limiting subclasses

	Symbol ¹	Subclass Description	Variable Derivation ²
Lakes	S	Shoreline configuration allows buildup of waves.	· RS _L
	0	Outlet not regulated by beaver $dam(s)$.	$\mathtt{w}_{\mathtt{L}}$
Streams	W G	Width restricts damming. ³ Gradient restricts damming. ³	WS _S GI _S
Both	F	Absence of major food species.4	${{{}^{TASR}_L}, \ {{}^{A}_S}} $ ${{}^{N}_L}, \ {{}^{NSS}_S}$
		Special Subclasses	٠
	Н	Human disturbance of shoreline (e.g., roads, railways, land clearing) restrict food gathering and/or lodge construction.	
	T	Natural topography limiting as above.	
	, D	Lake depth limiting. Freezes to bottom in winter.	

May not be same variable codes used in analysis.

 $^{^2}$ From Equations 3 and 4, p. 52.

 $^{^3{\}rm These}$ factors result in water level instability. Limitations imposed by stream width are largely dependent on stream gradient (i.e., flow rate).

⁴Aspen, alder and willow.

DISCUSSION

A) Beaver Habitat Requirements

The success of the regression analyses indicates that some of the biophysical factors used in the analyses were measures of, or were themselves, beaver habitat requirements. Although the models given are not definitive representations of beaver habitat requirements, a more precise definition of the habitat requirements can be given within the realm of the components of the models. The accuracy of the models as predictive tools implies an accuracy of their components as measures of habitat requirements. Other factors, which caused outliers in the analyses, may be used as subjective descriptors of beaver habitat. Measurement techniques may have introduced some bias in the model by causing poorly measured variables to be underrated. The habitat requirements of the beaver will thus be discussed in light of the limitations of the models.

Aquatic Habitat

The prerequisite of beaver habitat is water. Large lakes (with more area and shoreline length) and long stream sections are expected.

to provide more beaver habitat than smaller lakes and shorter stream sections. In a sense, the above factors are measures of suitable aquatic habitat. Special limiting factors such as water depth (which must be sufficient to allow access to the food cache in the winter), and shoreline topography (which must support lodge or den construction and allow access to the food supply) normally vary in a random fashion along the shores of lakes and streams. Thus the fact that they were not measured per se did not significantly affect the accuracy of the models. Where water depth and shoreline topography occurred as non-random limitations, as they did on Nilkitwa Lake (beaver colonization limited by shallow water) and Trembleur Lake (and many lakes of the Interior Plateau from Babine Lake east, where steep shoreline was limiting), the errors of estimation showed the sample sites to be outliers. Other components of suitable aquatic habitat for beaver were measured more directly. Beavers prefer a seasonally stable water level. For this reason low gradient streams are preferred. The most stable environment for beavers is one which they can control themseaves by damming. Thus, low gradient, narrow streams and lakes with dammable outlets (also narrow) are preferred. The unregulated aquatic environment is rarely stable (see surface water data, Fig. 3 and Appendix B). Wave action on lakes also has an effect on stability. A convoluted shoreline which prevents the buildup of large waves or provides refuges from large waves for

colony sites is also a beaver habitat requirement on large lakes.

Food and Construction Materials

In addition to a stable aquatic habitat, the presence of an adequate supply of food and building materials is necessary for the establishment and maintenance of beaver colony sites. Willow and alder are the key plants in the beavers habitat. These are the edaphic climax species of lake and stream shorelines which are disturbed by seasonal and beaver caused water fluctuations. The latter fluctuations are the result of cyclic beaver habitat occupancy and abandonment (due to food depletion or trapping). Willows also grow well in marshy areas, common along lake shores and low gradient streams, including areas flooded by beavers. Typical alder--and willow--beaver habitat is shown in Plates 1, 2, and 3. Beaver dams which cause the flooding of low forested areas create new aquatic habitat (Plates 4 and 5), as well as new willow habitat (Plates 6 and 7), thereby increasing beaver land capability.

Aspen, the most preferred food species, provides only temporary beaver habitat. Aspen depends primarily on fires to open up new areas for its colonization (Graham et al., 1963). As the timing and locations of fires are essentially random, aspen stands usually succeed to conifer forests. Beaver utilization of aspen accelerates this process. The magnitude of aspen cutting by beaver is shown in Plates 8 and 9. If the aspen is not allowed to regenerate (i.e., if the suckers are cut), the stand will be destroyed and conifers will be able to invade the site (Plate 10). The current high population of beavers in the study area (especially in the CALPDF biogeoclimatic zone) is dependent primarily on transient aspen stands.

Plate 1

Class 1 beaver-willow habitat on Howsen Creek (S29). Mooseskin Johnny (I10, background) is Class 4 beaver habitat, beaver production limited primarily by shallow water (July 7, 1974).

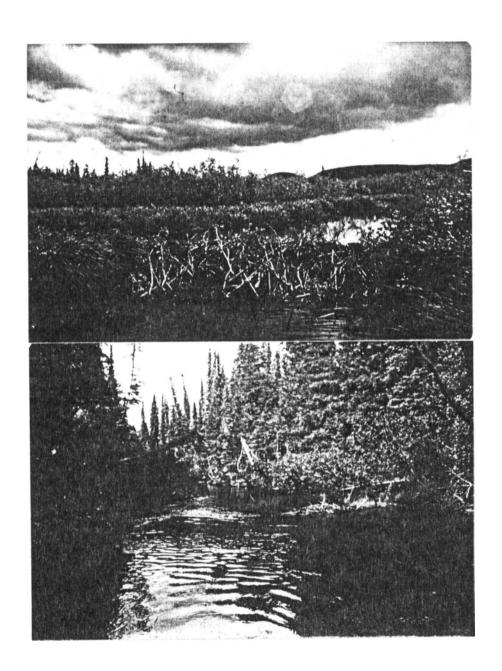


Plate 2

Beaver dam in willow habitat on Copper River at inflow of Dennis Lake (I8). Dam is constructed of willow. This colony made use of both lake and stream (August 23, 1974).

Plate 3

Beaver dam in alder habitat on Copper River at outflow of Dennis Lake (I8). The dam, partially destroyed by spring flooding, is constructed of alder (August 23, 1974).



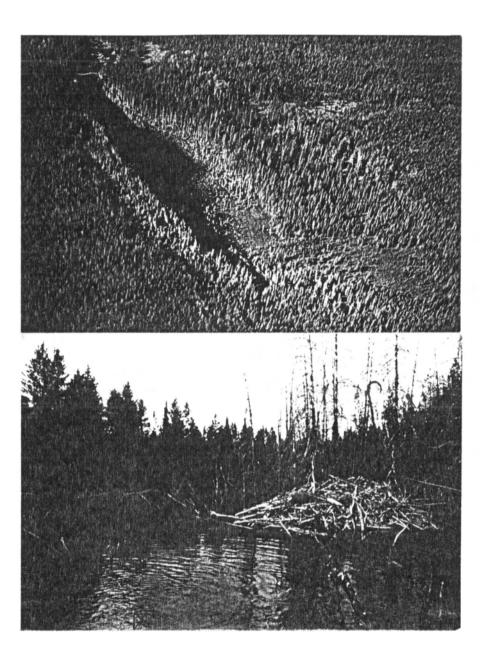
New aquatic habitat in low forested areas flooded by beaver dams.

Platé 4

Stream north of Prince George (1973).

Plate 5

Aldrich Lake (19; August 23, 1974).



New willow-marsh habitat created by beaver flooding.

Plate 6

Note aspen (light-green trees) cut back about 100 feet from the ponds and conifers growing on dams (indicating age). Netalzul Creek, about 6 miles northeast of Blunt Lake (I16; August 26, 1974).

Plate 7

Beaver lodge in marsh. Swans Lake (L8; August 20, 1974).





Depletion of aspen stands by beaver.

Plate 8

Note uncut birch near shore. Elwin Lake (L6; October 18, 1974).

Plate 9

Note uncut conifers and lodge near left-centre. Pond (L53; May 25, 1975).

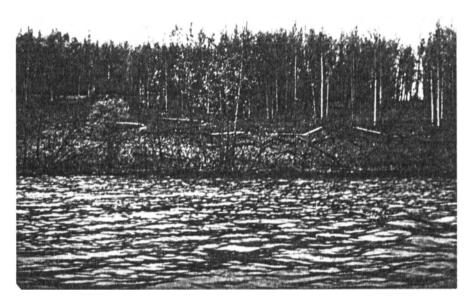


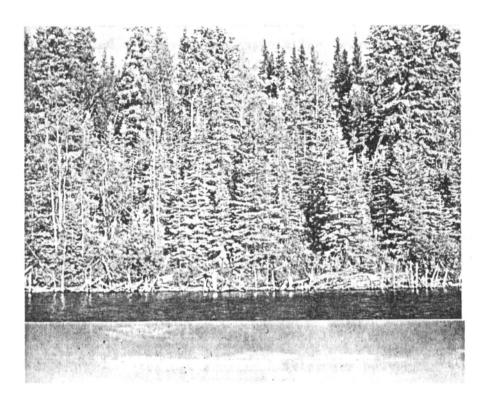


Plate 10

White spruce and subalpine fir invading overexploited aspen stand. Some aspen has been able to regenerate by suckering. Lodge is visible on the right. Elwin Lake (L6; August 18, 1974).

Plate 11

Class 1 beaver lake habitat on Swans Lake (L8).
Yellow pond lilies, willows, and aspen are
abundant (October 18, 1974).





A relatively stable base beaver population, which acts as a nucleus for expansion into new aspen areas, is supported by edaphic climax thickets of willow and alder. The stream shown in Plate 6 was probably originally colonized by beavers to exploit the aspen. Although the aspen is now depleted, beavers are able to subsist on willow-habitat which they created themselves (the dams were stable and willows replaced the conifer forest on the ponds edges). The relative resiliencies of alder, willow, and aspen habitat types to beaver exploitation are diagrammed on p. 79.

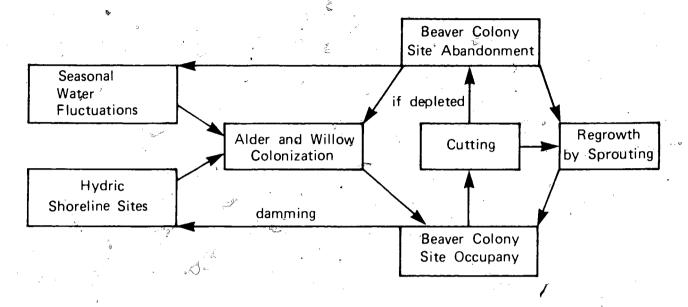
An example of Class 1 beaver lake habitat is Swans Lake (Plate 11). Favourable characteristics of this lake include:

- 1. A beaver dam on the outlet which
 - a) Stabilizes the water level
 - b) Creates new aquatic habitat for beaver
 - c) Creates new willow habitat for beaver use
 - d) Makes onshore woody species more accessible
- 2. A shoreline configuration which prevents wave buildup and protects the shore from wave action
- Abundant food species including aspen, willows, and yellow pond lilies

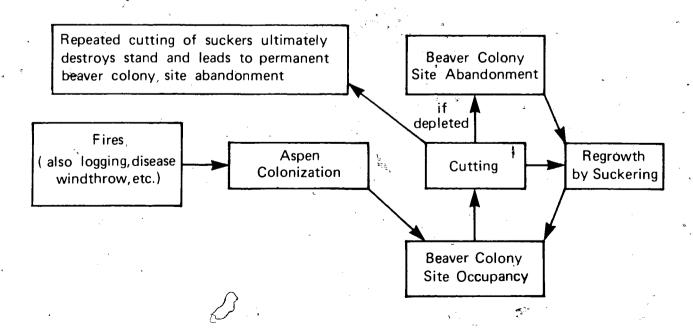
The Class 1 stream habitat of Howsen Creek (Plate 1) is suitable for beaver due to:

- 1. Low gradient and narrow width which permit damming; providing the same benefits of a dammed lake outlet
- 2. Abundant willow.

a) Alder-willow: permanent beaver habitat



b) Aspen: transient beaver habitat



Willow and alder are usually more abundant along streams than along lakes. Streams thus provide better beaver habitat than lakes in areas where aspen does not occur.

Cottonwood is not an important food species as it is not abundant enough to have a direct effect on beaver numbers. It is a preferred food, however, and is utilized where found in a similar way to willow. Birch (also not abundant in study area) and conifers are rarely eaten, although they are occasionally used in construction. Aquatic and terrestrial herbaceous vegetation, major summer foods, are rarely cached for winter use if woody species are available. Yellow pond lilies were observed in a few caches. Dennington and Johnson (1974) noted a cache entirely composed of lilies on an Arctic muskeg lake which lacked other food species.

Aspen and willow were the most common species found in food caches during the present study (Plates 12, 13, and 14). Less preferred foods, mainly alder, were often cached with aspen or willow, even though the latter species were available. Other authors reporting similar findings have concluded that alder was a major food species. On the basis of observations of winter food caches before and after their period of use I would suggest that the significance of alder in a mixed cache is not as a food, but as a construction material. Construction material is used to depress preferred food species under water where they will not freeze into the ice nor be rendered unavailable as a winter food supply. It may also help secure the cache in place, especially on fast flowing streams and on lake shores which are subject to extreme wave action. The following

Plate 12

Start of food cache, consisting of aspen and willow. Alder, present along shoreline, has not yet been cached. Swans Lake (L8; August 20, 1974).



Plate 13

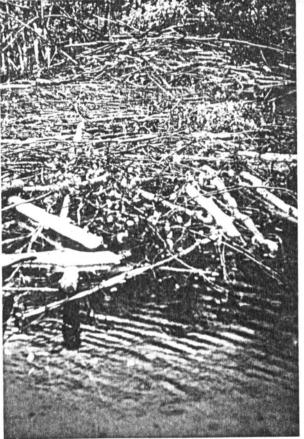
Mixed cache of aspen, willow, alder, birch, red osier dogwood and yellow pond lilies.

Alder, birch, red osier dogwood and peeled aspen logs are on top of cache. Seymour Lake (L27; October 17, 1974).

Plate 14

Cache of aspen, willow and alder near completion. Alder and peeled aspen logs are placed on top of cache. Sunset Lake (L7; October 17, 1974).





observations were made on the utilization of alder in food caches.

Citations indicate similar observations.

Beaver Food Cache Composition and Structure (Fall Observations)

- Although alder was often cached with aspen and/or willow, it was never the sole species cached (e.g., Novakowski, 1967; Aleksiuk, 1970; Northcott, 1971).
- 2. Alder was usually placed, in the cache, on top of aspen and/or willow (Plates 13 and 14).
- Peeled aspen logs were occasionally placed on top of food caches along with other less preferred species such as white birch and conifers (Plates 13 and 14). Dennington and Johnson (1974, p. 31) noted two caches of pond lilies which were "capped" with mats of black spruce. In the only such reference found in the literature they proposed "spruce is used only to cover and submerge more desirable species." Other authors have not reported on the locations (i.e., availability) of species in food caches.
- where floating marshes occur, caches are often placed under the vegetation mat, which is capped with mud and sticks. In other cases larger cuttings, such as aspen logs, are fixed into the substrate if possible. Both situations indicate attempts by beavers to submerge the cache by other means.

Beaver Food Cache Remains (Spring Observations)

- Many food caches are not completely browsed (Townsend, 1953; Northcott, 1971; Dennington and Johnson, 1974).
- 2. The most common unbrowsed species found in cache remains was alder (Northcott, 1971). The significance of cache remains has not heretofore been interpreted. In northern latitudes, where adult beaver have a depressed metabolism in the winter (Aleksiuk and Cowan, 1969), beaver colonies are able to survive on stored quantities (which may be minimal) of more preferred food species.
- 3. The cache remains are occasionally left in place and used to secure and submerge fresh food for the following winter (Townsend, 1953).
- 4. Cache remains are more commonly used for lodge and dam renovation.

The preferred use of alder for the construction and repair of beaver dams and lodges is well known. The size of alder stems (averaging about 2 inches in diameter) makes it an ideal building material (2 inches is the preferred size of aspen used in construction (Aldous, 1938; Hodgdon and Hunt, 1953; Hall, 1960)). Although succulent alder leaves and twigs are occasionally eaten during the summer (Tevis, 1950; Lawrence, 1964), alder cutting is not proportional to its use as a food, but as a structural material (Hazeltine, 1950; Jackson, 1953a, 1954). Alder bark is rarely eaten at any time. O'Brien (1938), who raised beavers on various foods, had to remove beavers

from an alder diet as they were rapidly losing weight and he feared for their lives. Indeed evidence of the use of alder as a major food by beaver is scanty and has been limited to its common occurrence in food caches. Evidence presented here indicates that alder, conifers, and possibly other less preferred species such as white birch serve primarily as structural components of beaver food caches. Such materials are also important buffers to the exploitation of preferred winter foods.

The feeding habits of beaver should thus be evaluated in the future with consideration for the presence of construction materials in winter food caches.

Clamate

Climate is probably not a significant factor influencing beaver habitat selection. The micro-environment of the beaver pond (or lake) and lodge effectively isolate the animals from the macro-environment during the winter (Stephenson, 1969). Extreme temperature conditions regularly occur in the study area (Fig. 2, Appendix A) and are of little consequence to the beaver populations there.

B) Beaver Inventory

Application of the regression models as an aid in beaver inventory is a logical extension of the regression technique. The-prediction method is superior to aerial reconnaissance where ground inventory is not practical (Table 7). The wildlife manager must realize, though, that the models predict the number of potential

colony sites, not the present population of beavers. Although colony sites are rarely all active simultaneously (temporary abandonment may be due to trapping, food depletion, or death of the breeding female (Townsend, 1953)) this number may be directly related to the present beaver colony carrying capacity of the land over a large area. Data presented in Appendix Il shows that 39% of the colony sites on 8 lakes (surveyed in October, 1974) were active. Dennington and Johnson (1974) found a similar occupancy rate for lake colony sites in the Mackenzie Valley and northern Yukon, while 75% of the stream colony sites were active (Appendix I2). The relationship of active sites to total sites is linear (Appendix I3) making it possible to estimate the numbers of active sites from counts of total beaver colony sites. Estimates would probably only be accurate for counts over large areas and should not be applied to specific lakes or stream sections. An overestimate of total colony sites is possible as the deterioration of lodges will lag behind a decline in carrying capacity (e.g., after depletion of a transient aspen stand). As aspen depletion has just started in the study area, all counts of beaver colony sites should be accurate and show a direct relationship to the present beaver colony carrying capacity. Beavers prefer to reoccupy old lodges rather than to build new ones unless a new food source (e.g., aspen) becomes available (personal observation), so an overestimate from this source is unlikely.

