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thesis entitled

PRE-SETTLEMENT BEAVER POPULATION
DENSITY IN THE UPPER GREAT LAKES REGION

presented by

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has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Zoology

Major professor

Date June 25, 1981

# PRE-SETTLEMENT BEAVER POPULATION DENSITY IN THE UPPER GREAT LAKES REGION

By

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A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1981

## ABSTRACT

# PRE-SETTLEMENT BEAVER POPULATION DENSITY IN THE UPPER GREAT LAKES REGION

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The objective of this study was to develop a reliable method to quantitatively assess the population density of beaver (Castor canadensis Kuhl) in the Upper Great Lakes Region during the pre-settlement period prior to the fur trade, ca. 1600. The methodology developed in this study involved the use of regression analysis techniques to demonstrate the relationship between beaver lodge density and specific habitat characteristics. This correlation was extended to reconstructed vegetation associations during the historic period to estimate the historic population density of beaver during the period.

Historic beaver population density in the Upper Great Lakes Region was estimated based on the contemporary correlation between beaver abundance and habitat associations combined with historic vegetation reconstructions. Contemporary beaver populations were surveyed to collect precise lodge density and habitat

data. Beaver lodge density counts were obtained from active traplines where the dominant tree species abundance was known. These data were correlated using bivariate analysis to characterize the relationship between lodge density and habitat associations. The predictive value of this correlation was established based on a step-wise multiple regression program for each of 23 tree species examined. Reconstructions of historic vegetation associations for the Upper Great Lakes Region were then used to describe pre-settlement forest conditions in the Great Lakes watershed. The vegetation reconstructions were entered into the multiple regression program to arrive at the estimated beaver lodge density. The actual population density estimate was calculated on the basis of the number of individuals known to occur in active lodges in the Great Lakes Region.

It was determined that approximately two million beaver represents a reasonably accurate assessment of beaver density in the drainage area of the Great Lakes during the pre-European settlement period, ca. 1600.

ACKNOWLEDGEMENTS

I would like to express my gratitude and appreciation to Dr. Rollin Baker, chairman of my graduate committee and to the other members of my committee, Dr. Charles Cleland, Dr. Alan Holman, and Dr. Jack Bain. The advice and criticism which they provided in the development and completion of this research was invaluable. Acknowledgements are also extended to Dr. Roger Pitblado and Mr. Wade Blake of Laurentian University for their assistance in the programming and statistical analysis of the data. The cooperation and effort exerted by Ms. Verna Brunet in the typing of the manuscript deserves special recognition for without her excellent assistance the preparation of the dissertation would have been difficult. The patience and support given to me for the completion of this work by my wife Joan and members of the Heartland community were important in providing the encouragement and determination to finish this study. Recognition must also be given to the faculty and staff of the Native Studies Department of the University of Sudbury for their cooperation.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

## INTRODUCTION

The great quantity and quality of furbearing animals in the Upper Great Lakes Region have been suggested as one of the primary factors in the exploration and settlement of North America (Schorger, 1965; Longly and Moyle, 1963). The states of Michigan, Minnesota, Wisconsin and the Canadian provinces of Ontario and Quebec have often been discussed with reference to the trade in beaver furs and the general observation that beaver were numerous and probably occurred in all waters of the Great Lakes watershed (Winterhalder, 1980; Heidenreich and Ray, 1976; Innis, 1927). Studies of the fur trade have not dealt with the actual abundance of beaver in the Upper Great Lakes Region. The competitive interactions between rival fur companies and Native people for the fur resources of the Upper Great Lakes Region have previously relied on inference and extrapolation to estimate the availability of beaver and other fur bearers in this region (Martin, 1978; Ray, 1975; McManus, 1972).

Early explorers and traders often aluded to the high abundance of beaver in the Great Lakes (Biggar, 1923). Historic records for the amount of furs collected during short periods of time generally reflect the high population levels which must have been present in the region (Schorger, 1965; Innis, 1927). One of the first explorers to travel the "Great Northwest" was Pierre Radisson. During one of his expeditions to the Upper Great Lakes Region between 1665 and 1670 he obtained some 60 canoes filled with peltries which equaled approximately 10,000 pelts (Johnson, 1971). Other trade accounts also attest to high beaver availability. For example the upper Mississippi district produced more than 100,000 good beaver skins during the 1734-1735 season alone (Hocquart, 1906).