Aerial inventory will be considerably more accurate for surveys of active sites than it will be for total colony sites. For example, in the U.S.S.R., Zharkov (1963) reported that on streams, 44% of the active colonies could be seen (90% for the river proper, 39% for the floodplain). In the present study only 17% of total stream colony sites were seen (Table 7, p.66). Vatolin (1970) surveyed 40 lakes (1,420 miles in 16 flight hours) and observed only 9% of the 277 active colonies which were present. In a discussion of some unpublished Canadian Wildlife Service reports by various authors, Dennington and Johnson (1974) reported comparable inaccuracies for surveys of active beaver colonies in the Mackenzie delta. Active colony sites are best seen in the fall when broken dams are reconstructed, new mud is placed on lodges to provide a winter seal against predators and the weather, and food caches are built. visibility of lodges, whether active or not, also depends on characteristics of the shoreline vegetation. A dense forest canopy lining the shore obstructs the view of more lodges than a cleared-off or marshy shoreline. The locations of stream colonies can also be determined by the presence of active dams. Inactive dams may remain indefinitely, as signs of beaver habitat suitability on small, low gradient headwater streams. No matter how accurate surveys of active colony sites are, they may still be poor indicators of beaver habitat suitability because of variation in degree of habitat saturation by beaver in different areas.

The use of aerial photographs for delineating colony sites (active or potential) has many of the limitations flying does. Many lodges and dams are not visible on aerial photographs because they are obscured by vegetation or because they are taken from such an altitude that they lack detail. In addition, air-photos primarily show those colony sites which were active at the time they were taken. With a combined knowledge of beaver habitat requirements and air-photo interpretive skills, one can recognize, however, areas of general suitability to beavers. The use of aerial photographs for the recognition of potential colony sites is discussed by Dickinson (1971). The value of aerial photographs lies in the detection of population trends (by comparing photos taken in successive years) rather than as a census technique.

For an inventory of potential beaver colony sites and subsequent land capability classification, very little, if any, field work is required. As described in the Methods section of this thesis, most of the variables used in the models were taken from readily available government maps (topographic and forest cover maps) and standard aerial photographs (e.g., flown at a particular height for a particular purpose). Only two of the significant variables in the models (Equations 3 and 4) required ground measurements. These were the water level stability index for lakes (W_L) and a width variable for stream sections (WS_S). When W_L was dropped at Step 11, R^2 dropped by only 0.0078. In other words, at that step W_L was accounting for only 0.78% of the 92.60% of the variation (in COLS_L) which was being explained (Table 4a). When WS_S was dropped at

Step 15 (Table 4b) the equation for streams remained significant. Thus, for a slight sacrifice in the accuracy of prediction, field work is not required for the inventory of total beaver colony sites. Anomalies in the general characteristics of lakes and streams (outliers) may escape detection if fieldwork is completely abandoned. Therefore, to avoid gross errors in estimation, large lakes and lengthy stream sections should be surveyed for anomalies before the prediction is made. The survey may involve aerial reconnaissance, ground checks, or communication with people familiar with the area. Common causes of outliers, such as rocky shoreline topography (Plate 15) and many human activities (Plate 16), should be focused on in the survey. Roads, railways, and land clearings invariably follow waterways and are major limiting factors to beaver habitat suitability. Artificial water regulation with man-made dams and the artificial removal of beaver dams can produce severe water fluctuations, decreasing the capability of many naturally suitable areas to support beaver. 1

Many of the variables requiring field measurements may be taken more quickly (i.e., economically) and with comparable accuracy from low level colour aerial photographs (e.g., 70 m.m. photos, taken at 400 feet A.M.S.L.). These include measurements of horizontal distances (stream width), heights (water depth and stream gradient), and local geology, physiography and bank vegetation (D.A. Currie,

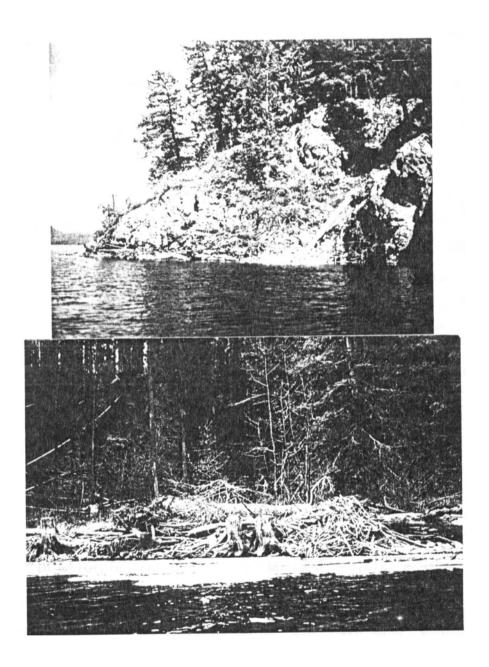
¹Beavers attempt to accommodate the fluctuations by extending their lodges vertically on the shoreline, thus maintaining underwater entrances and above water living space at all times.

Plate 15

Colony site on fault in rocky shoreline in area sheltered from wave action. Pinchi Lake (L88; June 3, 1975).

Plate 16

Artificial water level control by the Fisheries Service (Canada Department of the Environment) on Taltapin Lake (L46) produces severe water fluctuations (May 17, 1975).



1976, pers. comm.). Possibilities for the use of such photographs in beaver habitat modelling, inventory and land capability classification are considerable and should be pursued in future studies. The accuracy of most forest cover maps, topographic maps, etc., although limited, was sufficient for the present study (see Elimination Analyses and Final Models section). Some of the subjective variables, such as the water level stability (W_L) and flow rate (F_S) indices, might increase the accuracy of prediction if they could be measured more accurately.

- C) Beaver Land Capability Classification and Beaver Management

 The beaver land capability classification system presented
 in this thesis is intended for the following uses:
 - (1) Land use planning in the study area.
 - (2) As a methodology for other land capability classification projects involving beaver, other wildlife, or other resources.
 - (3) As a basis for beaver management, including beaver habitat conservation and improvement.

Land capability classifications are presumably meant to play a major role in multiple land use studies where a decision must be made as to which resource(s) should receive priority as a land use. A discussion of the bases on which these decisions are made, whether social, economic, or aesthetic, is not within the scope of this study, although certainly relevant to the future of the beaver. It is left to the land use planners to evaluate beaver in the appropriate

 $^{^{\}mathrm{l}}\mathrm{Dept}.$ of Forest Hydrology, Faculty of Forestry, University of British Columbia, Vancouver.

categories (above), compare the results with results from other resources and make their decisions regarding land use. Unfortunately, conflicts of beaver with other land uses are common. These are well documented in the literature (see Jackson, 1953b; Knudsen, 1954, 1962; Laramie, 1963; Vesall, 1947; Yeager and Hill, 1954). Land use decisions have traditionally not favoured the beaver.

The beaver land capability ratings given (Fig. 7; Tables 8 and 9) reflect present land capability. Natural succession, natural catastrophes (fire, windthrow, insect outbreaks, etc.) and management practices (see below) may alter the capability from its present state. Management techniques, in fact, may be used to improve the capability of a given area for a specific resource, such as wildlife. For example, Luckhurst (1974, p. 1) specifies the following technological controls to improve land capability for ungulates:

- "1) prescribed burning or grazing
- "2) logging or slashing
- "3) protection, including protection from fire or any other land use practice that will damage the land base or reduce the potential productivity of ungulates."

Although these controls were directed towards ungulate management, they are also relevant to other herbivores, such as the beaver.

Since an important factor limiting animal populations is food supply (Lack, 1954), it is to be expected that management improvement of the food base would have significant benefit to animal

¹A specified management input is assumed in many land capability classifications (e.g., Luckhurst, 1974). The term "present" capability doesn't apply in these cases.

populations. This is certainly true in the case of beaver where the availability of food species determines beaver numbers on physically suitable areas.

Food supply can affect the population size through density-dependent changes in mortality (Lack, 1954). The main effect is on juvenile beavers which are forced, through territoriality, to seek out unoccupied suitable sites to establish colonies (Aleksiuk, 1968). Density-dependency in this case assumes that territories are set up to optimize food utilization over a long period of time with the function of maintaining a stable population at or below the carrying capacity of the environment. There is no evidence in the literature which contradicts this theory, even though the exact nature of territoriality in beavers is still unclear (Hall, 1960; Aleksiuk, 1968). The major mortality factor of migrating individuals is opportunistic predation. Starvation is rare in all beavers (Novakowski, 1967).

Other density-dependent and -independent mortality factors such as weather, parasites, and disease appear to have only minor effects on beaver populations. Epidemics of Tularemia and other bacterial diseases have been noted in extremely dense populations of beaver (Longley and Moyle, 1963). These were always rare and are even less common today when trapping keeps populations at moderate levels.

In order to maintain optimal populations of beaver and maximize productivity for commercial fur trappers, the food supply must be managed and the physical habitat protected. As shown earlier, alder and willow populations are stable and are able to coexist with beaver. Aspen, on the other hand, is only a temporary occupant of lake and

stream shorelines. Continuous exploitation of aspen by beavers (usually termed "overexploitation" by game managers) accelerates the process of local extinction of aspen. A prolongation of the lifetime of aspen stands is potentially the most powerful beaver management tool. Equations 3 and 4 indicate that every X-miles of shoreline that is not already 10% gross volume aspen could support $1.79 \times \sqrt{\text{X-miles}}$ COLS_L or $0.954 \times \text{X-miles}$ COLS_S.

In many areas of North America overexploitation of aspen has already occurred. This is most evident in eastern North America where trapping was banned to insure repopulation of beavers in areas where they had been extirpated through unrestricted trapping during colonial times. There are only a limited number of alternatives available for beaver-aspen management. They involve the stimulation of natural regeneration, planting, and beaver harvest strategies.

The majority of aspen forests present in North America today are the result of natural forest fires which made aspen habitat available for colonization. In the past beavers have depended on fires to maintain early seral stage vegetation. Fire is especially important in mountainous areas where stream courses are relatively stable. Where stream courses change frequently, aspen often regenerates on the disturbed sites. In British Columbia, stands of aspen are typically fire-induced. The current practice of provincial and state governments to attempt to extinguish forest fires, along with beaver overutilization of aspen, will cause the extinction of many aspen forests throughout the beavers range in North America.

A resultant decline in beaver populations can be expected if

beaver-aspen management is ignored. Any disturbance that results in an increase in soil temperature, including fire, cutting of trees, removal of associated vegetation and scarification, will stimulate aspen suckering (Maini, 1968). The suckering response increases with an increase in the intensity of the fire. The possibility of using fire for purposes of aspen reforestation has not been employed to date either for beaver, other wildlife or forest management. It is likely that native Indians and, more recently, even big-game guides have employed fires to maintain high quality forage material (in both the grassland and aspen forest) characteristic of early seral stage vegetation.

Another possible means of regenerating aspen on devastated watersheds involves planting. There are two major problems associated with this method: 1) It would be difficult to keep beavers out of an area during reforestation (Graham et al., 1963) and, 2) Ungulates would retard reforestation (Gese and Shadle, 1943). Artificial propagation of aspen is best done with cuttings rather than with seeds or root suckers (Gese and Shadle, 1943). The cuttings could be taken from strains which are best suited to growth in the swampy conditions surrounding most beaver colonies. Before letting beavers back into an area, tree size and density could be optimized to give optimal production. Gese and Shadle (1943) give 35 years as the optimum age of aspen from the standpoint of amount of beaver food produced. The optimum age of aspen for complete utilization is 20 years (Hiner, 1938). Quantity utilized per year of growth should be maximized in the planting strategy, but no information on this subject was found in the literature.

Aspen harvesting and planting is not practiced in British

Columbia. According to Smith (1968), this is because the merchantable

volume of aspen here is low. He states that aspen planting could be

justified if better and more economical wood was produced.

A third possibility for beaver-aspen management involves preventing the devastation of aspen stands by rotating trapping localities. This would provide aspen with the chance to regenerate on some areas while it is being harvested by beavers on other areas. Boyce (1974) suggests that a rotation period of no less than 4-5 years is required to give a maximum sustained yield. It is important to prevent beavers from feeding on the aspen suckers that follow their cutting. Since small trees are preferred for construction materials (Aldous, 1938; Hall, 1960), suckers are often cut and regeneration thus prevented (Christensen et al., 1951). Graham et al. (1963) proposed integrated beaver-aspen management as a solution to the problem in the Great Lakes States where both are commercial resources. Cutting plans for beaver could be comparable with the cutting schedules under a forest management plan.

A final possibility for management exists. If a trapper could hold the population on his trapline at a level low enough so that in any one year the animals would harvest only the amount of aspen equivalent to the annual growth of the forest, then a rotation of areas being trapped may not be needed.

The last two suggestions seem most practical for use in North

America today as they involve the local provincial and state governments as well as the trapper. The government bureau responsible for

fur-bearer management, the Fish and Wildlife Branch in British Columbia, could regulate trapping methods which will preserve the aspen-beaver community. Registered trapline systems, as in British Columbia, stimulate trappers to be responsible for the management of animals on their own lines. A dialogue between government and trapper may be all that is needed to initiate integrated resource management in the interest of both the trapper and the beaver.

Perpetuation of aspen for the benefit of several wildlife species, including deer, moose, elk, porcupine, snowshoe hare, and woodland birds as well as beaver, is an additional worthwhile objective, which would justify all types of aspen management.

CHAPTER 7

SUMMARY AND CONCLUSIONS

- 1. The purpose of the study was to develop a land capability classification system for the beaver.
- 2. The nature of beaver habitat and habitat selection satisfy the assumption that all suitable beaver habitat has been, or is being, exploited. The characteristics of beaver structures insure that visible signs of exploitation remain.
- 3. The characteristics of beaver habitat were described from the literature.
- 4. The study area, covering over 10,000 square miles in the northern interior of British Columbia, provided a range of biophysical conditions sufficient to develop and test the capability classification system. A total of 134 lakes (approximately 266,000 acres, 1,100 shoreline miles) and 45 stream sections (90 stream miles) were sampled.
- 5. Beaver colony site density is shown to be a practical measure of the intensity of beaver land use. A total of 643 lake colony sites and 145 stream colony sites were observed.

- 6. Biophysical Variables representing the habitat requirements of beaver were measured. The variables are described on p. 40.
- 7. The relationships of biophysical variables to beaver colony site density on lakes and on stream sections were tested and modelled using backwards stepwise regression analysis. The regression equations are given on p. 52.
- 8. An independent check of the validity of the lake model was made on a random sample of 34 lakes.
- 9. Sample sites which did not fit the situation described in the models were interpreted in the analysis of residuals and provided valuable information.
- 10. Statistically significant environmental factors were aquatic habitat with a stable water level and an adequate food supply.
- 11. Colony densities indicated that edaphic climax communities
 (such as alder-willow associations) provided the most stable habitats
 for beaver while temporary plant communities (such as aspen associations)
 support high but transient populations.
- 12. Evidence was presented which suggests that alder is important as a construction material not only in dams and lodges, but in food caches where it is used to submerge more preferred food species (willow and aspen). The presence of alder is a significant buffer to the exploitation of willow and aspen.
- 13. The use of the models as an aid in beaver inventory was discussed and compared with other methods. Inventory by prediction is considered both more accurate and economical than aerial reconnaissance and aerial photograph inventory of potential beaver colony sites.

- 14. A beaver land capability classification system was devised (pp. 67-68) and a capability map for the study area was constructed (Fig. 7, appended). Management techniques which can be applied to increase beaver land capability were discussed.
- 15. Aspen is the most important beaver management tool. The stimulation of natural regeneration and aspen planting are not considered practical management techniques unless wildlife values in general are high. Conservation of existing aspen stands can be acheived with various harvest strategies, as discussed.

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Appendix A.--Climate data from six weather stations in the study area^a

Element and Station	Jan.	Feb.	Mar.	Apr.	Мау	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year	Length of Record ^b
Babine Lake		Latitude	le 55 19 N	Longi	Longitude 126	37 W E	Elevation	2360 Ft.	A. S. L.	. `				
Mean Daily Temperature (Deg. F.) Mean Daily Maximum Temperature Mean Daily Minimum Temperature	5.1 13.5 -3.3	17.2 27.7 6.7	24.2 35.8 12.6	34.4 45.7 23.0	44.1 57.2 30.9	51.7 65.1 38.2	55.2 68.3 42.2	54.1 66.9 41.2	46.8 58.4 35.1	36.7 44.8 28.5	24.8 30.8 18.8	13.5 20.3 20.3	34.0 44.5 23.4	е е е е е е е е е е е е е е е е е е е
Extreme Maximum Temperature No. of Years of Record Extreme Minimum Temperature No. of Years of Record	21 -47 -21	47 20 -38 20	60 21 -39 21	67 -7 -7	84 21 13 21	91 20 21 19	91 20 29 19	91 20 20 20	83 19 18 19	68 19 · 1 20	51 -29 22 22	47 22 -44 22	, 16	
No. of Days with Prost	31	28	30	29	19	٥	. 1	m '	10	22	29	31	238	3
Mean Rainfall (inches) Mean Snowfall Mean Total Precipitation	24.2	0.04 18.1 1.85	0.10 11.3 1.23	0.64 5.2 1.16	1.55 0.2 1.56	1.80 0.0 1.80	2.12 0.0 2.12	1.88 0.0 1.88	1.95 0.2 1.97	2.11 4.9 2.59	0.68 16.7 2.35	0.07 25.7 2.65	13.01 106.5 23.65	. 000
Greatest Rainfall in 24 Mrs. No. of Years of Record Greatest Snowfall in 24 Hrs. No. of Years of Record	0.45 26 9.6 26	30.5	\$ 0.46 25 8.0 26	1.08 24 7.0 26	1, 50 26 1, 9	1.45 25 0.0 25	1.23 22 0.0	1.89 - 24 0.0 24	1.04 23 1.6	1.51 25 8.0 25	1.21 27 9.0	0.42 27 10.6 27	1.89	~ ~
Burns, Lake	*	Latitude	de 54 15 N	Long	Longitude 125	48 W E	levation	2320 Ft.	A.S.L.,		•			
Mean Daily Temperature (Deg. F.) Mean Daily Maximum Temperature Mean Daily Minimum Temperature	7.5 17.1 -3.6	19.8 31.6 8.4	26.3 38.4 14.2	36.2 47.5 24.9	45.8 59.0 32.2	52.9 66.7 39.1	55.5 68.9 42.0	55.3. 69.0 41.5	48.7 61.0 36.3	38.8 48.0 29.6	26.9 33.7 20.0	14.3 22.3 6.3	35.7 46.9 24.2	111
Extreme Maximum Temperature No. of Years of Record Extreme Minimum Temperature No. of Years of Record	50 16 -52 17	57 16 -41 17	61 18 -41 18	74 18 -6 18	87 13 . 15	90 16 16 16	89 15 27 15	90 16 28	84 14 18 15	72 ¢ 14 5 15	61 18 -34 18	48 17 -49 17	90.	4 4
No. of Days with Frost	31	28	30	26	16	5		. 7	10	. 21	27	16 .	228	· · 7
Mean Ratnfall (inches) Mean Snowfall Mean Total Precipitation	0.15 20.0 7 2.15	11.8	0.18 9.3 1.11	0.60 2.6 0.86	1.38 0.5 1.43	1.79 0.0 1.79	2.32 0.0 2.32	1.76 0.0 1.76	1,59 0,1 1,60	1.36 3.1 1.67	0.96 10.9 2.05	0.26 19.1 2.17	12.44 ° 77.4 20.18	,
Greatest Rainfall in 24 Hrs. No. of Years of Record Greatest Snowfall in 24 Hrs. No. of Years of Record	0.55 16 9.6 . 16	0.51 6.0 16.0	0.19 15 5.5 15	1.60 16 6.6 16	0.70 13 3.6 14	1,50 15 0,0	1.90 15 0.0	1.27 17 - 0.0 17	0.85 13 .1.0.	0.88 17 6.0 17	0.57 17 7.0 16	1.14 16 9.4 16	1.90	4 4
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Element and Station	Jen.	Feb.	Mar.	Apr.	May	June	July	Aug.	Se pt.	Oct.	Nov.	Dec.	Year	Length of Record
Fort St. James		Latitude	e 54 27 N		Longitude 124	15 W	Elevation	2250 Ft.	A.S.L.					
Mean Daily Temperature (Deg. F.). Mean Daily Maximum Temperature Mean Daily Minimum Temperature	16.8	17.8 27.7 7.8	26.0 36.8 15.2	36.9 - 47.8 25.9	47.2 59.9 34.5	54.7 67.2 42.1	58.2 70.7 45.7	56.0 68.5 43.4	48.7 60.1 37.2	39.0 48.0 30.0	25.6 32.5 18.6	15.1 22.5 7.7	36.2 46.5 25.7	د د نر
Extreme Maximum Temperature No. of Years of Record Extreme Minimum Temperature No. of Years of Record	50 76 -57	. 55 76 -57 76	62 76 -39	76 76 -21 76	88 76 11 76	93 ° 76 21 76	98 74 22 75	96 75 18	85 75 8 . 75	78 76 -5 76	61 76 -36 76	50 76 - 53 76	98	
No, of Days with Frost	31	. 82	30	. 56	13		i 1		6	70	28	31	519	-
Mean Rainfall (inches) Hean Snowfall Mean Total Precipitation	0.07 16.1 1.68	0.10 12.1 1.31	0.21 7.6 0.97	0.51 3.0 0.81	1.24 0.2 1.26	1.77	1.88 0.0 1.88	1.81 0.0 1.81	1.84 0.1 1.85	1.26 2.8 1.55	0.39	0.11 18.2 1.93	11.19 73.1 18.52	
Greatest Rainfall in 24 Hrs. No. of Years of Record Greatest Snowfall in 24 Hrs. No. of Years of Record	1.31 75 13.0 74	2.20 75 6.5 74	" 0.70 76 7.5 76	1.10 76 9.7 76	15.27 75 4.0 76	1.05 75 2.0 75	2.18 73 0.0	1.48 75 0.0 75	1.39 75 4.0 76	0.99 76 10.7 75	2.00 76 9.8 75	1.30 76 8.0 75	2.20	
New Hazelton		Latitude	e 55 14 N		Longitude 127	36 W	Elevation	1030 Ft.	A.S.L.				,	-
Mean Daily Temperature (Deg. F.) Mean Daily Maximum Temperature Mean Daily Minimum Temperature	14.3 21.0 7.5	24.3 33.0 15.5	32.5 ·42.6 22.4	40.8 52.8 28.8	50.1 63.7 36.4	\$6.2 69.2 43.0	59.4 72.1 46.6	58.0 70.7 45.2	50.4 62.3 38.6	41.3 49.9 32.5	30.0 36.1 23.9	20.0 25.5 14.3	39.8 49.9 29.6	, ,
Extreme Maximum Temperature No. of Years of Record Extreme Minimum Temperature No. of Years of Record	53 -52 -49 52	8 X 3 X	68 -21 53	. 53 - 11 - 52	8424	95 22 52	ዩ ዴ ዬኔ	% 253 % % 2633	88 56 17 53	74 55 0 55	53 -24 53	25 ¥ ½ ¥	67-	
No. of Days with Frost	30	27	29	22	6	7	;	-	9	. 15	25	30	195	. 2
Mean Rainfall (inches) Mean Snowfall; Mean Total Precipitation	0.39 14.4 1.73	0,33 8,0 1,13	0.29 3.0 0.59	0.75 0.7 0.82	1.22 T 1.22	1.81 0.0 1.81	2.00	1.82 0.0 1.82	2.42	2.14	1.14 6.8 1.81	0.31 13.7 1.69	14.62 47.3 19.28	888
Greatest Rainfall in 24 Hrs. No. of Years of Record Greatest Snowfall in 24 Hrs. No. of Years of Record	1.22 47 12.0 47	1.87 53 11.0 52	1.00 48. 13.0 49	0.87 53 4.5 53	1,35 52 0,5 53	1,25 53 0,0	1.46 54 0.0 54	1.52 52 0.0 53	1,33 54 0,0 55	2.18 . 51 7.0 54	1.75 51 11.2 51	0.91 54 12.0 54	2.18	
Smithers		Latitude	N 77 75 a	*	Longitude 127	M 90	Elevation 1690 Ft	1690 Ft.	A.S.Ł.	•	. 1			·.
Mean Daily Temperature (Deg. F.) Mean Daily Maximum Temperature Mean Daily Minimum Temperature	13.1 22.0 4.2	21.6 32.2 11.0	28.9 39.6 18.2	38,8 50,2 27,4	47.8 61.5 33.9	53.4 66.9 39.8	57.3 71.0 43.6	56.4 70.5 42.2	49.5 62.8 36.8	39.8 49.1 30.4	27.0 34.3 19.7	17.3 25.5 9.0	37.6 48.8 26.3	108
	٠					-					٠	ø		

Suttilize Continued State Stat	Element and Station	, san,	Feb.	Mar.	Apr.	Мау	June ,	July	Aug.	Sept.	0ct.	Nov.	· Dec.	Year	Length of Record
A characteristic control of the char	Smithers (continued)		,							•					
The control of the co	Extreme Maximum Temperature	26	54	19	7.5	30	88 2	99	76	87	75	59.	. 50	66	-
Ted 30 31 31 31 31 31 31 31 31 31 30 30 30 30 30 30 30 30 30 30 30 30 30	Extreme Minimum Temperature	84-	-36	-30	57.	91	22	28	24	71.	C	-30	30 -42	-48	-
30 28 30 24 13 5 1 2 10 19 28 31 24 13 13 13 13 13 13 13 1	No. of Years of Record	30	31	31	 	31	31	31	30	30	29	30	30		,
(inches) 0,33 0,20 0,28 0,58 1,36 1,74 1,89 1,64 1,54 1,59 1,99 0,82 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,	No. of Days with Frost	30	28	, 30	24	13	2		2	10	19	28	31	221	2
15.7 9.0 6.0 2.3 0.1 0.0 0.0 0.0 0.0 0.1 1.9 12.7 38.0	Mean Rainfall (inches)	0,33	0.20	0.28	0.58	1:36	1.74	1.89	1.64	1.54	1,99	0.82	A.O	12,75	2
of Record 1.20 0.50 1.20 1.04 1.55 1.29 1.31 1.55 1.10 1.55 1.10 1.97 2.00 1.29 11 in 24 Hrs. 16.6 15.0 34, 31 31 31 31 31 30 30 30 30 30 30 30 30 11 in 24 Hrs. 16.6 15.0 34, 5.0 2.0 2.0 0.0 0.0 0.0 0.0 3.5 11.0 16.5 11 in 24 Hrs. 16.6 15.0 34, 5.0 2.0 2.0 3.0 0.0 0.0 0.0 3.5 11.0 16.5 11 in 24 Hrs. 16.6 15.0 34, 5.0 2.0 2.0 0.0 0.0 0.0 0.0 3.5 11.0 16.5 17 in 24 Hrs. 18.4 13.0 2.0 2.0 2.0 3.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1	Mean Snowfall Mean Total Precipitation	15.7	9.0	6.0 0.88	2.3 0.81	0.1 1.38	0.0	0.0	0.0 1.64 *	0.0	1.9 2.18	12.7 2.13	18.0 2.19	65,7	2, 7
of Record 1 30 31 31 31 31 31 30 30 30 29 30 30 50 6 6 6 6 6 6 6 6 6 7 6 7 6 7 6 7 6 7 6	Greatest Rainfall in 24 Hrs.	1.20	0.50	1.20	1.04	1.55	1.29	15.31	1.55	1, 10	1 97	00	1 23	,	-
16.6 15.0 13.0 13.1 13.1 13.1 13.0 10.0 0.0 0.0 5.5 11.0 16.5 11.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0	No. of Years of Record	30	31	'n.	31 .	31	31	31	30	30	30	29	330	7.00	-
Hay	Greatest Snowfall in 24 Hrs. No. of Years of Record	16.6 30	15.0 31	2.5 2.5 3.5 5.5 5.5 5.5 5.5 5.5 5.5 5.5 5.5 5	5.0 31	2.0 31	0.0 31	0.0 31	30.0	0°0	5.5 30	11.0	16.5	16.6	, - ,
Hamilton				ė · ~											
Perature (Deg. F.) 13.6 22.0 28.8 38.1 47.3 53.7 57.6 56.7 49.6 39.2 26.2 17.6 flmum Temperature 6.2 11.2 39.0 48.9 60.0 66.2 70.4 69.7 61.6 47.6 32.3 23.8 flmum Temperature 6.2 12.8 18.5 27.1 34.5 44.7 43.6 46.6 46.6 46.6 47.6 47.6 37.6 37.8 33.8 49 10.0 93 88 73 88 49 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 4	Telkva		Latitud	e 54 39 N	Longi	tude 126				A.S.L.					-
thunn, Temperature 20.9 31.2 39.0 48.9 60.0 66.2 70.4 69.7 61.6 47.6 32.3 23.8 thunn, Temperature 6.2 12.8 18.5 27.1 34.5 41.1 44.7 43.6 47.6 47.6 20.2 11.3 in Temperature 53 55 63 88 90 89 100 93 88 73 58 49 11.3 45 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46	Mean Daily Temperature (Deg. F.)	13.6	22.0	28.8	38.1	47.3	53.7	57.6	56.7	4.6.6	39.2	26.2	17.6	37.5	2
fmum Temperature 6.2 12.8 18.5 27.1 34.5 41.1 44.7 43.6 37.6 30.7 20.2 11.3 n Temperature 53 55 63 88 90 89 100 93 88 73 58 49 11.3 of Record 45 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46 46	Mean Daily Maximum Temperature	20.9	31.2	39.0	6.87	0.09	66.2	70.4	. 2.69	61.6	47.6	32.3	23.8	47.6	7
n Temperature 53 55 63 88 90 89 100 93 88 73 58 49 10 10 10 10 10 10 10 10 10 10 10 10 10	Mean Daily Minimum Temperature	6.2	12.8	18.5	27.1	34.5	41.1	44.7	43.6	37.6	30.7	20.2	11.3	27.4	7
of Record 45 46 46 46 46 46 46 46 46 46 46 46 46 46	Extreme Maximum Temperature	53	55	, 63	88	06	89	100	93	88	73	58	67 .	100	-
n Temperature -42 -34 -22 -6 20 26 29 27 8 -3 -23 -37 - 6 of Record 46 46 46 46 46 46 46 46 46 46 46 46 46	No. of Years of Record	45	9,7	4.5	4.5	77	45	45	. 94	97	94	97	97		
th Frost 31 28 30, 7 25 13 2 7 19 29 31 7 2 [10.04e] 1.18 1.95 2.06 1.64 1.50 1.44 0.43 0.18 1.95 [10.14] 1.95 2.06 1.64 1.50 1.44 0.43 0.18 1.95 [10.14] 1.95 2.06 1.64 1.50 1.44 0.43 0.18 1.95 [10.14] 1.95 2.06 1.64 1.50 1.90 1.80 1.95 1.95 [10.14] 1.95 1.95 1.95 2.06 1.64 1.50 1.90 1.80 1.95 1.95 [10.16] 1.95 1.95 1.95 1.95 1.95 1.95 1.95 1.95	Extreme Minimum Temperature No. of Years of Record	-42	- 34	-22	9 - 7	20	26 45	29 . s	27	æγ	£ - 3	-23	-37	-42	-
th Frost 31 28 30, 7, 25 13 2 7 19 29 31 2 (inches), 0.13 0.12 0.16 0.46 1.18 1.95, 2.06 1.64 1.50 1.44 0.43 0.18 0.18 1.6.1 9.2 6.2 3.1 0.7 0.0 0.0 T T 4.6 13.7 17.6 17.6 1.91 1.74 1.05 0.77 1.25 1.95 2.06 1.64 1.50 1.90 1.80 1.95 1.95 2.06 1.64 1.50 1.90 1.80 1.95 2.06 1.64 1.50 1.90 1.80 1.95 2.06 1.64 1.50 1.95 1.95 2.06 1.64 1.50 1.90 1.80 1.95 2.06 1.64 1.50 1.95 1.95 2.06 1.64 1.50 1.95 1.95 2.06 1.64 1.50 1.95 1.95 2.06 1.64 1.50 1.95 1.95 2.06 1.64 1.50 1.95 2.06 1.64 1.50 1.95 2.06 1.64 1.50 1.95 2.06 1.64 1.50 1.95 2.06 1.64 1.50 1.95 2.06 1.64 1.50 1.95 2.06 1.64 1.50 1.95 2.06 1.64 1.50 1.95 2.06 1.64 1.50 1.95 2.06 1.64 1.50 1.95 2.06 1.64 1.50 1.95 2.06 2.08 2.0 1.95 2.06 2.0 2.0 2.0 2.0 2.0 2.0 2.0 2.0 2.0 2.0		!		?	})	?	ì) †)	2	· · · ·		
(inches), 0.13 0.12 0.16 0.46 1.18 1.95 2.06 1.64 1.50 1.44 0.43 0.18 1.18 1.18 1.18 1.18 1.18 1.18 1.18	No. of Days with Frost	31	28.	30.	25	13	5	;	:	7	19	59	31	215	7
Topitation 16.1 9.2 6.2 3.1 0.7 0.0 0.0 T T 4.6 13.7 17.6 17.6 18.1 17.7 17.6 17.6 18.1 17.7 17.6 17.6 17.7 17.6 17.7 17.6 17.7 17.6 17.7 17.6 17.7 17.6 17.7 17.6 17.7 17.6 17.7 17.6 17.7 17.7	Mean Rainfall (inches),	0.13	0.12	0.16	97.0	1,18	1.95	2.06	1.64	1.50	1.44	0.43	0.18	11,25	. 2
0.76 0.48 0.70 0.78 0.98 1.48 2.43 1.61 1.18 1.80 0.91 0.65 44 46 46 42 44 43 39 41 41 38 42 43 17.0 8.5 8.0 7.0 3.3 0.0 0.0 0.2 0.8 9.0 10.6 8.0 45 43 46 42 45 45 46 46 45 41 41 43	Mean Snowrall Mean Total Precipitation	16.1	9.2 1.05	6.2 0.78	3.1	0.7 1.25	0.0 1.95	0.0 2.06	T 1.64	T 1.50	1.90	13.7	17.6 1.95	71.2	7 7
7. 5 45 46 46 42 44 43 39 41 41 38 42 43 17.0 8.5 8.0 10.6 8.0 0.7 45 45 45 45 45 45 45 45 45 45 45 45 45	Greatest Rainfall in 24 Hrs	92 0	α,	0,0		0	0 7		17.	0.		ā	3		-
17.0 8.5 8.0 7.0 3.3 0.0 0.0 0.2 0.8 9.0 10.6 8.0 45 43 46 42 45 45 46 46 45 41 41 43	No. of Years of Record	44	94	7.97	42	0. °0 44	43	39	10 . 1	41	38	42	43	64.7	-
45 43 46 42 45 45 46 46 45 41 41 43	Greatest Snowfall in 24 Hrs.	17.0	8,5	8.0	7.0	3,3	0.0	0.0	0.2	8.0	0. 6	10.6	8.0	17.0	1
	No. of Years of Record	4.5	43	97	4.5	4.5	45	97	94	. 5,	41	41	43		

^aData from Atmospheric Environment Service (1973), ^bKey for "Length of Record:"

30 years between 1941 and 1970, 25-29 years between 1941 and 1970, 20-24 years between 1941 and 1970, 15-19 years between 1941 and 1970, Adjusted,

Appendix B.--Surface water data from selected gauging stations in the study areal

Mean	4740	7640	1690
Dec.	2830	2480	955
Oct. Nov.	3050	55 W 4070 3890 rember 25	1110
Oct.	3540 W 3540	55 W 4070 vember	40 W 1280
Sept.	124 16 30 W 4920 354(N 126 53 55 W 5370 4070 ctober 26, November 5 (8 years to 1974)	126 37 40 W 1650 1280
Aug.	N 7440 0	N 5370 ctober 5 (8 y	N 2410
July	08JE011 54 25 05 N 124 16 4180 9230 10,400 7440 4920 3,430,000 AC - FT June 13-July 21 December 31-April 30 44 years to 1973 5400 square miles January 12-February 2 (1974)	08EE004 54 37 05 N 126 53 55 W 0,800 13,200 8310 5370 3770 4070 389 3,580,000 AC - FT April 27-June 28, October 26, November 25 December 31-May 2 44 years to 1973 2800 square miles November 21-April 25 (8 years to 1974)	08EC001 55 19 25 N 126 37 1960 4210 3460 2410 1650 1,220,000 AC - FT June 1-July 17 December 28-May 1 32 years to 1973 2500 square miles
June July	08JE011 54 25 (4180 9230 10,400 3,430,000 AC - FT June 13-July 21 December 31-April 44 years to 1973 5400 square miles January 12-Februar	08EE004 54 37 0,800 13,200 8310 3,580,000 AC - FT April 27-June 28, December 31-May 2 44 years to 1973 2800 square miles November 21-April	08EC001 55 19 1960 4210 346 1,220,000 AC - FT June 1-July 17 December 28-May 1 32 years to 1973 2500 square miles
Мау	08JE011 4180 9 3,430,0 June 13 Decembe 44 year 5400 sq January	08EE004 54 37 0 10,800 13,200 8310 3,580,000 AC - FT April 27-June 28, December 31-May 2 44 years to 1973 2800 square miles November 21-April	08EC00 1960 1,220, June 1 Decemb 32 yea 2500 s
Apr.	1730	2600	540
Mar	1670 * 1730	983	568
Feb.	2090	1210	
Jan.	2540	1510	764
Element and Station 2	Stuart River near Fort St. James Discharge3 Mean Annual Total Discharge Dates of Maximum Discharges Dates of Minimum Discharges Period of Record Drainage Area Dates of Ice Conditions	Bulkley River at Quick Discharge Mean Annual Total Discharge Dates of Maximum Discharges Dates of Minimum Discharges Period of Record Drainage Area Dates of Ice Conditions	Babine River at Babine Discharge Mean Annual Total Discharge Dates of Maximum Discharges Dates of Minimum Discharges Period of Record Drainage Area