To date, there has not been an attempt to quantify the abundance of beaver prior to the fur trade in North America. The availability of this important resource needs further study to better understand the events which led to near extinction of the species as a result of the fur trade.

The objective of this study was to develop a reliable method to quantitatively assess beaver population density in the Upper Great Lakes Region during the pre-settlement period prior to the fur trade, ca. 1600. To determine such an estimate, it was first necessary to assess contemporary beaver colonies within the Upper Great Lakes Region, and to acquire precise habitat data for each area where colonies were surveyed. These data were used to examine the statistical correlation between beaver lodge density and specific habitat characteristics which influence beaver site selection. The relationship between beaver lodge density and contemporary vegetation associations was combined with pre-settlement forest reconstructions to estimate beaver lodge density in the Upper Great Lakes Region prior to the fur trade and European settlement. This calculated value was used to estimate beaver population density based on the average number of individuals known to occur in active lodges in the Upper Great Lakes Region.

# METHODS

Contemporary beaver colonies in the Upper Great Lakes Region were examined to acquire precise data on lodge density and obtain accurate descriptions of the habitats selected by beaver for occupancy. The Ontario Ministry of Natural Resources cooperated in this effort by providing access to trapping records, habitat data, and other information concerning beaver populations in the trapping district of North Bay, Ontario. This area, located within the drainage basin of Lake Huron, was selected for study due to the availability of data and because it represented the general ecological conditions characteristic of the Upper Great Lakes Region. All information was recorded in English units of measure. This system of measurement was used in the study to maintain continuity with the original data.

Beaver lodge density was derived from records provided by the Ministry of Natural Resources. The number of beaver lodges observed within the boundaries of surveyed traplines were taken from aerial census records. Standardized aerial survey techniques were employed by Ontario Ministry of Natural Resources personnel to census the traplines. The reliability of these aerial census methods has been established by other researchers for the study of animal populations distributed over large areas (Evans, Troyer and Lensink, 1966; Hay, 1955; Swank and Glover, 1948).

The boundaries of all traplines to be surveyed were located on topographic maps provided by the Canadian Department of Energy, Mines and Resources prior to aerial surveys. Small fixed wing aircraft were used to fly over each trapline until all active beaver lodges had been observed and recorded on the map representing the trapline. Lodges were counted and assumed to be active at the time of the survey if the presence of food caches in the immediate vicinity of the lodge could be positively confirmed by the observers. Each active lodge located on the topographic map was counted as one colony. Lodge counts were thus compiled for each trapline surveyed. The number of lodges observed within each trapline was then compared with the area in square miles for the trapline established by the Ministry of Natural Resources. This comparison provided the necessary information to calculate the lodge density for each trapline by dividing the number of observed lodges by the total number of square miles represented by each trapline.

The reliability of the aerial census data was maximized by conducting all surveys during October and November of 1972, prior to the onset of the winter trapping season. There are a number of reasons why beaver lodge counts are most reliable during this period of time. Food caches, which are a major factor in the classification of lodges as active, are more readily observable at this time due to the greater visibility afforded by the loss of deciduous foliage in areas adjacent to the lodges (Novak, 1977; Brandt, 1938). In addition to lodge visibility, the age structure of the beaver population appears to be most stable in the fall of the year. Dispersing juveniles and other individuals isolated due to the previous trapping seasons are most likely to have found companions and begun to reestablish abandoned lodges. Existing pairs and females with young have also been shown to begin maintainance of existing lodges at this time (Brandt, 1947; Warren, 1932).

To correlate beaver lodge density with ecological conditions, it was necessary to determine which specific habitat characteristics may be associated with site selection. The suitability of sites for beaver occupancy depends upon a broad spectrum of ecological parameters, however, the principal environmental factors which determine the suitability of habitats for beaver occupancy have been shown to be associated with appropriate vegetation, compatible stream conditions, and topographic relief (Gill, 1972; Arner, 1964; Retzer, 1955). The data required to accurately describe the habitat characteristics of each of the surveyed traplines was collected from forestry inventory studies obtained from the Department of Forestry Branch of the Ministry of Natural Resources.