Appendix B.--Continued

Mean	146	46.3	163
Dec.	9 6 E	11.5	· α
Nov.	104	25.6	20.3
Oct.	10 W 110	04 W 30.5	04 W 54.4
Sept. Oct.	126 18 10 W 108 11(N 126 20 04 W 12.5 18.6 30. r 15	126 39 04 W 27.0 54.
Aug.	N 1 59 1	•5 15	N 20.8
July Aug.	55 10 20 N 105 30 (69) 1970 miles -(January 2	54 30 59 N 30.6 12 12 -September 1973 miles April 24 (6	54 23 52 N 84.0 20 - FT miles April 20 (
June	08EC008 55 10 600 362 10 May 12-May 30 April 4 (1969) 6 years to 1970 160 square miles December 22-(Jan	08EE009 54 30 59 269 101 30.6 33,600 AC - FT May 14-June 12 December 31-Septembe 10 years to 1973 66.7 square miles	3 537) AC er 31 are
May	08EC008 55 10 20 N 126 18 10 W 600 362 105 59 108 110 May 12-May 30 April 4 (1969) 6 years to 1970 160 square miles December 22-(January 20+)4 (1969-1970)	08EE009 54 30 59 N 269 101 30.6 12 33,600 AC - FT May 14-June 12 December 31-September 10 years to 1973 66.7 square miles October 29-April 24 (6	08EE013 1010 537 118,000 AC May 17 December 31 1973 250 square November 3-
Apr.	95	i.	127
Mar.	30	5.6 28.9	, 21•0
Feb.	41	3° 8°	11.4
Jan.	45	5.0	16.5
Element and Station	Morrison River at Outlet of Morrison Lake Discharge Dates of Maximum Discharges Dates of Minimum Discharges Period of Record Drainage Area Dates of Ice Conditions	Richfield Creek near Topley Discharge Mean Annual Total Discharge Dates of Maximum Discharges Dates of Minimum Discharges Period of Record Drainage Area Dates of Ice Conditions	Buck Creek at the Mouth Discharge Mean Annual Total Discharge Dates of Maximum Discharges Dates of Minimum Discharges Period of Record Drainage Area Dates of Ice Conditions

Appendix B.--Continued

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	Mean	63.7	7.9		- :		11
	Dec.	14.4	ი ზ	energia de la composición del composición de la			
	Nov.	34.1	7.0				
	Oct.	35 W 52.2	55 W 8.4	1974) 59 W	30 W	10 W	49 W
	Sept.	127 07 35 W 46.7 52.	127 11 55 W 7.4 8. 2	6 years to 19 127 07 59 971)	126 42	126 42	26 N 127 07 13 (1973, 1974)
	July Aug.	66.8 66.8 22	03 N 127 1 6.4 0ctober 22 8, August 26	26 (6 y 3 N 7 (1971	5 N 25 (197	N (1973)	5 N 3 (1973
	1	08EE008 54 39 14 N 127 07 35 182 198 127 66.8 46.7 5 46,100 AC - FT May 8-July 28 December 17-March 22 14 years to 1973 51 square miles November 3-May 8 (6 years to 1974)	08EE010 54 49 03 N 1 14.1 19.6 12.1 6.4 5,760 AC - FT May 10-June 26, October 22 December 31-May 8, August 7 years to 1973	9.5 square miles November 21-April 26 (6 years to 1974) 08EE005 54 46 48 N 127 07 59 W 3450 square miles December 6-April 27 (1971)	08EE003 54 23 45 N 12 850 square miles November 27-April 25 (1971)	08EC013 55 25 30 N 2620 square miles January 8-April 21 (1	
	June	08EE008 54 39 182 198 12 46,100 AC - FT May 8-July 28 December 17-Marc 14 years to 1973 51 square miles November 3-May 8	08EE010 54 49 (14.1 19.6 12.1 5,760 AC - FT May 10-June 26, Oc December 31-May 8 7 years to 1973	9.5 square miles November 21-April 08EE005 54 46 3450 square miles December 6-April	08EE003 54 23 850 square miles November 27-Apri	08EC013 55 25 25 2620 square miles January 8-April 2	re ≡ r 3-
	Apr. May	08EE008 182 19 46,100 AC May 8-Jul December 14 years 51 square	08EE010 14.1 1 5,760 A May 10- December 7 years	9.5 squar November 08EE005 3450 squa December	08EE003 850 squa November	08EC013 2620 sq January	08EE014 65 squa Novembe
	Apr.	21.0					;
	Mar.	7.3	2.9				
_	Feb. Mar.	6.9 7.3	2.3 2.9			<i>a</i> ke	
*	- 1		4 2.3			La La	
	Feb.	6.9	above Simpson Creek 2.4 2.3 otal Discharge mum Discharges ord	Drainage Area Dates of Ice Conditions Bulkley River near Smithers Drainage Area Dates of Ice Conditions	Bulkley River near Houston Drainage Area Dates of Ice Conditions	Babine River at Outlet of Nilkitwa Lake Drainage Area Dates of Ice Conditions	Canyon Creek near Smithers Drainage Area Dates of Ice Conditions

Appendix B.--Continued

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Maxan Creek above Bulkley Lake Drainage Area Dates of Ice Conditions	08EE018 54 21 25 N 126 10 12 W 142 square miles November 20-(December 31 ⁺) ⁴ (1974)
Foxy Creek above Lu Creek Drainage Area Dates of Ice Conditions	08EE015 54 12 46 N 126 15 30 W 6.2 square miles 0ctober 28-(December 31 ⁺) ⁴ (1974)
Lu Creek near the Mouth Drainage Area Dates of Ice Conditions	08EE016 54 12 49 N 126 15 53 W 2.8 square miles November 7-(December 31 ⁺) ⁴ (1974)
Stuart Lake near Fort St. James Dates of Maximum Water Levels Dates of Minimum Water Levels Period of Record	08JE003 54 27 00 N 124 16 00 W June 28-July 17 April 3-April 19 6 years to 1974
Babine Lake at Topley Landing Dates of Maximum Water Levels Dates of Minimum Water Levels Period of Record	08EC003 54 48 35 N 126 08 20 W June 10-July 12 December 19-April 23 6 years to 1974
Kathlyn Lake near Smithers Dates of Maximum Water Levels Dates of Minimum Water Levels Period of Record	08EE011 54 49 03 N 127 11 55 W May 18-June 25, October 20 December 31-March 8 6 years to 1974

 $^2\mathrm{Station}$ name, number and location (Lat. and Long.). 4 Records end.

 $^{\rm l}{\rm Data}$ from Water Resources Branch (1970-1975).

³Discharge in Cubic Feet Per Second.

Appendix C.--Sample sites and data for untransformed variables used in the analyses 1

C₁ Lakes

	00.0 00.0 59.	• 35 0.00 .65 0.00	.35 0.00 0.00 .35 4.	.00 0.00 0.00 .50 0.	.35 0.00 .65 2.	.00 0.00 0.00 1.65 2.	.00 2.35 .35 0.00 2.	.50 .65 "1.15 .15 3.	.00 0.00 0.00 1.00 0.	. 0.00 .35 0.00	.00 0.00 .35 0.00 2.	00 0.00 0.00 0.10 0.	.00 0.00 0.00 .25 0.	• 00 00 00 00 07	00.0 00.0 00.0	25 0.00 0.00 0.00	0.00 0.00 0.00	. 35 .35 0.00	. 15 0.00 0.00	0.00 0.00 .35	0.00 0.00 0.30	00.0 00.0 00.0	0.00 0.00 0.00 0.0	.25 0.00 0.00	.00 0.00 0.00 0.00 00.0	00 0.00 0.00 .50 0.	.35 .35 0.00 0.00 1.	. 35 0.00 0.00	.50 0.00 .35 1.	4
$M_{\rm L}$	c ,	1	က	က	က	٣	ო	က	2	3	ņ	ო	ო	က	က	ო		ന	<u>ش</u>	സ	ന്	က	m _.	က	9	3	Э. Э.	ش	٦.	
${f A}_{f \Gamma}$	155	51	1335	17	675	099	275	365	₹ 82	12	620	1	-	5	7			✓						7	10	∞	155	, 15	240	
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EL	27																													
$_{ m TSTOO}$	9 .	I	∞	0	13	18		22	5	က	∞	–	0	_	_	_	0	_	_	7	_	0	7	7	0	0	7	· `	7	
Photograph Number ²	5195-254	5281-096	5296-184	5296-194	5300-148	5300-150	5300-198	5300-200	5300-211	5300-240	5301-006	5301-032	5301-032	5301-068	5301-070	5301-070	- 1	7		5301-118	1	5301-146	\$301-146	/5301-210	/ 5302-036	- 1	1	302-2	5302-274	
Маше	Holland	Bulkley	Maxan	Pond	Day	Elwin	Sunset	Swans	Goosley	Pond	Owen	Burbridge	Pond	Pond	Pl	P2	Tsalitpn	Round	Dorsay	McDowell	Pond	Pl	P3	Pond	Silvern /	/ Lond	Seymore /	Bigelow /	Kathlyn	
Number L:	٠ ٦	7	က	4	ک	9	7	∞	6	10	11	12	13,	14	15	16	17	18	19	20	21	22	23	24	25	26	27	78	29	-

Appendix C.--Continued

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Number L:	Мате	Aerial Photograph Number	$_{ m COLS_L}$	T _H	PL	A _L	ML	$_{ m TA_L}$	$^{ m T_{ m O}}$	Γ_{N}	T_{S}	TARANKL
30	Farewell	5306-082	> ~		•	3	2	. 50	.35	00.00	.35	. 25
31	McQuarrie	5306-082	7	35	7.25	525	2	1.85	.85	00.00	00.00	1,40
32	Pond	5306-084	0		•	7	7	0.00	00.00	00.00	00.00	00.00
33	Pl	5306-086	7		1.75	75	33	. 65		00.00	00.00	. 35
34	P3	5306-086	1		. 50	11	33	. 50		00.00	.10	04.
35	P5	5306-086			25	10	3		00.00	00.00	• 05	•
36	P7	5306-086	-		• 50	12	33	00.00	00.00	00.00	00.00	00.0
37	P8	2306-086	1		.75	12	m		00.00	00.00	00.00	•
38	Pll	5306-086	-		_	7	က		00.0	00.00	.35	•
39	Hankin	5307-120	. 7		_	4	7		00.00	00.00	00.00	•
70	Chapman	5308-142	11		_	1350	_		1,35	• 65	1.00	•
41	Ogston	5036-143	~ 1		_	9	ന	.20	00.0	00.0	• 55	• 20
42	Pond	5036-143	-		_	4	7	•	00.0	00.00	00.00	•
43	Grassham	5036-143	7		22,50	1745	7	00.00	00.00	0.4.	0.00	00.0
77	Tatin	i	11		_	4	m	•	0.00	• 55	00.00	•
45	P1	5197-176	4		_	17	က	. 95	00.00	00.0	04.	09.
97	Taltapin	5197-201	12		_	9	-	7.90	2,65	0.00	0.00	•
47	Co-op	5216-029	7		_	9	თ		0.00	00.00	00.00	00.00
48	Tchesinkut	5216-041	18			7300	7	20,05	7.90	1,50	00.00	•
65	Pond	5216-161	J		_	m	സ		00.00	00.00	• 75	•55
20	Burns	5216-046	53		-	2335	7		13,15	7,50	1,50	21,25
51	P2	5216-111	ŋ		.25	2	-	.25	00.00	00.00	00.00	.25
52	Pl	5216-046	7		.25	2	ش	.25	.25	00.00	• 25	.25
53	P2	5216-046	7		• 50	∞	M	. 50	.25	00.0	00.00	• 50
54	P3	5216-046	1		. 25	, _ 1	ო	80.	00.00	00.0	.15	. 08
	P3	5216-157	-		1,25	22	က	•	• 55	00.00	00.00	•
95	Augier	5216-053	2		•	1415	ű	•	•	.20	00.0	•
57	Pl	_	7		• 75	26	7	•	•	00.0	00.00	•
58	P2	5216-086	0		1.00	13	က	00.0	00.00	00.0	1.00	00.0
29	P3	5216-086	1		I.25	40	က	•	•	00.00	•20	•

C_l Lakes

•	00.00		.10	00.00	00.00	00.0	00.0	3.80	75	, 20	1,90	. 07.	1,35	00.00	.20	00.00	00.00	07.	00.0	•	• 55	3.85	•35	00.00	16,30	5.25	00.0	20.85	ં
07.	00.0	•	00.00	• 20	• 20	• 55	• 55	00.00	00.00	000.0	07.	• 20	00.00	• 20	07.	. 50	.75	00.00	• 50	•20	00.0	.15	00.00	• 50	•	.75	•	00.00	•75
00.00	00.00	00.00	0.00	00.00	00.0	00.00	.20	00.00	00.00	00.00	• 20	• 20	.55	00.00	00.00	0.00	00.00	00.00	00.00	00.00	00.00	00.00	00.0	00.00	6. 40	0.00	0.00	3.00	.75
00.00	00.00	00.00	0.00	00.00	00.00	00.00	0.00	07.	00.00	00.00	00.00	00.00	00.00	00.00	.20	00.00	00.0	04.	00.00	00.00	00.0	00.0	00.0	00.00	.95	0000		07.	5.45
00.00	00.00	00.00	.20	00.0	00.00	00.0	00.00	4. 35 \	. 75	.20	3.40	• 75	2.65	•	.20	•	00.00	07.	00.00	1.90	• 55	00.9	.70	00.0	18,00	5.25	00.0	21.95	·
3.	2	ന	1	3	3	က	3	7	က	₩	1	7	1	1	ω, ·	3	3	٠ ش	ω	1	რ	1	7	က	-	7	3	1	1
180	9	က	1285	27	10	09	∞	825		_	0	9	755	√ t	\sim	26	10	8	9	215	105	5400·	43	5	15200	1800	∞	10460	6120
2,50	•.50	.25	•	1.25	. 50	•	2.75	•	.75	•	•	•	7.00	•	•	. 50	.75	£ 05°	. 50		2.75		1.50	•	43.00	•	. 50	36.00	9.
31	33	32	31	31	31.	31	31	28	28	29	28	28	28	38	23	22	22	28	59	29	30	28	28	28	26	31	32	24	24,
0	2	7	7	7	1	7	က	7	ლ	က	13	* •	9	1	7	က	2	ო	7	1	2	, 11	2	1	37	10	_	22	17
5216-086	5216-116	5216-116	5216-119	5216-153	5216-153	5217-205	5217-205	5218-165	5218-182	5306-004	5306-037	5306-048	5306-048	5306-077	5307-191	5307-232	5307-232	5308-158	5308-159	5008-159	5308-160	5621-080	5621-080	5621-129	5621-147	5626-002	5626-002	5626-016	5626-025
P4	Pl	P3	Pinkut	P1	P2	Top	Peta	Ormond	Pond	Tanglechain	Parrot S.E.	Parrot S.W.	Parrot N.	Guess	Kitseguecla	Toltzen	Mold	Pond	Pond	Doris	Boomerang	Tocha	Pond	Pond	Tezzeron	Camsell	Pond	Pinchi	Cunningham
09	61	62	63	9	65	99	6 7	89	69	70	71	72	73	74	75			, 78	79	80	81	82	83	84	85	98	87	88	89

Appendix C.--Continued

								,				
Number L:	Name	Aerial Photograph Number	$^{ m T}_{ m COTS}$	EL	$^{ m L}_{ m T}$	$^{ m A}_{ m L}$	WL	\mathtt{TA}_{L}	J.	T _N	$^{ m T}_{ m S}$	TARANKL
06	Rubvrock	5626-026	5	38	12,00	780	. 2	00,0	00 0	00.00	7.0	00.00
91	Whitefish	5626-022	۰ ۲۰	26	6	1420	2	4,30	2,45	. 55	00.00	3.20
92	Stuart	5621-214	28	23	5.	66820	1	85.00	10,50	. 55	8.05	83.00
. 93	_	23555-161	18	24	20.00	2280	1	20,00	5.50	00.00	0,00	15,15
94	Pond	23556-105	ო	24	1,25	32	က	.85	04.	00.00	00.00	. 85
, 95	Pond	23\$55-161	1	54	• 20	۳	က	00.00	00.00	00.00	00.00	00 ° 0
96	Pond	23/555-185	7	56	. 50	9	. 7	00.00	00.00	00.00	00.00	00.00
26	Natowite	2/3555-185	19	56	•	2420	_	10,65	00.00	1,15	00.00	7.00
86	Pond	23556-008	.·	27	1.00	55	ო	00.00	00.0	00.00	1.00	00.00
66	Pond	23556-103	က	59	• 50	16	ന	• 50	00.00	00.0	00.00	• 20
100	Pond	23556-104	7	30	1.00	21	ന	• 20	00.00	00.00	.80	•20
101	Nilkitwa	23556-120	1	23	10,50	140	1	8.65	3.00	00.0	1,35	00.9
102	Babine	23555-106	53	23 .	287.00	91350	7	•	94.40	1.00	5.50	197.85
		•	•									
C2 Inde	Independent Sample	Sample of Lakes		. ,			,	ž Ž				·
		Aerial										
Number I:	Name	Photograph Number ²	$_{ m COLS_L}$	$_{ m L}$	$^{\mathrm{PL}}$	$^{ m AL}$	WL	$\mathtt{TA}_{\mathbf{L}}$	$^{ m C}$	$_{ m N}^{ m T}$	$^{7}\mathrm{S}$	TARANKL
,	Torkelsen	5195-254	7	28	•	310	٣	.65	00.00	00.00	.85	. 65
2	Pond	5195-254	1	28	•	15	က်	00.00	00.00	00.00	.25	, 00°0
æ	Nez	5296-194	5 @	41	8.00	425	<i>.</i> ຕ	00.0	00.00	• 50	00.0	. 00.0
7	Gilmore	5300-198	2	26	2.25	120	Ű,	1.50	00.00	00.00	00.00	1.40
2	Pond	5300-198	,	29	• 20	10	m ·	00 ° 0	00.00	00.00	• 50	00.00