Forest inventory maps available from the Department of Forestry Branch were used to accurately describe the vegetation associations for each of the surveyed traplines. Based on the 1972 forest inventory, Forest Stand maps were compiled for all townships within the North Bay trapping district. It was therefore possible to locate and outline the specific boundaries for all traplines examined. Each Forest Stand map provided detailed information concerning the dominant woody vegetation of the trapline. The maps contained a description of the dominant vegetation species occurring in the township. Each individual stand was labelled by number and contained the species composition of the stand, represented by a percentage of the area of the stand in acres, mean height of tree species in feet, and the average estimated age of the overall stand.

A vegetation profile was constructed to represent the plant associations of each trapline by using the Forest Inventory maps and a standard sampling technique appropriate for the forest stand mosaic available from the inventory data. Using the line transect sampling technique outlined by Oosting (1956) a pair of transects were drawn on the inventory map(s) within the boundaries of the trapline. The transects were distributed over the trapline area to include as large an area as possible, and thus adequately describe the vegetation associations. Each stand encountered along a transect was tabulated separately. The number of the stand, species composition, age and total area were then recorded on the data forms.

When the required information was recorded for each stand sampled along the transects, the data were combined to describe the plant associations of each trapline. The species composition, represented by a percentage was converted to area units to reflect the total acreage of each species observed from all stands sampled within the trapline. The combined acreage of all stands sampled from a trapline was divided into the total acreage representing each species to obtain a profile of the species composition of each trapline represented as a percent of the total acreage sampled. The mean

age of stands sampled from the trapline was calculated by dividing the total age of each stand by the number of stands sampled.

Stream abundance was also determined for each trapline and assumed to be an important factor in the selection of suitable sites for occupancy by beavers. Each trapline was located on a 1:50,000 scale topographic map which clearly illustrated the location of streams and other waterways. The number of streams within each of the trapline boundaries was determined by a method of stratified random sampling (Snedecor and Cochran, 1967). Four quadrats, of one square mile each, were randomly distributed throughout each trapline. The total number of stream miles present in each quadrat was measured and recorded. The average number of stream miles per trapline was obtained by dividing the total number of stream miles sampled by the number of quadrats. Using this method, the average stream density in miles of stream per square mile and the total number of stream miles occurring in each trapline were obtained.

Harvest data represented by the number of beaver taken from each trapline were also obtained from Ministry of Natural Resources records. These data were based on the actual trapping results for the 1972-1973 trapping season. The total number of individuals removed from each trapline was divided by the total number of square miles of the trapline to determine the mean harvest from each trapping area. No information was available concerning the intensity of trapping effort expended by individual trappers.

The statistical correlation between beaver lodge density and specific habitat characteristics was examined using four statistical analysis techniques. The first statistical operation was a bivariate correlation, that provided a summary statement about the overall relationship between the habitat characteristics and lodge density. The second operation was a general multiple regression which could be used to predict lodge density as a function of the total set of habitat characteristics. The next analysis conducted was the step-wise multiple regression. This statistical technique allowed for the prediction of lodge density based on the independent contribution of each habitat variable to lodge density. The above statistics predicted beaver lodge density as a function of the habitat characteristics encountered in each of the traplines. The chi-square test of dispersion was used to examine the difference between the predicted value calculated for lodge density and the observed trapline densities.

The initial bivariate correlation analysis provided a summary of the relationship between habitat characteristics, which were the independent variables, and lodge density, the dependent variable. In this regression analysis, predicted values for the dependent variable were obtained using the following linear function:

$$Y' = A + BX$$

where Y' is the estimated value of the dependent variable Y, B is a constant, multiplied by all values of X, and A is an additive constant (Klecka, Nie and Hull, 1975).

The bivariate regression program involved the selection of A and B in a manner which insured that the sum of squares for the residuals, the difference between the actual and estimated values of Y for each case, was smaller than any possible alternative values. With the results of this analysis it was possible to: 1) arrive at a measure of the degree of association between the variables by the use of the correlation coefficient (r), 2) quantify the variation explained by (r) with the use of the coefficient of determination ($r^2$), and 3) obtain an estimate of the statistical significance of the associations between the dependent and independent variables.