Appendix C.--Continued

-	00.00	00.00	00.00	00.00		00.00	•	04.	00.00	00.00	00	00.0	00.0	• 20	.20	• 25	• 95	00.00	00.00	00.00	00.00	.25	•	1.40	•	00.00	07.	• 55	22.70	•	
		.25		6.		•35	00.00	00.00	• 50	00.00	.25	.15	• 55	00.00	•25	• 20	00.00	• 75	.25	00.00	• 50	00.0	1,90	• 75	00.0	• 50	00.00	07.	00.00	00.00	
	00.00	00.00	00.0	00.00		00.0	00.0	00.0	00.00	• 15	00.00	0.00	00.00	00.0	00.00	00.00	00.00	00.00	00.00	00.0	00.00	.25	3,75	.40	04.	00.00	00.00	00.00	4.15	00.0	
	00.00	00.00	00.00	00.00		00.0	• 50	00.0	00.00	00.00	00.00	00.00	00.00	00.00	00.00	00.00	00.00	00.00	00.00	00.00	00.00	00.00	3, 75	00.00	• 20	00.00	•	•	2.05	•	
	00.00	00.0	00.0	00.00		00.00	.25	• 65	00.00	00.00	00.00	*35	00.00	.20	.25	.25	1,15	00.00	00.00	00.0	00.0	. 25	•	•	7.15	•	07.	• 55	25.90	•	
	<u>့</u> က	ന -	5	2		<u>।</u>	m)	(9)	c	-	က	7	ن. س	٣	ω	7	ന	m	m	٣	e C	1	7	7	7	ന	m	m	7	1	
. *.	. 38	. 1	205	205		200	15	37	10	465	12	145	55	20	Ţ	7	31	145	7	55	9	œ	1265	345	820	12	21	115	22120	1260	
	1.00	.25	2,50	.7		3,25		1.00	. •	6. 50	• 50	2,25	1,50	1,00	.25	• 50	1.25	•	.25	1,50	• 50	• 50	•	3,75	•	• 50	•	•	57,25	•	
	. 31	31	28	5.9		33	31	31	37	28	. 29	33	28	30	54	56	27	31	35	32	27	25	24	56	28	33	23	30	23	29	
-	7	1	2	1		. 2		_	1	m	.	94	J	7	9	7	.	M	-	1	m	- 1	6	m	œ	J	. 7	2	13	13	
	5300-211	5301-146	5302-032	5302-034		5302-162	5306-086	5306-086	5306-086	5307-196	5307-196	5308-084	5195-247	5197-176	5216-111	5216-157	5216-157	521.6-086	5216-116	5216-118	5216-159	5216-162	5216-237	5217-224	5218-182	5306-002	5307-191	5308-160	5621-135	23556-104	
,	Pond	P2	Dennis	Aldrich	Mooseskin	Johnny	P4	P6	P9	McDonne 11	Secret	Blunt	Pete's	P2	Pl	Pl	P2	Ling	P2	Division	Pond	Pond	Decker	Stern	Oona	Pond	Pond	Pine Tree	Trembleur	Nakinilerak	
	9	7	œ	6	10		11	12	13	14	15	16	17	18	. 61	20	21	22	23	24	25	26	27	28	29	30	31	32	33 .	34	

C3. Stream Sections

.40 12.35 5.65 1.50 0.00 0.00 ...55 0..00 1..75 0..00 0..00 0.00 .65 .40 0.00 0.00 .95 .55 0.00 1.50 AS NSS .55 .30 0.00 .75 0.00 0.00 0.00 0.00 35 200 250 20 20 20 10 15 15 250 30 30 WS FS 1.25 14.00 7.00 2.00 5.00 • 50 1.50 .25 1.00 1.00 4.00 1,00 10,00 00. LS. GS COLSS Photograph Number² 5306-096 5300-155 23555-185 5302-149 5306-094 23555-184 23555-184 23555-185 5217-238 5621-238 5621-136 5302-212 5300-152 5217-237 5216-007 5626-010 5307-197 5302-212 5302-212 5302-151 5301-141 5301-141 5301-121 5302-151 5307-227 5621-151 Aerial Gloyazikut Tches inkut Driftwood Driftwood Richfield Sakeniche Bulkley 2 Bulkley] Name Sanokawa Vecoslie Hautêțe Miller Spruce 2 Miller 2 Spruce Silvern Buck 2 ratin l Duncan **Tachie** Middle Copper Passby Buck 1 Str 2Nizik 0cock Number ŝ

Appendix C. 4-Continued

Sections
Stream
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o c		7 [_	7 5	α ····	7.5	0
67	Howsen I	2302-102	7	٢/•	ָר פּי רי	C/•	00.0
30	Howsen 2	5302-162	2 1	•	3 40	00.0	00.0
31	Maxan	5296-185	16 1	7,50	1 20	1.90	5,25
32	Crow	5296-187	4 1		1 15	1.00	2,25
33.	Puport	5301-096	3	. 75	2 8	.25	00.0
34	Str 1	5302-212	0 3	• 50	2 6	00.00	00.0
35	Sunset	5300-198	. 1	• 50	1 5	.20	• 30
36	Hankin	5307-120	1 2	• 50	1 15	.25	00.00
37	Fulton	5308-142	4 , 1	1,00	1 35	1,00	00.00
38	Endako	5216-157	4 1	1,25		1,25	1,25
39	Pinkut	5216-053	0 1	1.00	2 50	00.00	00.0
. 05	Fleming	5621-155	2 1	1.00		.85	.15
41	Grostète	5621-147	5	1.00		• 75	1.00
42	Hyman	5626-016	4	1.00		.75	.55
43	Noran	23555-161	0 5	50		00.0	• 50
77	Sutherland	7-1	4 1	15/2	1 50	1,75	.55
45	Morrison	-1	3 1	1.00	2 100	1.00	• 33
lRefer	to Table 2	for definitions.	- - - পুন				
2_	,	3.				٠	
-Dates	tes of photos are	••					lands of
40 Chain:		September	r 1961	80 Chain:	BC	l August-Sept	pt. 1974
	BC 5195	June	7				
		July	1966		A23555-2355		1
		September			-		
		May	1968				
		July	-	√ -			
	5301,	6 July-August	1				,
		5308	1968				•
			1				

Appendix D

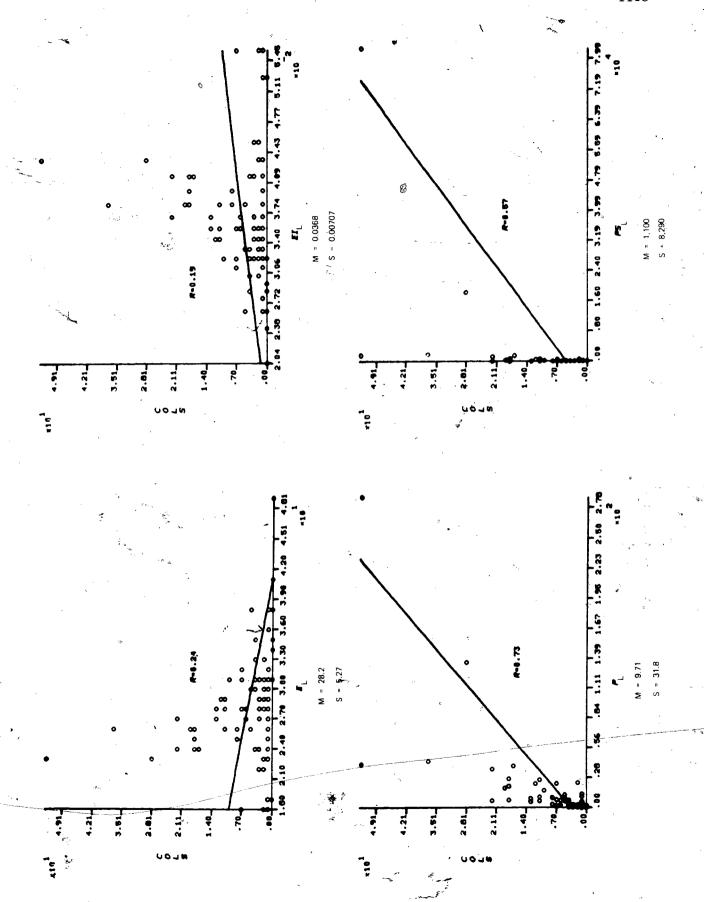
Plots of COLS against independent variables with correlation coefficients, $^{\rm l}$ and means and standard deviations $^{\rm 2}$ of independent variables.

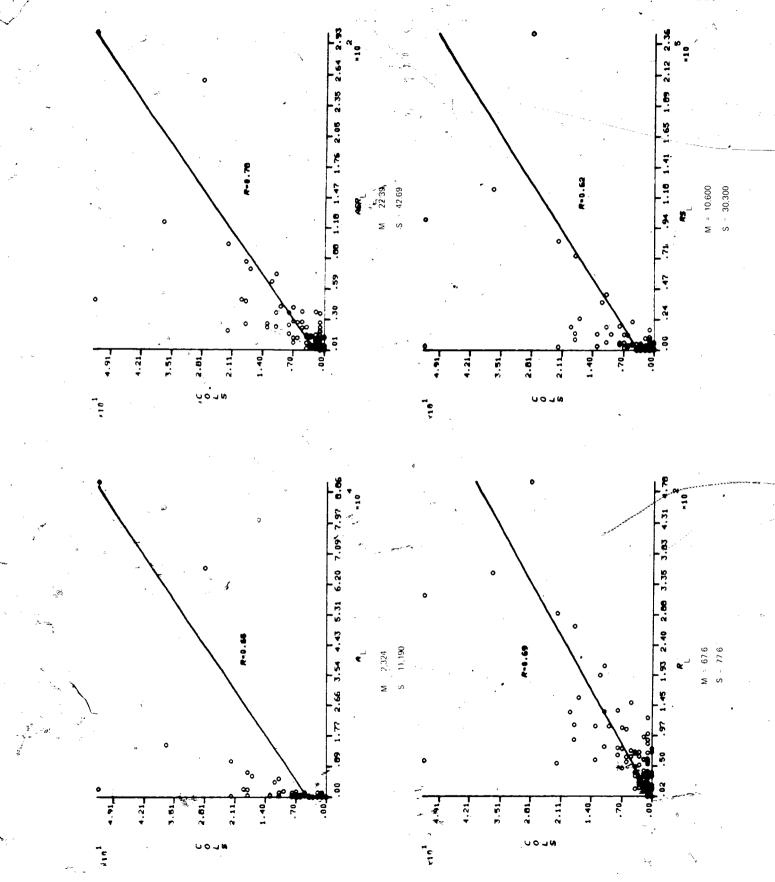
¹From Table 3.

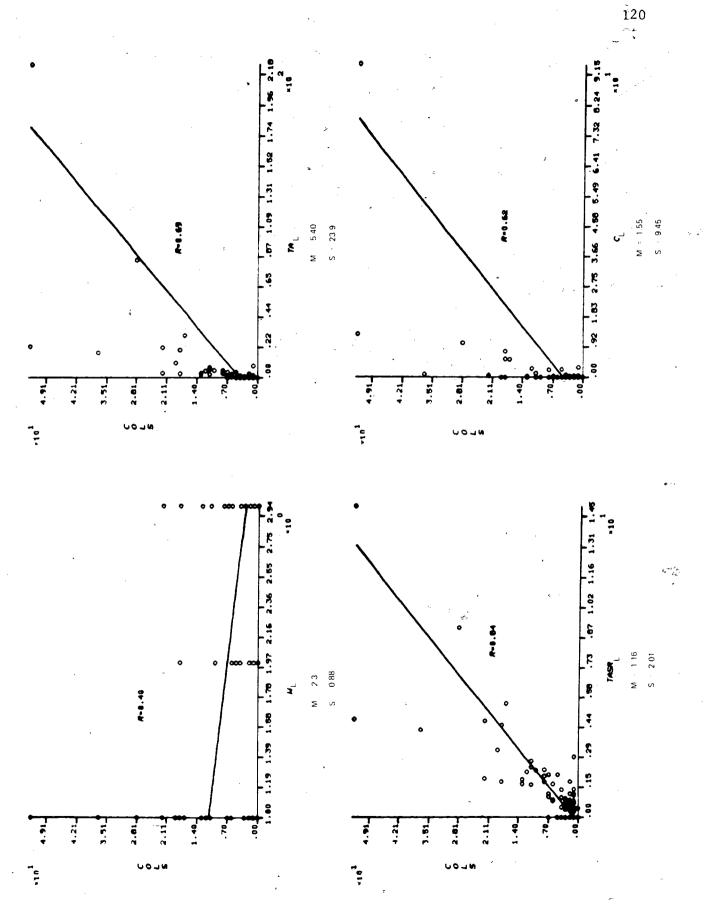
 2 Mean = M, Standard Deviation = S

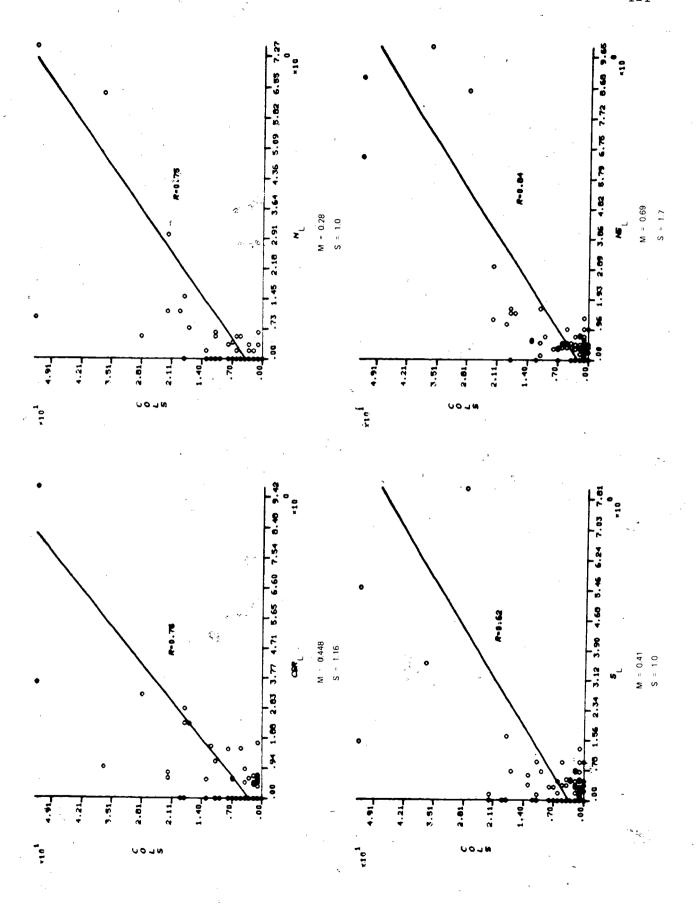
 $\texttt{M(COLS}_{L}) = 5.69$, $\texttt{S(COLS}_{L}) = 9.31$