A general multiple regression analysis was performed on the data to further clarify the relationship between the dependent variable, lodge density, and the set of independent variables represented by the habitat characteristics. This program provided a method to evaluate the contribution of the habitat characteristics to the variability observed in lodge density. This method is an extension of the bivariate analysis in that the total set of habitat characteristics could be used to provide an estimate of the lodge density. The general form of this function was as follows:

$$Y' = A + B_1X_1 + B_2X_2 + \ldots. + B_nX_n$$

where Y' represented the estimated value of lodge density, A the Y intercept, and B the regression coefficients for the values of X, which were the habitat characteristics. The results of this analysis yielded the following information; 1) a multiple regression coefficient, which described the degree of association between the independent and dependent variables, 2) a multivariate coefficient of determination which provided an explanation for the amount of variation in the dependent variable, explained by the independent variables, and 3) the level of confidence which indicated how significant the relationship was between the variables (Klecka, Nie, and Hull, 1975).

A stepwise multiple regression analysis was also conducted on the data to determine the combinations of independent variables which accounted for the greatest amount of explained variation in lodge density. This program entered the independent variables only if they met certain statistical criteria. The independent variables were selected according to the levels of significance in a cummulative series, while the order of inclusion was determined by the respective contribution of each variable to the explained variance (Klecka, Nie, and Hull, 1975). The resulting statistics were the same as those obtained from the general multiple regression program, except that each independent variable could be examined separately. This statistical analysis provided sufficient information to arrive at a quantitative description of the relationship between lodge density and environmental parameters. Using these data, the regression equation was used to predict lodge density as a function of habitat characteristics.

To evaluate the accuracy of the regression analysis as a predictor of lodge density, the data were subjected to the Chi-square test for dispersion to determine if the predicted value for lodge density actually represented the observed lodge densities of the traplines. This test is designed to examine whether or not the predicted frequency of a sample accurately depicts the observed frequency of the sample. The general form of the equation is:

$$\chi^2 = \Sigma (f-F)^2/F$$

where $\chi^2$ represents the ratios between the sum of the squared deviation between f, the observed sample frequency and F the predicted sample frequency divided by the predicted sample frequency F (Snedecor and Ochran, 1967).

To estimate the number of beaver expected to occur in the Upper Great Lakes Region, based on lodge density, it was necessary to determine the average number of individuals known to occur within a single lodge. Recent ecological studies of the population dynamics of beaver in the Upper Great Lakes Region were used to arrive at an estimate of the number of beaver which could be expected to occur within the drainage basin of the Great Lakes (Novak, 1977; Brandt, 1947).

The abundance of beaver in the Upper Great Lakes Region during the pre-settlement period prior to 1600 was estimated. The relationship demonstrated between beaver populations and habitat characteristics for contemporary beaver colonies were combined with a reconstruction of the vegetation associations for this region developed by Veatch (1959). This reconstruction was based on the classification and distribution of soil types in the state of Michigan. The vegetation types described by Veatch (1959) were classified into three categories which would represent the major plant communities of the Great Lakes Region. These were dominant deciduous, dominant coniferous, and mixed coniferous-deciduous. It was assumed that the relationship between contemporary beaver populations and habitat characteristics was relatively constant through time. The regression equation involved in the prediction of beaver lodge density based on contemporary vegetation profiles was used to obtain an estimate of lodge density as a function of the differential species composition of the three historic vegetation associations identified.

The determination of an estimate for the pre-settlement population density of beaver in the Upper Great Lakes Region was based on the number of lodges predicted to occur within the historic vegetation classifications identified for the region, the total number of square miles of forested area within the drainage area of the Great Lakes and the average number of beaver known to occur within a single lodge in this area of the animal's range based on recent population estimates.

The methodology developed for the determination of this estimate of beaver lodge density during the early historic period represents a unique approach to the study of past faunal associations. To clarify the process involved in estimation of beaver population density the following summary is presented.

It was first necessary to survey contemporary beaver populations and collect data on the density of lodges observed in an area where the variability of habitat conditions could be measured quantitatively. Precise data concerning vegetation abundance by dominant tree species and stream availability was obtained from 49 traplines. The specific habitat characteristics for each individual trapline were examined using bivariate analysis to determine the correlation between ecological conditions and beaver lodge density. The correlation obtained in this manner was tested using multiple regression statistics to establish the predictive value of the relationship between lodge density and habitat characteristics.

The estimation of historic beaver lodge density required the use of reconstructed vegetation associations of the Great Lakes Region. This data was abailable in a form comparable to the contemporary environmental data used to establish the initial correlation. The multiple regression statistics were used to predict an estimate of beaver lodge density based on the reconstructed vegetation associations. The estimate of beaver lodge density was used as an index for beaver population density by multiplying the average number of individuals known to occur in lodges by the total number of lodges estimated.

# RESULTS

Beaver census data based on 82 separate traplines were collected from the North Bay Trapping District. After a detailed examination of these records, 49 of the traplines were selected for this study which had been surveyed using standardized techniques. The location of each trapline within the trapping district is presented in Figure 1. The results of the aerial census of these traplines indicated that a total of 2,874 active beaver lodges occurred in an area of more than 2,205 square miles. The average trapline was determined to be 45 square miles in area and contained 1.52 active lodges per square mile. The variance for this density value was 0.91. Each trapline is represented separately in Table 1.

Vegetation profiles were constructed for each trapline based on forest stand maps available from the Ministry of Natural Resources. The dominant vegetation types encountered along sample transects established on forest stand maps were tabulated for all traplines. Total acreage, represented by each species and the acreage of all stands within a trapline,

Table 1. North Bay District Traplines Descriptive Data

| Trapline No. | Size(Sq. Mi.) | Total Lodges | Lodge Density |
|---|---|---|---|
| 01 | 32.4 | 53 | 1.6 |
| 02 | 39.2 | 50 | 1.3 |
| 03 | 35.6 | 73 | 2.1 |
| 04 | 26.4 | 57 | 2.2 |
| 05 | 31.2 | 52 | 1.7 |
| 06 | 42.4 | 39 | 0.9 |
| 07 | 76.8 | 18 | 0.2 |
| 08 | 72.8 | 60 | 0.8 |
| 09 | 84.4 | 70 | 0.8 |
| 10 | 45.6 | 46 | 1.0 |
| 11 | 61.6 | 44 | 0.7 |
| 12 | 94.8 | 41 | 0.4 |
| 13 | 47.2 | 145 | 3.1 |
| 14 | 25.6 | 91 | 3.6 |
| 15 | 41.2 | 68 | 1.7 |
| 16 | 20.0 | 17 | 0.8 |
| 17 | 12.4 | 13 | 1.1 |
| 18 | 71.2 | 48 | 0.7 |
| 19 | 42.0 | 33 | 0.8 |
| 20 | 33.6 | 16 | 0.5 |
| 21 | 58.0 | 44 | 0.8 |
| 22 | 85.6 | 40 | 0.5 |
| 23 | 34.0 | 39 | 1.2 |
| 24 | 14.8 | 08 | 0.5 |
| 25 | 45.2 | 77 | 1.7 |
| 26 | 73.6 | 116 | 1.6 |
| 27 | 40.0 | 78 | 2.0 |
| 28 | 40.0 | 70 | 1.8 |
| 29 | 56.0 | 66 | 1.2 |
| 30 | 132.8 | 280 | 2.1 |
| 31 | 30.4 | 24 | 0.8 |
| 32 | 40.8 | 138 | 3.4 |
| 33 | 94.4 | 49 | 0.5 |
| 34 | 32.8 | 21 | 0.6 |
| 35 | 32.8 | 17 | 0.5 |
| 36 | 53.6 | 42 | 0.8 |
| 37 | 26.4 | 12 | 0.5 |
| 38 | 22.4 | 77 | 3.4 |
| 39 | 16.4 | 26 | 1.6 |
| 40 | 19.2 | 20 | 1.0 |
| 41 | 12.0 | 24 | 2.0 |
| 42 | 14.0 | 56 | 4.0 |
| 43 | 14.4 | 44 | 3.1 |
| 44 | 40.0 | 83 | 2.1 |
| 45 | 36.4 | 96 | 2.6 |
| 46 | 28.0 | 58 | 2.1 |
| 47 | 38.0 | 62 | 2.2 |
| 48 | 14.8 | 22 | 1.5 |
| 49 | 11.6 | 28 | 2.4 |

were used to arrive at percent abundance values for the 23 vegetation species observed in the 49 traplines sampled (see Table 2). The average number of stands sampled within each trapline was 16.1, while the average acreage per stand was 180.0. The total acreage sampled for the traplines ranged from 6342.6 to 1412.0. The mean acreage sampled per trapline was 2865.3.