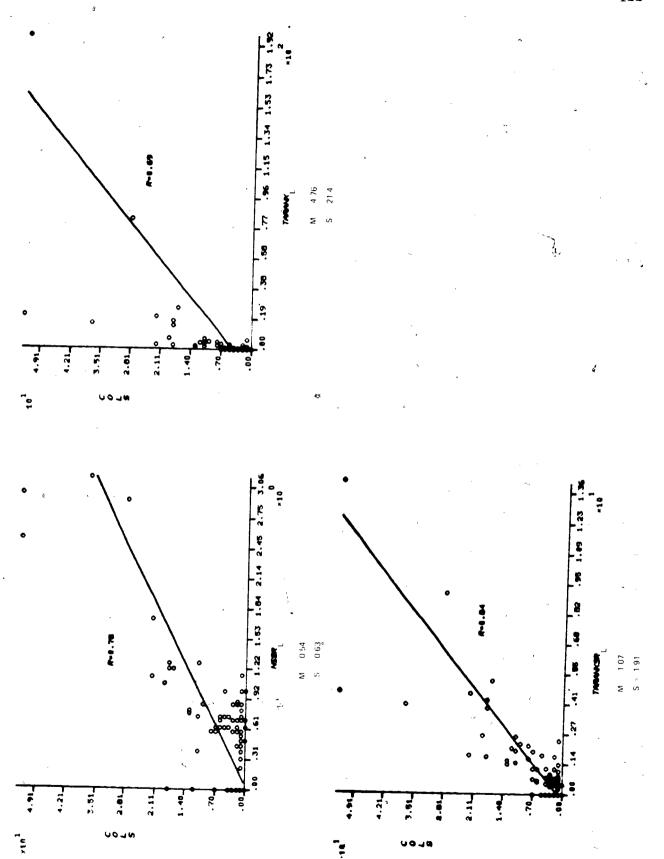
 $M(COLS_S) = 3.22$, $S(COLS_S) = 3.72$

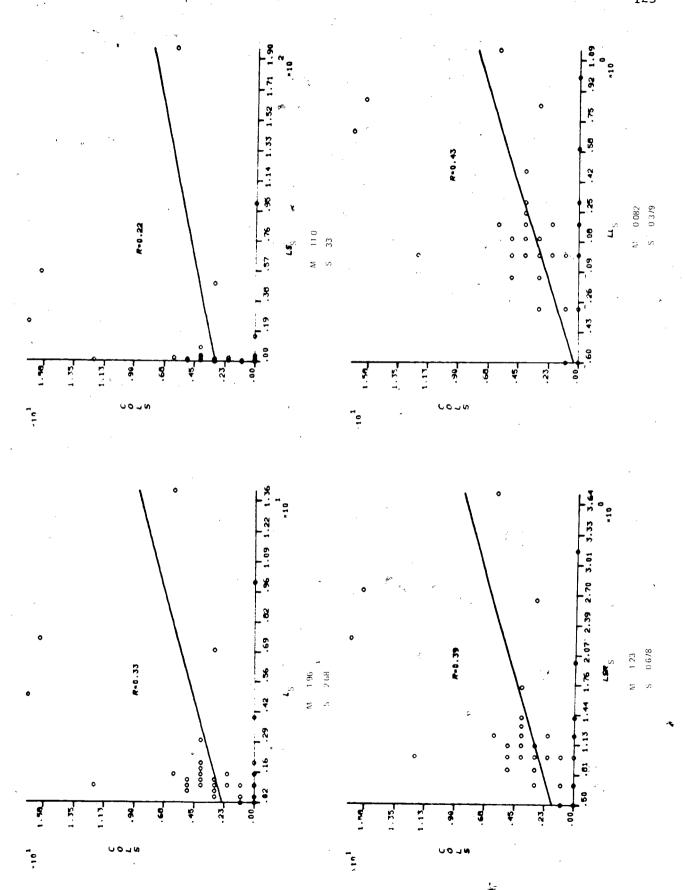


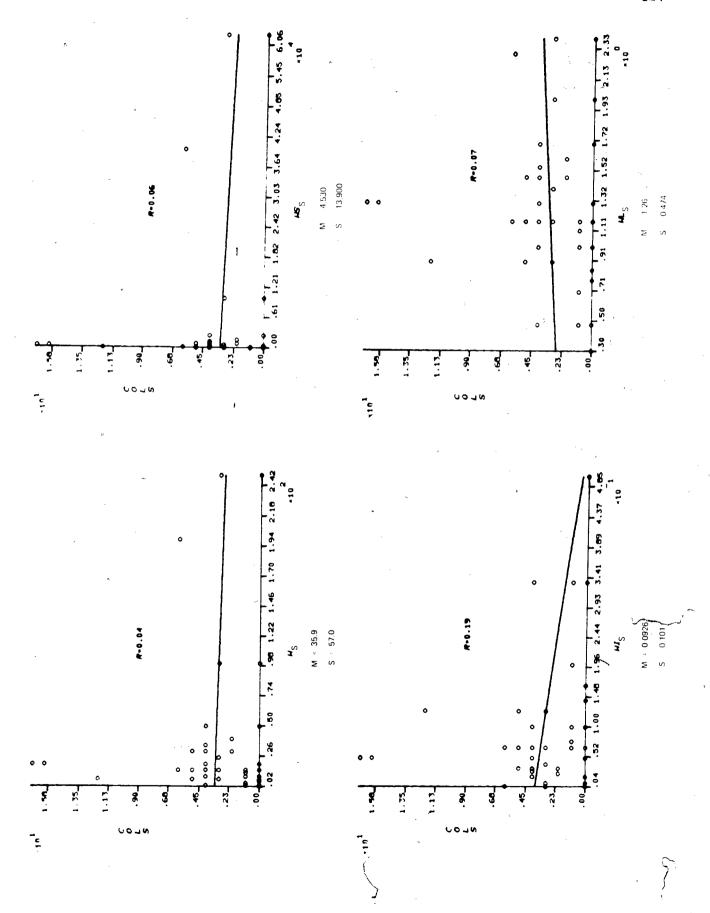


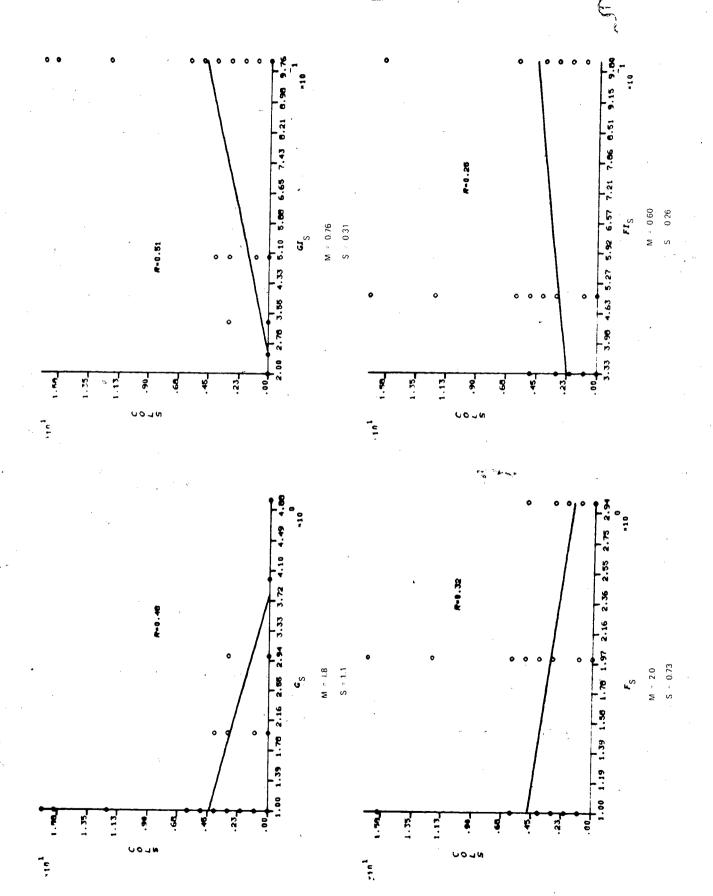


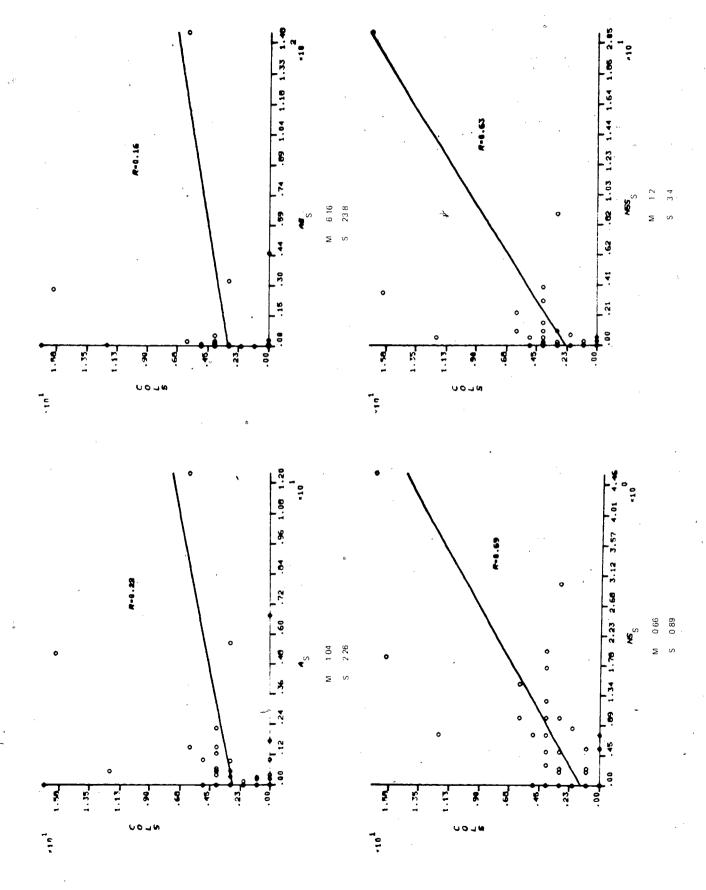












Appendix E.--Regression coefficients and null t-values for variables in all steps of elimination analyses (Tables 4a and b)

E₁ Lakes

Step:	1		. 2	2	_ 3	
Variable	Coefficient	Null t	Coefficient	Null t	Coefficient	Null t
$\mathtt{E}_{\mathtt{L}}$	-0.106	-0.55°	-2.96E-2	-0.50	ساسي	
EIŢ.	-59.7	-0.42				~-
$P_{ m L}$	-0.965	-2.73 ^{\(\)}	-0.993	-2.88 ^{\(\lambda\)}	-0.958	-2.85 ^{\(\)}
PŠ _{I.}	-9.83E-4	-1.44	-9.88E-4	-1.45	-9.36E-4	-1.40
$^{ m A_L}$	1.73E-3	2.96 ^{\(\lambda\)}	1.76E-3	3.06 ^{\lambda}	1.72E-3	3.04 ^λ
${\tt ASR}_{ m L}$	0.719	3.22 ^{\(\lambda\)}	0.738	3.38 ^{\(\lambda\)}	0.710	3.38 ^{\(\lambda\)}
	-2-73E-2	-0.87	-2.95E-2	-0.96	-2.74E-2	-0.90
R _L RS _L	-5.36E-4	-4.31λ	-5.43E-4	-4.43 \	-5.31E-4	-4.44λ
$\mathtt{W}_{\mathrm{L}}^{L}$	1.39	3.31^{λ}	1.38	∘3.32 λ	1.37	3.32 h
$ extbf{TA}_{ extbf{L}}$	-0.199	-0.96	-0.212	-1.04	-0.224	-1.11
TAŠR _{I.}	2.31	2.65 ^{\(\lambda\)}	2.37	2.75 ^λ	2.51	3.12 ^λ
$^{ m C}_{ m L}$	1.31	2.17 ^{\(\lambda\)}	1.36	2.29^{λ}	1.31	2.25 ^{\(\lambda\)}
cšr _L	-2.40	-1.80	-2.50	-1.92	-2.38	-1.86
$^{'}^{ m N_L}$	6.32	8.35 ^{\(\lambda\)}	6.33	8.41 ^{\(\lambda\)}	6.28	8.46 λ
ΣΥ.	1.57	1.51	1.57	1.51	1.55	1.50
n Š€ R _L	-1.74	-1.36	-1.71	-1.34	-1.64	-1.30
Constant	1.45	0.14	-2.93	-1.34	-3.79	-2.93 ^{\(\)}

	=					
Step	4		5		6	
Variable	Coefficient	Null t	Coefficient	Null t	Coefficient	Null t
_ = ±						
$\mathtt{P}_{\mathtt{L}}$	-0.769	-2.94 ^{\(\)}	-0.808	-3.13 ^λ	-0.746	-2.89 ^λ
$\mathtt{PS}_{\mathbf{L}}$.	-1.18E-3	-1.92	-1.14E-3	-1.86	-1.10E-3	-1.79
$\mathtt{A}_{\mathtt{L}}$	1.73E-3	3.05 ^λ	1.56E-3	2.89 ^{\(\)}	1.61E-3	2.96 ^{\(\chi'\)}
$\overline{ASR}_{\mathrm{L}}$	0.568	·4.12λ	0.592	4.36 ^λ	0.538	4.04 ^{\(\lambda\)}
RS_{L}	-5.28E-4	-4.42 ^{\(\)}	-5.33E-4	-4.47 ^{\(\)}	-5.06E-4	-4.24 ^{\(\)}
W_{L} .	1.39	3.37 ^{\(\lambda\)}	1.41	3.42 h	1.23	3.06λ
$ ilde{ t TA}_{ extbf{L}}$	- 0.199 ~	-1.00				
$ ilde{ t TASR}_{ m L}$	2.51	3.12λ	1.92	3.50 ^{\(\lambda\)}	1.82	3.31 λ
$c_{\mathbf{L}}$	1.24	2.16λ	1.00	1.92	8.76	1.67
$ ilde{CSR}_{ extsf{L}}$	-2.44	-1.91	-2.18	-1.74	-1.75	-1.42
$^{ m N_L}$	6.20	8.42 ^{\(\)}	6.36	8.84 \lambda	5.83	8.98 \lambda
$_{*}$ S $_{ m L}^{-}$	1.60	1.56	1.79	1.76	0.563	0.81
nssr _{t.}	-1.77	-1.42	-2.03	-1.65		
Constant	-4.05	-3.21 \lambda	-3.98	-3.16 h	-3.71	-2.94 ^{\(\lambda\)}

E₁ Lakes

Step	7		8		9	
Variable	Coefficient	Null t	Coefficient	Null t	Coefficient	Null t
	,	2		3		
$\mathtt{P}_{\mathbf{L}}$	-0.793	-3.16 ^{\(\lambda\)}	-0.751	-3.00 ^{\(\lambda\)}	-0.676	-2.88 λ
${\tt PS}_{ m L}$	-1.16E-3	-1.89	-4.87E-4	-1.25	-2.20E-4	-0.92
$\mathtt{A_L}^-$	1.81E-3	, 3.71 ^λ	1.58E-3	3.42 ^{\(\lambda\)}	1.41E-3	3.37 λ
AŠR _{T.}	0.561	4.33λ	0.554	4.26 ^{\(\lambda\)}	0.517	4.21^{λ}
RS_{L}^{L}	-5.34E-4	-4.69 ^{\(\)}	-5.26E-4	-4.60 ^{\(\lambda\)}	-5.02E-4	-4∙53 ^λ
$w_{ m L}^{-}$	1.28	3.23 ^λ	1.28	3,21 ^λ	* 1.29	3.24 ^{\(\)}
$ar{ t TASR}_{f L}$	1.77	3.22 ^{\(\lambda\)}	1.53 =	2.93 \	1.78	4.07 ^ኢ
${ m c_L}$	0.871	1.67	0.246	0.87		- -
CSR _{T.}	÷1.74	-1.42				-'-
$N_{ m L}$	6.04	10.27 հ	6.16	10.52 λ	6.17	10.55 ^λ
Constant	-3.76	-2.99 \lambda	-3.89	-3.08 ^{\(\lambda\)}	-3.87	-3.08 ^λ

· Step	10		11 -		12	
Variable	Coefficient	Null t	Coefficient	Null t	Coefficient	Null t
$^{ m P}_{ m L}$	-0.781	-3.82 ^{\(\lambda\)}	-0.695	-3.28 ^{\(\lambda\)}	-3.68E-2	-0.97
$^{-}$ A $^{-}$	1.43E-3	3.43 λ 💌	1.38E-3	3.15 ^λ	 .	
${\sf A\overline{S}R_L}$	0.555	4.81 ^{\(\)}	0.453	3.91 $^{\lambda}$	0.124	$^{2}.35$ $^{\lambda}$
RS_{T}	-5.10E-4	-4.62 ^{\(\)}	-4.48E-4	-3.95 λ	-1.05E-4	-3.15 $^{\lambda}$
\mathbb{V}_{L}	1.24	3.14 ^{\(\lambda\)}				~ -
W _L TASR _I	1.79	4.09 ^ኢ	1.96	4.31 ^{\(\)}	2.16	4.61 ^{\(\lambda\)}
N_{L}	6.32	11.23 λ	6.12	10•47 ^ኢ	4.56	14.16 $^{\lambda}$
Conștant	-3.84	-3.05 λ	-0.160	-0.33	0.584	1.32

E₁ Lakes

Step	13		14		15	
Variable	Coefficient	Null t	Coefficient	Null t	Coefficient	Null t
ASRL	8.23E-2	2.69 λ	••			
$\mathtt{RS}_{ extbf{L}}$	-8.16E-5	-3.49 \lambda	-3.17E-5	-2.16λ		
$\mathtt{TASR}_{\mathbf{L}}$	2.20	4.69 ^{\(\lambda\)}	3.31	14.76 ^{\(\lambda\)}	2.97	18.10λ
$^{ m N_L}$. 4 • 60	14.50 ^{\(\chi\)}	4.40	13.84 հ	4.32	13.43 λ
Constant	0.865	🚣 2.60 λ	0.939	2.74 A	1.02	2.94λ

Step Variable	16	
Variable	Coefficient	Null t
TASRL	3.90	15.66 λ
Constant	1.15	1.99 հ

λ <u>P≤</u>0.05

Appendix E_{\bullet} --Continued

E₂ Stream Sections

Step	1		2	1	3 .	
'Variable	Coefficient	Null t	Coefficient	Null t.	Coefficient	Null t
\mathtt{L}_{S}	26.0	2.79 λ	26.0	3.52 λ	26.0	3.58 λ
LSS		-1.97	-0.610	-3.55 λ	-0.610	-3.61 λ
LSR _S	-106	-2.85 h	-106	-3.30 λ	-106	-3.36 λ
\mathtt{LL}_{S}	61.4	2.80 λ	61.4	3.10 λ	61.2	3.16 λ
₩ _S	0.113	1.18	0.113	1.24	0.116	1.37
₩Š _S	-5.21E-4	-1.99	-5.21E-4	-2.07 ^{\(\lambda\)}	-0.529E-4	-2.25 ^{\(\lambda\)}
WIS	-11.5	-0.85	-11. 5	-0.89	-12.1	-1.07
WLS	-8.34	-1.28	-8. 35	-1.34	-8.60	-1.50
G_{S}	-8.31E-2	-0.11	-8.31E-2	-0.11		
GIS	5.12	1.71	5.12	1.75	5.40	4.15^{λ}
${}^{\cdot}\mathbf{F}_{\mathbf{S}}$	-0.200	-0.13	-0.201	-0.13	-0.230	-0.16
FIS	-1.90	-0.45	-1.90	-0.46	-1.96	-0.48
A_{S}	0.868	1.00	0.870	1.22	0.867	1.24
$^{\mathtt{AS}}_{S}$	4.86E-4	0.00			·	
- \mathtt{NS}_{S}	0.723	0.62	0.723	0.64	0.706	0.64
\mathtt{NSS}_{S}	0.423	1.31	0.423	1.33	~ 0 . 425	1.36
Constant	89.6	3.15λ	89.6	3.46 ^{\(\chi\)}	89.4	3.52 ^λ

Step	4		5		6	
Variable	Coefficient	Null t	Coefficient	Null t	Coefficient	Null t
τ	26.1	3.68 ^{\(\lambda\)}	26.7	3.76 λ	25.0	2 72)
LS		-	26.4	- • .	25.9	3.73 λ
LŠ _S	-0.613	-3.71 λ	-0.624	-3.84 \	-0.600	-3.87 λ
\mathtt{LSR}_{S}	- 106	-3.48 λ	-108	-3.58 λ	-107	-3.56 λ
\mathtt{LL}_S	61.6	3.28 λ	63.1	3.41λ	62.9	3.42 λ
w_{S}	0.117	1.42	0.126	1.57	0.141	1.80
WSS	-5.34E-4	-2.33 λ	-5.61E-4	-2.51 λ	-5.88E-4	-2.68 \
WIS	-12.3	-1.11	13.8	-1.29	-15.1	-1.43
$\mathtt{WL}_\mathbf{S}$	-8.70	-1.56	-9.36	-1.72	-10.5	-2.01
GIS	5.47	4.52 λ	5.60	4.75 λ	5.28	4.81 λ
FI_S	-1.38	-0.91	-1.14	≈0.78		
$\mathtt{A}_{\mathtt{S}}$	0.910	1.44	1.09	1.94	0.869	1.80
$\mathtt{NS}_{\mathtt{S}}$	0.651	0.63				
$\mathtt{NSS}_{\mathtt{S}}$	0.445	1.60	0.605	5.43 X	0.588	5.42 \\
Constant	89.3	3.57 λ	91.4	3.73 λ	91.2	3.74 λ