Harvest intensity, expressed as the total number of beaver taken from each trapline, was also obtained from the Ministry of Natural Resources records. During the 1972-1973 trapping season, a total of 3343 beaver were harvested from the 49 traplines. The mean harvest was determined to be 1.75 beaver per square mile with a variance of 1.78. Total and mean harvest values for all traplines are presented in Table 3.

The number of stream miles was determined for each trapline as an index of the availability of suitable sites for beaver lodges. The average number of stream miles observed within the quadrats sampled from each trapline were used to calculate mean stream density for each trapline (see Table 3). The mean stream density as measured by stream miles was found to be 2.19 linear miles of stream per square mile with a variance of .09.

A summary of the statistically significant variables from the bivariate analysis is presented in Table 4. When

Table 2. Vegetation Species Abundance and Area Values

| Vegetation Species | Mean Abundance | Total Acreage | Mean Acreage |
|---|---|---|---|
| Hard Maple | 16.10 | 27,169.4 | 5554.5 |
| White Birch | 15.17 | 26,527.6 | 541.4 |
| Poplar | 13.09 | 22,002.1 | 449.0 |
| Balsam Fir | 6.68 | 8,935.2 | 182.4 |
| White Pine | 5.89 | 8,857.2 | 180.8 |
| Black Spruce | 5.42 | 7.485.4 | 152.8 |
| Yellow Birch | 5.12 | 9,008.4 | 183.8 |
| White Spruce | 3.57 | 5,325.1 | 108.7 |
| Jack Pine | 3.06 | 4,349.1 | 88.8 |
| Soft Maple | 2.66 | 3,306.0 | 67.5 |
| Alder | 2.74 | 3,239.8 | 66.1 |
| Hemlock | 2.36 | 3,254.4 | 66.4 |
| Red Pine | 1.66 | 2,576.8 | 52.6 |
| Cedar | 1.54 | 2,172.4 | 44.3 |
| Mixed Hardwood | 1.51 | 1,884.0 | 38.4 |
| American Beech | 1.03 | 1,090.4 | 22.4 |
| Red Oak | .74 | 1,095.0 | 22.3 |
| Ash | .36 | 403.8 | 8.2 |
| Basswood | .32 | 430.6 | 8.8 |
| Elm | .29 | 450.4 | 9.2 |
| Ironwood | .26 | 314.5 | 6.4 |
| Black Cherry | .19 | 276.4 | 5.6 |
| Larch | .09 | 104.0 | 2.1 |

Table 3. North Bay Trapline Harvest and Stream Abundance

| Trapline No. | Total Harvest | Mean Harvest | Stream Density |
|---|---|---|---|
| 01 | 30 | 0.93 | 2.2 |
| 02 | 123 | 3.14 | 2.2 |
| 03 | 36 | 1.01 | 2.3 |
| 04 | 98 | 3.71 | 2.4 |
| 05 | 72 | 2.34 | 1.5 |
| 06 | 46 | 1.08 | 2.1 |
| 07 | 32 | 0.42 | 2.1 |
| 08 | 26 | 0.36 | 2.1 |
| 09 | 38 | 0.45 | 2.0 |
| 10 | 58 | 1.27 | 2.3 |
| 11 | 13 | 0.21 | 2.5 |
| 12 | 45 | 0.47 | 1.9 |
| 13 | 98 | 2.08 | 1.8 |
| 14 | 203 | 7.93 | 2.0 |
| 15 | 50 | 1.21 | 2.1 |
| 16 | 16 | 0.78 | 2.3 |
| 17 | 11 | 0.89 | 2.2 |
| 18 | 107 | 1.50 | 2.8 |
| 19 | 29 | 1.86 | 2.1 |
| 20 | 23 | 0.68 | 1.9 |
| 21 | 46 | 0.79 | 2.7 |
| 22 | 115 | 1.34 | 2.1 |
| 23 | 27 | 0.79 | 1.6 |
| 24 | 25 | 1.69 | 2.5 |
| 25 | 59 | 1.31 | 2.5 |
| 26 | 336 | 4.57 | 2.1 |
| 27 | 68 | 1.70 | 1.7 |
| 28 | 77 | 1.92 | 2.1 |
| 29 | 123 | 2.20 | 2.7 |
| 30 | 363 | 2.73 | 2.9 |
| 31 | 21 | 0.69 | 2.0 |
| 32 | 63 | 1.54 | 2.1 |
| 33 | 164 | 1.74 | 2.6 |
| 34 | 23 | 0.69 | 2.1 |
| 35 | 23 | 0.69 | 2.1 |
| 36 | 75 | 0.74 | 2.3 |
| 37 | 50 | 1.40 | 2.1 |
| 38 | 71 | 3.17 | 2.4 |
| 39 | 26 | 1.59 | 2.4 |
| 40 | 39 | 2.03 | 2.4 |
| 41 | 24 | 2.00 | 2.2 |
| 42 | 63 | 4.50 | 2.2 |
| 43 | 43 | 2.99 | 2.2 |
| 44 | 94 | 2.35 | 2.1 |
| 45 | 49 | 1.35 | 2.3 |
| 46 | 52 | 1.86 | 1.6 |
| 47 | 21 | 0.75 | 2.4 |
| 48 | 32 | 2.16 | 2.4 |
| 49 | 17 | 1.47 | 1.9 |