E₂ Stream Sections

_				-	A 100 A	
Step	7		8		9	4
Variable	Coefficient	Null t	Coefficient	Null t	Coefficient	Null t
\mathtt{L}_{S}	25.6	3.63 ^{\(\lambda\)}	23.8	3.47 ^{\(\lambda\)}	24.1	3 . 45λ
$^{\mathtt{LS}}\mathtt{S}$	- 0 . 573	-3.58 ^{\(\lambda\)}	- 0.524	-3.41 ^{\lambda}	-0.554	-3.57 ^{\(\lambda\)}
LSRS	-107	-3.51 ^λ	÷99 . 5	-3.35λ	-98.5	-3.26 ^{\(\lambda\)}
$_{ m LL_S}$	63.7	3.41 ^{\(\lambda\)}	59.1	3 _• 24λ	56.2	3.05 ^{\(\lambda\)}
$^{-}$ W_{S}^{-}	5.12E-2	1.07				- ·
$\mathtt{Ws}_{\mathtt{S}}$	-3.62E-4	-2.33 ^{\(\lambda\)}	-2.02E-4	-4.60 ^{\(\)}	-2.43E-4	-6.91 λ
\mathtt{WL}_{S}^{S}	-3.68	-1.68	-1.64	-1.51	·	
GI _S	5.24	4.70 ^{\(\)}	5.10 ·	4.59 ^{\(\)}	4.42	4.28λ
A_{S}^{-}	0.730	1.52	0.751	1.56	0.954	2.03λ
NŠS _S	0.580	5.27 ^λ	0.590	5•36 ^λ	0.600	5.37λ
Constant	83.8	3.46 ^{\(\lambda\)}	77.0	3.29 ^{\(\lambda\)}	74.2	3.13λ

Step	10		11	•	12	
Variable	Coefficient	Null t	Coefficient	Null t	Coefficient	Null t
\mathtt{L}_{S}	22.3	3.10 ^{\(\lambda\)}	3.89	1.90	1.09	1.82
\mathtt{LS}_{S}	-0.481	-3.06 ^{\(\lambda\)}	-0. 105	-1.42		
\mathtt{LSR}_{S}	-89.0	-2.86 ^{\(\)}	-7.27	-1.52	-1.31	-0.56
LL_S	50.3	2.65 ^{\(\lambda\)}				many
WSS	-2.25E-4	-6.34 ^{\(\)}	-1.94E-4	-5.38 ^{\(\lambda\)}	-1.78E-4	5.13λ
GIS	4.79	4 . 54 ^ኢ	5.28	4.72 h	4.91	4.45λ
NSSS	0.517	4.77 ^{\(\lambda\)}	0.468	4.07 ^{\(\lambda\)}	0.533	4.99λ
Constant	66.4	2.72λ	2.00	0.76	-0.861	-0.49

E₂ Stream Sections

Step Variable	13 Coefficient	Null t	14 Coefficient	Null t	15 Coefficient	Null t
L _S WS _S GI _S NSS _S Constant	0.776 -1.75E-4 4.76 0.511 -1.71	4.18 ^λ -5.14 ^λ 4.49 ^λ 5.19 ^λ -2.07 ^λ	-6.99E-5 5.34 0.616 -1.23	-2.57 ^{\(\lambda\)} 4.29 ^{\(\lambda\)} 5.47 ^{\(\lambda\)} -1.27	 4.74 0.578 -1.05	 3.64λ 4.86λ -1.02

Step	1 6	
Variable	Coefficient	Null t
NSS_{S}	0.691	5.31^{λ}
Constant	2.39	5.12 ^λ

Appendix F.--Path coefficients from first elimination steps containing all significant variables

F₁ Lakes (Step 10)

	\mathtt{P}_{L}					
$^{\mathrm{A}}\mathrm{_{L}}$	-0.98%	A_L .				
ASRL	-0.94%	0.887-	$\mathtt{ASR}_{\mathtt{L}}$		*	
\mathtt{RS}_{L} .	0.98	-0.95 ³	-0.97%	$\mathtt{RS}_{\mathtt{L}}$	•	
W_{L}	-0.13	0.04	_0.28 ^{\(\lambda\)}	-0.18	$\mathtt{w}_{\mathtt{L}}$	
TASRL	0.17	-0.15	-0.39 $^{\lambda}$	0.27 ^{\lambda}	-0.12	$\mathtt{TASR}_{\mathtt{L}}$
$N_{\rm L}$	-0.83 [\]	0.85	٥.76 [٪]	-0.83 ^{\lambda}	0.11	-0.29 ^{\lambda}

 F_2 Stream Sections (Step 9)

 $-\mathbb{R}_{0.05}$, v = 95 (lakes) and v = 37 (stream sections).

^aFrom output of REGR07 (Statistics Canada); Partial F-values of all variables significant, $P \le 0.05$.

Appendix G.--Estimate, error, standardized error, and 95% confidence interval for estimate of COLS

																												T	٠.
	Possible Estimates	4-5	7-10	8-10	1-2	8-9	6-1	8-10	13-16	2-5	7-7	10-12	0-1		ı	1-2	ŀ	0-1	. 4-5	1-2	4-5	1-2	- 1	2-2	ı	. 1-1	1-1	4-5	
	nce Límits Upper Límit	5.61	10.19	10.69	2.06	8.29	9,73	10.23	16.82	5.30	4.92		60.1		2.15	2,92	2,36	1.47	5.27	2,59	5.03	2,62	2,37	2.94	2,67	1.91	1,80	5.40	
	95% Confidence Limits Lower Limit Upper Lim	3.76	6.78	7,40	0.37	5.79	6.87	7,58	12,89	•	3,16	9,37	-1.01	0.95	0,35	0,75	0,31	-1,65	3.06	0.91	3,23	96*0	0.50	1,27	0.85	0,20	0.08	3,54	
	Standardized Error ^b	0.50	-2,84	-0,39	97.0-	2,26	3,68	-0,34	2,71	0.51	60.0	-1.09	0.36	-0.03	-0.10	-0.32	÷0.13	0.03	-1.20	-0.28	1.09	-0.30	-0.54	-0.04	0.85	-0.40	-0,36	96*0	
	Error	1,31	-7.49	-1.04	-1,21	5.96	9.70	-0.91	7,14	1,95	-1.04	-2	96.0	-0.07	-0.25	-0.84	-0.33	0.	-3,17	-0.75	2.87	-0,479	-1.44	-0.11	2,24	-1.05	-0.94	2,53	3
	Estimate ^a	 69.4	8.49	9.04	1.21	7.04	8.30	8.91	14.86	3,65	, 70°	10,86	0.04	0.07	1.25	1.84	1,33	60.0-	4.17	1.75	4,13	1.79	1.44	•	1.76		76.0	•	•
	COLSL	9	1	80	0	13	18	∞	22	5	3	80		,	1	1	1	0		1	7	7	0	2	7	0	0	7	•
G _l Lakes	Lake Number L:	1	2	ლ	7	5	9	7	80	6	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	

Appendix G.--Continued

 G_1 Lakes

Láke Number L:	COLSL	Estimate	Error	Standardized Error	95% Confidence Limits Lower Limit Upper Lim	nce Limits Upper Limit	Possible Estimates
28		1,89	-0.89	-0,34	1,08	2,70	, 2-2
29	5	1,77	0,23	60.0	0.20		1-3
30	_	2,96	-1.96	-0,74	2,15	3,77	3-3
31	4	6.21	-2.21	-0.84	5.23	7.19	2-9
32	0 . ,	0.31	-0.31		69*0-	1,31	0-1
33	2	3,93			3,10	4.76	7-7
34	-1	2,36	-1,36	-0.52	1,41	3,31	2-3
35	-1	0.64	0.36	0.14	-0.26	1,54	0-1
36	1	1,13	-0.13	-0.05	0.29	1,98	1-1
37	1	1.10	-0.10	-0.04	0.25	1.96	1-1
38	1	3.04	-2.04	-0.77	1.86	4.22	2-4
39	, • 7	2,55	1,45	0.55	1,30	3,80	2-3
70	11	11,64	- 0.64	-0.24	10,04	13,23	11-13
41	1	4.44	-3,44	-1.30	3,20	5.68	4-5
42		-0.42	1,42	0.54	-2.07	1,23	0-1
43	7	4° 98	2.02	0.76	2,11	7,86	3-7
77	11	11,35	-0.35	-0.13	6.67	13,03	10-13
45	7 ,	.4.77	0•77	-0.29	3.87	2,66	. 4-5
. 97	12	7.69		1.63	5,55	9,83	6-9
47	7	2,28	1.72	0.65	1,31	3,24	, √ 2-3
48	, 18	15.67	2,33	0.88	12,17	19.17	13-19
67	1	3,16	-2.16	-0.82	2,33	4.00	3-4
50	53	50.31	2.70	1.02	45,33	55,28	46-55
51		-1.15	2,15	.0.81	-3.20	0.91	0-0
52	-	.1,33	-0.33	* , 0.13	0.31	2,36	1-2
53	2	2,20	-0.20	-0 <u>.</u> 08	1,22	3,19	2-3
54	1	08.0	0.20	0,08	-0.19	1.80	0-1

Appendix G.--Continued

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G Cont
Appendix

Lake Number L:	$^{\mathrm{T}}$ STOO	Estimate	Error	Standardized Error	95% Confid Lower Limit	95% Confidence Limits er Limit Upper Limit	Possible Estimates
8.7	-	76 0	90.0	0.02	0.76	1.80]-1
88	22	25,36	-3,36	-1.27	22,86	27.86	23-27
89	17	21.23	-4.23	-1.60	18,63	23,83	19-23
90	5	3,74	1,26	0.48	1,80	5.67	2-5
91	5	6.97	-4.97	-1.88	8.93	11.01	9-11
92	28	26.91	1.09	0.41	21,26	32,56	22-32
93	18	12,93	5.07	1.92	10,40	15.47	11-15
76	3	3,40	05.0-	-0.15	2,47	4.33	3-4
95	1	.77.0	0.56	0.21	-0.51	1,38	0-1
96	1	-1.69	2.69	1.02	-3,57	0.18	0-0
97	19	18,01	66.0	0.37	15.94	20,08	16-20
86	1	1.75	-0.75	-0.28	0.86	2,64	1-2
66	က	2,47	0.53	0.20	1,56	3,39	2-3
100	2	2,25	-0.25	60*0-	1.45	3.04	2-3
101		8.09	-7.09	-2.69	6.14	10.04	7-10
102	53	53,54	-0.54	-0.21	47.56	59.52	48-59
Totals	280				/ .		502-676

Appendix G. -- Continued

G₂ Independent Sample of Lakes

Possible Estimates	5-6 6-9 6-9 1-1 1-1 1-1 2-2 1-1 2-3 3-4 0-1 0-1
95% Confidence Limits er Limit Upper Limit	6.19 9.44 6.11 1.91 1.91 1.90 2.93 4.13 3.17 3.39 4.44 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91 1.91
95% Confide Lower Limit	4.06 0.41 5.38 4.12 0.20 0.95 -0.12 0.46 -0.11 -0.54 1.26 1.27 1.27 1.85 -0.04. -1.06 -0.12
Standardized Error ^b	0.71 -0.10 -0.91 -0.04 -0.02 0.09 0.19 0.09 -0.05 -0.05 -0.05 -0.09 -0.09 -0.09 -0.09
Error	1.87 -0.26 -2.41 -0.11 -0.05 0.16 0.24 0.50 0.11 0.93 -1.09 -0.30 -0.30 -0.13 -0.27 -1.22 -1.22 -1.22 -1.22 -1.22 -1.22
Estimate ^a	5.13 1.26 7.41 1.05 1.05 1.07 1.07 1.03 1.05 1.13 1.05 1.13 1.05 1.13 1.05 1.13 1.05 1.13 1.05 1.13 1.05 1.13 1.05 1.13 1.05 1.13 1.05 1.13 1.05 1.13 1.05 1.13 1.05 1.07 1.07 1.07 1.07 1.07 1.07 1.07 1.07
${f T}_{ m STOO}$	131131504151311151515217
Lake Number I:	10 22 11 12 13 13 14 16 27 28 29 20 20 21 22 23 24

Appendix G.--Continued

	Possible Estimates	29-37 6-7 11-13 1-1 2-3 4-4 22-31 6-7	124-175	Possible Estimates	1-5 3-6 3-6 4-7 3-4 2-11
	95% Confidence Limits er Limit Upper Limit	37.05 7.85 13.37 1.98 3.20 4.92 31.12 7.83		95% Confidence Limits er Limit Upper Limit	5.07 6.20 6.16 7.30 ^C > 4.55 11.05
,	95% Confi Lower Limit	28.04 5.99 10.15 0.29 1.43 3.23 21.27 5.11		95% Confi Lower Limit	0.81 2.86 2.62 3.78 2.07 1.16 -1.53
	Standardized Error	-8.93 -1.49 -1.43 -0.05 -0.12 -5.00		Standardized Error ^b	0.58 4.07 0.33 0.25 0.38 -0.06
	Error	-23.55 -3.92 -3.76 -0.13 -0.31 0.92 -13.20		Error	1.06 7.47 0.61 0.46 0.69 -0.11
Sample of Lakes	Estímate	32.55 6.92 11.76 1.13 2.31 4.08 26.20 6.47		Estimateª	2.94 4.53 4.39 5.54 3.31 6.11
endent Sampl	$^{ m T}_{ m ST00}$	9 8 8 2 5 13	als 113 Stream Sections	COLSS	12 12 5 6 6 6 6 3
G ₂ Independent	Lake Number I:	27 28 29 30 31 33 34	Totals G ₃ Stream	Stream Section Number S:	

Sections
Stream
e_3

7	13-21	13-21	[- C	7-0	0-1		0-2	0-4	7-0	0-2	1 ° -	3.5	0 - 0		2-6	0-3	0-2	1-2	3.1	, ,	3-6	1-4	11-19	3-7	0-0		2 6) (- - - - - -	3-5
, 03	21.81	3,09	1.39	2.77	1.61	3,03,	2,34	4.41	4.77	2,44	3,25	5,42	4.30	5.23	4.39	3,43	2,50	2.88	5.86	1.40	6,16	4.10	19.46	7.46	2,71	2.52	6.30	3.29	5.29
4-07	12,15	0,37	-2,88	-3,70	-4.75	0.03	-1,42	-0.12	2,40	-1,13	0,15	2.79	-3,71	2,75	1,63	-1,56	-0.49	0.36	2,06	-3,32	2,62	0,75	10,18	2,33	-0.42	-0.50	2.24	0.18	2,69
-1.09	0.01	-0,40	0,40	0.80	98.0	0.80	-0.25	101	-0.65	-0.36	-0-38	09.0-	-0.16	0.01	1.09	-0.51	-0.55	-0.34	-0.52	0.52	. 0,33	-0.23	,9°0	67.0-	1.01	-0.55	-1.78	-0.40	0.01
-2.00	0.02	-0.73	0.74	1,47	1.57	1,47	95.0-	1,85	-1.18	-0-65	-0.70	-1.10	-0.30	0.01	1,99	-0 - 94	-1.01	-0.62	96.0-	96*0	0.61	-0.43	1.18	-0.89	1,85	-1.01	-3,27	-0.74	0.01
00.9	16.98	1.73	-0.74	-0.47	-1.57	1,53	94.0																						
4	17	1	0	1	0	က	0		0																				
8	6	01	11	- 5	[]	14	.5	9	[7	Σ (6 9	0 5		7		7	5	٥	7	φ,	ون ر	ο,	٦ ،	7 (η.	7 '	2	9	7

Appendix G. -- Continued

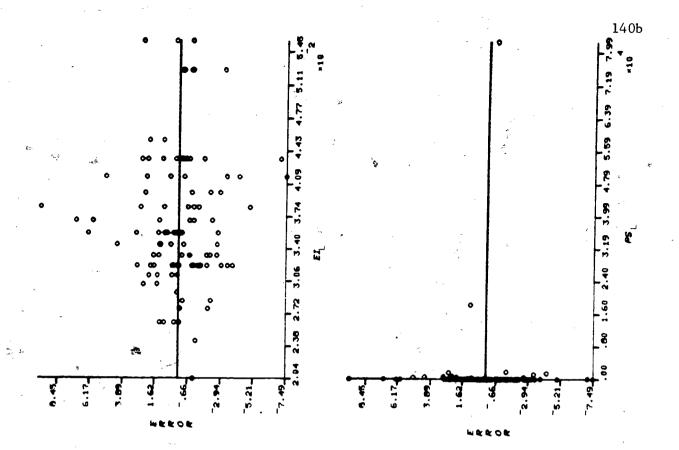
Sections	
Stream	
3	

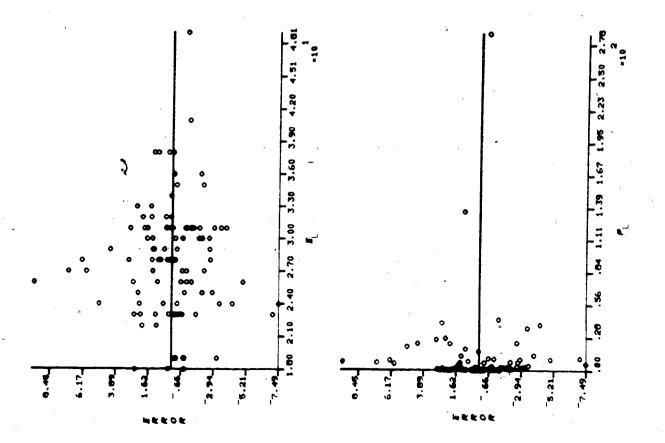
Possible Estimates	7-6	2-4	3-5	9-7	3-5	0-3	3-5	1-4	94-225
95% Confidence Limits ver Limit Upper Limit	6.74	4.59	5,25	6.32	5; 56	£ 3.81	2.88	7.06	· 100
95% Confide Lower Limit	3,53	1,56	2,83	3,52	2,94	-1.04	2,62	0.27	
Standardized Error	-0.62	-1.68	-1,11	0.04	-0.14	-0.75	-0,13	0.45	
Error	-1.14	-3.08	-2.04	0.08	-0.25	-1,38	-0.25	0.83	
Estimate	5.14	3.08	70.7	4.92	4.25	1,38	4.25	2,17	
COLSS	7	0	2	. 5	7	0	7	က	145
Stream Section Number S:	38	39	07	41	42	43	77	45	Totals

a Estimates from equations given at first elimination step containing all significant variables (Equations 3 and 4, p.52).

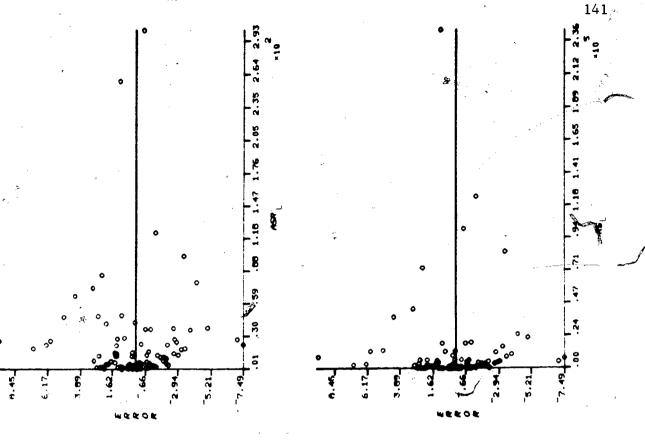
bStandardized Error \Rightarrow Error Standard Deviation) \Rightarrow Standardized Error \Rightarrow Error Standard Deviation from G_1 (Lakes) was used in the calculations of Standardized Error. Appendix H $^{\prime}$ Plots of residuals 1 against independent variables.

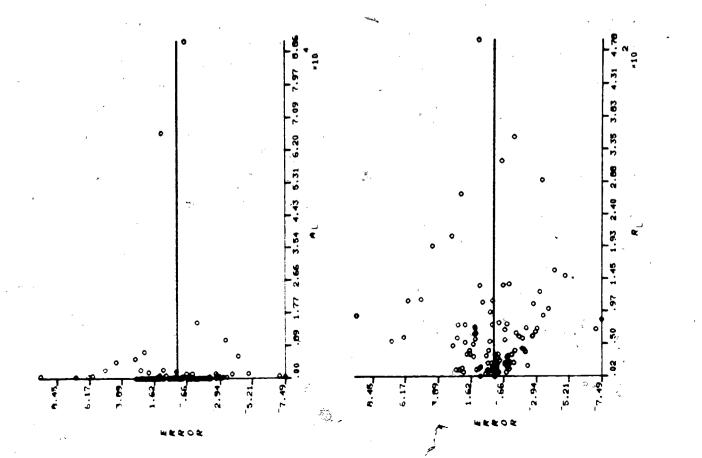
 $^{1}\mathrm{From\ Appendix\ G}_{1}$ and $^{G}_{3}$.

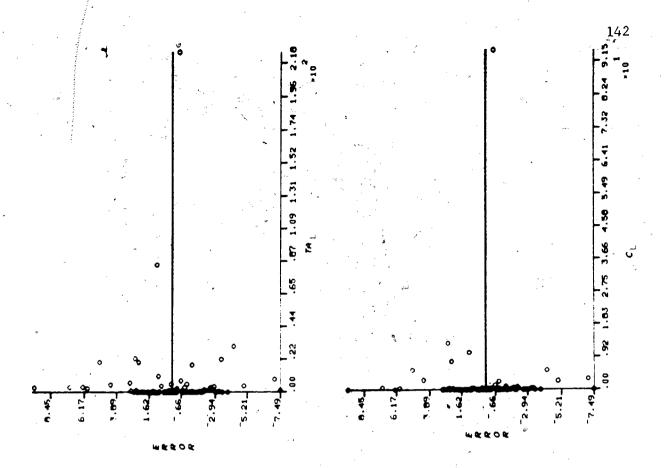


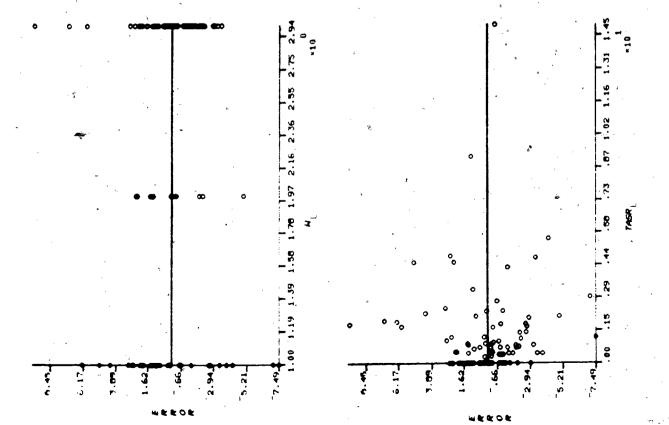


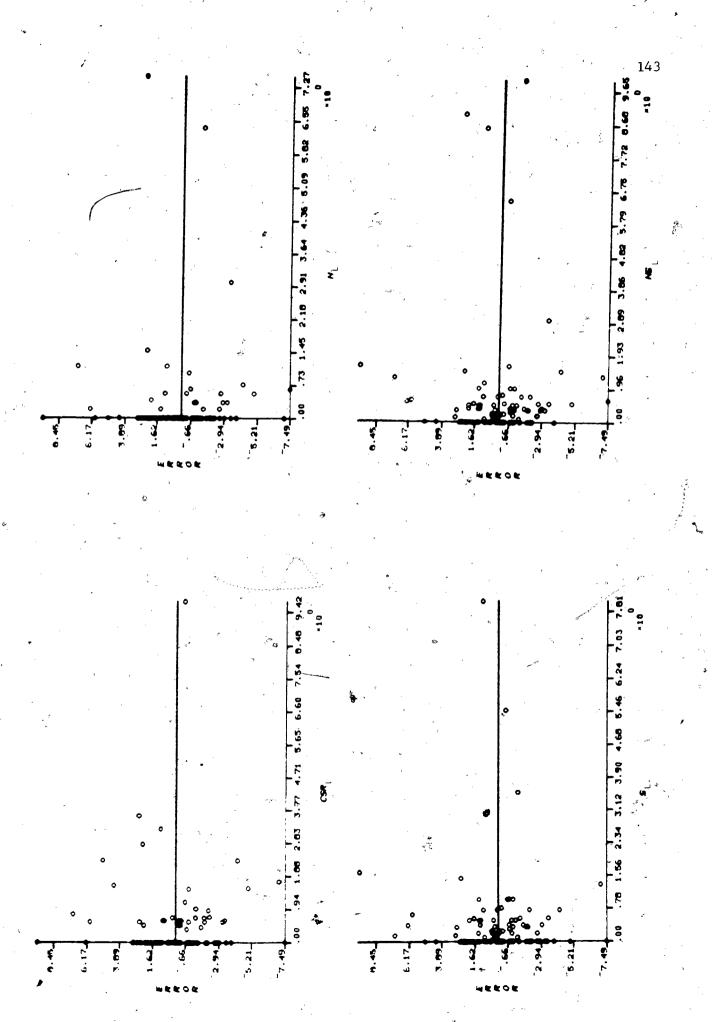


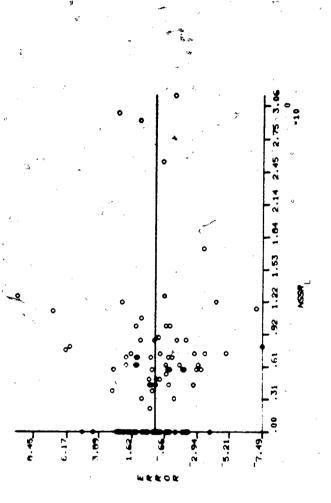


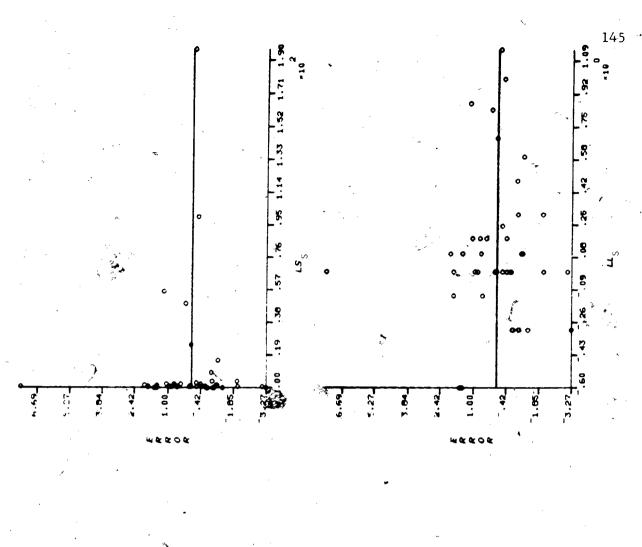


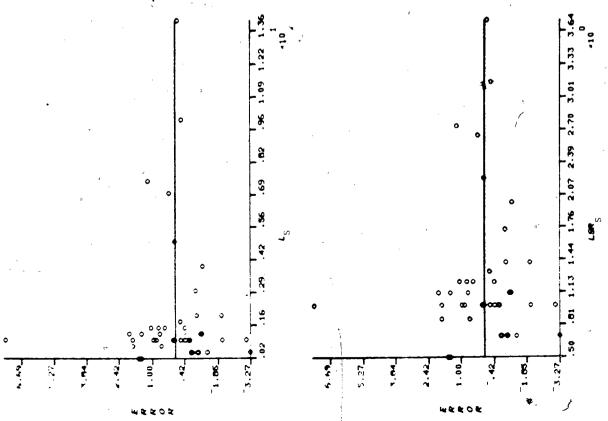




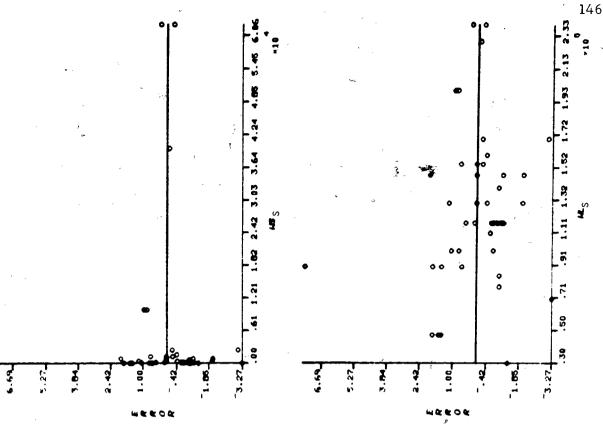


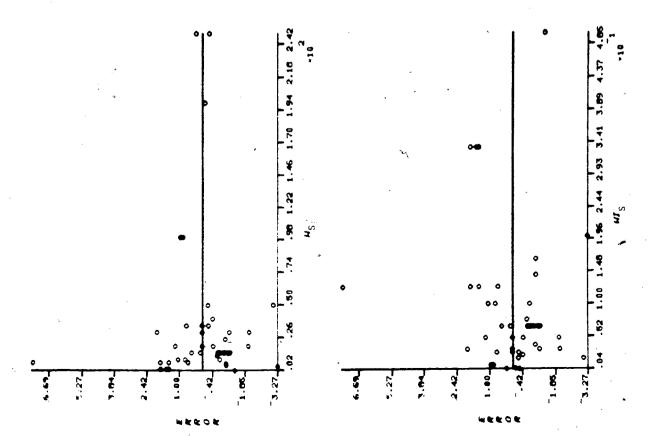


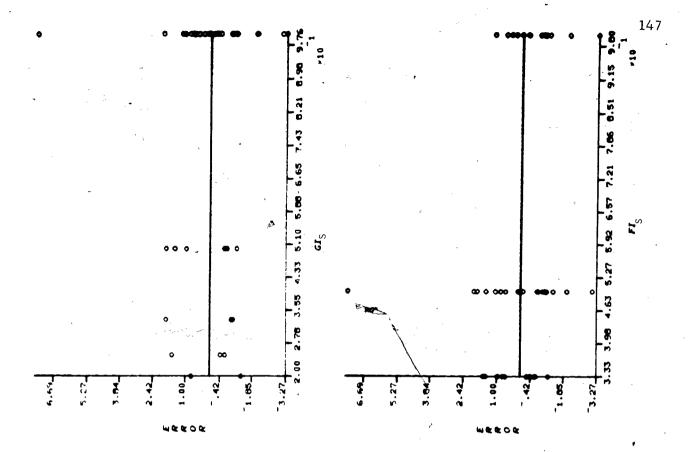


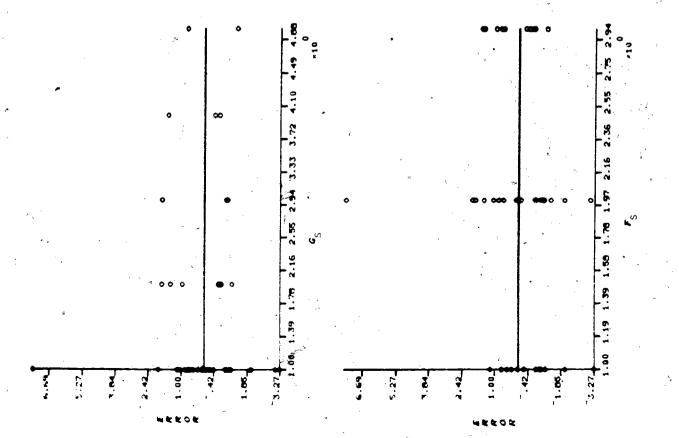




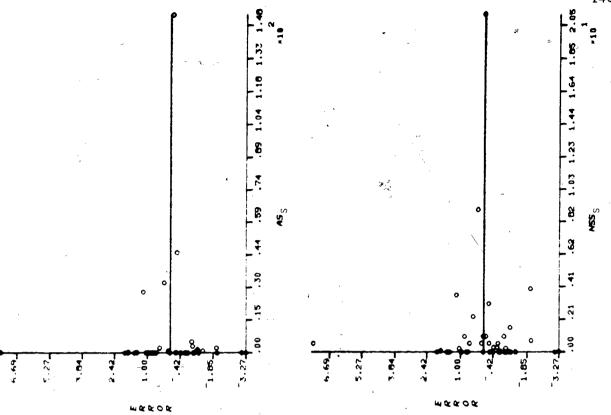


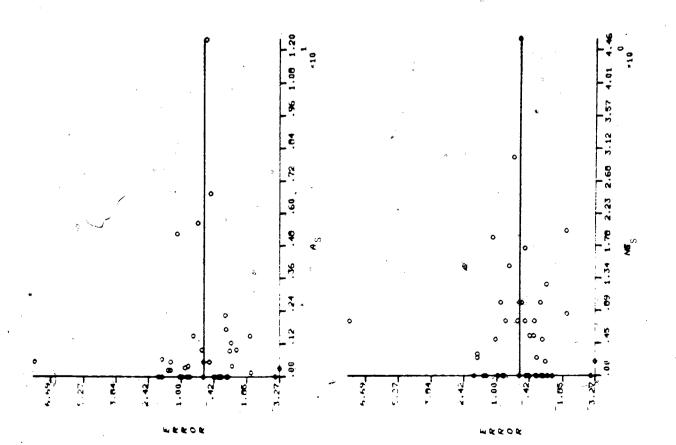












Appendix I.--Occupancy rate of beaver colony sites

 $\rm I_1$ Food cache observation from selected lakes in the study area. Data collected October 16-19, 1974.

Number	Name	cols _L	Active $\mathtt{COLS}_{\mathtt{L}}$	$\%$ Active COLS $_{ m L}$
L3	Maxan	8	4	50
L5	Day	~ 13	5	[*] 38
L6	Elwin	18	4	22.
L7	Sunset	8	3	38
L8	Swans	22	10	45
L27	Seymour	7	3	43
I1	Torkelsen	7.	3	43
14	Gilmore	5	2	40
Totals	2	88	34	39

I₂ Food cache observations in the Mackenzie Valley and Northern Yukon (after Dennington and Johnson, 1974).

			Lake	es	Stream	ms	
Survey Unit		COLSL	Active COLS _L	% Active COLS _L	COLSS	Active COLS _S	% Active COLS _S
1		61	19	31	5	3	60
2		29	6	21	14	14	100
3		0	0	, _	48	27	56
4		23	22	96	8	8	100
5		4	1	25	20	18	90
6		0	0	-	26	25	96
7		0	0	-	16	12	75
8	•	27	10	37	1	1	100
9		2	2	100	0	0	-
10		21	10	48	0	0	-
11		23	6	26	0	0	-
12		49	24	49	-	, _	-
13		105	42	40	1	0	0
14		33	8	24	0	0	-
15		,3	[*] 1	33	0	0	-
16	,	54	23	43	0	. 0	_
17		69	39	57	0	0	-
18		35	25	71	0	0	-

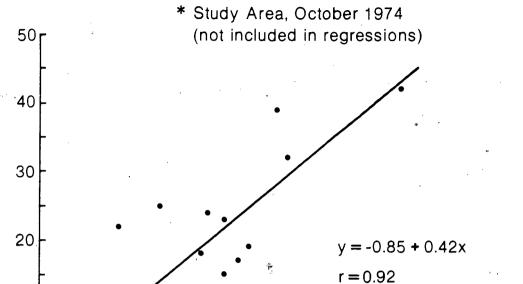
Appendix I.--Continued

 $\rm I_2$ Food cache observations in the Mackenzie Valley and Northern Yukon (after Dennington and Johnson, 1974).

		Lak	es	Stream	ns	
Survey Unit	COLSL	Active ${ t COLS}_{ m L}$	$\%$ Active COLS $_{ m L}$	COLSS	Active COLS _S	% Active
19	14	2	14	0	0	-
,20-21	58	17	29	-	-	_
^{-/} 21A .	6	2	33	0	0	-
23	0	0	-	2	1	50 ·
24 - 25	72	32	44	0	0	_
26	54	15	28	0	0	_
27	19	2	11	0	0	_
· 28	5	0	0	0	0	_
29	13	. 3	0 23	1	1	100
30	0	0	· -	0	. 0	_
31	0	0	-	9	5	56
32	12	2	17	1	0	0
32A	16	3	19	0	0	_
33	47	18	38	3	2	67
34	9	1	11	0	0	-
Totals	863	335	39	155	117	75

13 Regressions of active colony sites on total colony sites (after Dennington and Johnson, 1974).



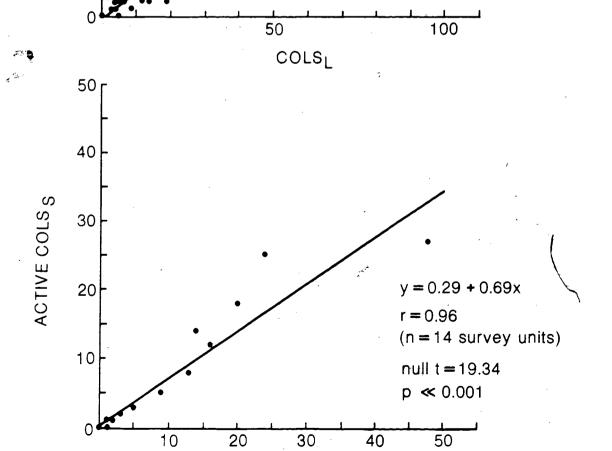


(n=27 survey units)

null t = 13.32p $\ll 0.001$

ACTIVE COLS_L

10



COLSS