lodge density was regressed with each of the independent variables, represented by vegetation species, mean age of stand, harvest and stream density, it was found that the most statistically significant associations were between vegetation species and lodge density. Seven significant independent variables, representing dominant vegetation types, were found to have a positive association with lodge density. These were Poplar (Populus sp.), Elm (Ulmus, sp.), Oak (Quercus sp.), Ash (Fraxinus sp.), Balsam Fir (Abies sp.), Beech (Fagus sp.), and mixed hardwoods. Three independent variables were found to exhibit low to moderate inverse associations with lodge density, White Birch (Betula papyrifera), Yellow Birch (Betula lutea), and Cedar (Thuja occidentalis). Balsam Fir and White Cedar both showed low associations with beaver lodge density. The coefficient of determination, presented in Table 4, represents the amount of variation accounted for by each of the selected variables.

A multivariate regression analysis was undertaken to regress the dependent and independent variables. Twenty-four independent variables, representing vegetation species and stand age, were regressed with the dependent variable, lodge density. The multiple regression coefficient (b) was found to have a value of

Table 4. Statistically Significant Associations for Independent and Dependent Variables measured by the Bivariate Analysis.

| Variable | Coefficient of Correlation | Coefficient of Determination | Significance | Confidence Level |
|---|---|---|---|---|
| Poplar | .2341 | .0548 | .052 | 95% |
| Elm | .2034 | .0413 | .080 | 92% |
| Ash | .3049 | .0930 | .016 | 98% |
| Red Oak | .2087 | .0435 | .075 | 92% |
| Balsam | .2064 | .0426 | .077 | 92% |
| American Beech | .2065 | .0426 | .077 | 92% |
| Mixed Hardwood | .2687 | .0722 | .030 | 97% |
| White Birch | - .2981 | .0888 | .018 | 98% |
| Yellow Birch | - .2408 | .0579 | .048 | 95% |
| Cedar | - .1854 | .0344 | .100 | 90% |
| Harvest | .6261 | .3921 | .001 | 99% |

.08737 which indicates a high positive association between the independent and dependent variables. Furthermore, the value of the multiple regression coefficient of determination ($b^2$) was .65185, which indicated that more than 65% of the variation in lodge density was explained by the variation in vegetation species. This result was found to be significant at the 90% confidence level (F-1.87) and demonstrated a high degree of accuracy for the analysis.

A third statistical analysis was conducted on the data. This program, a step-wise multiple regression, was used to clearly define which of the vegetation species had the greatest influence on lodge density. A summary of the results obtained from the 24 steps involved in this program is presented in Table 5. It can be observed from this table that a majority of the variables in the analysis were found to be significant at the 99% confidence level. The final stages of the analysis were found to be significant at the 90% confidence level.

The results of the step-wise regression analysis were used to obtain an estimate of beaver lodge density based on the vegetation analysis of the North Bay District traplines. A summary of the data involved in this determination is presented in Table 6. A predicted value of 1.64 lodges per square mile was compared to the

Table 5. Statistical Significance between Independent and Dependent Variables Measured by Step-wise Regression Analysis.

| Variable | Correlation Coefficient | Coefficient of Determination | F Distribution | Confidence Level |
|---|---|---|---|---|
| Ash | .304 | .0930 | 4.82 | 95% |
| Mixed Hardwood | .422 | .1776 | 4.96 | 95% |
| Yellow Birch | .488 | .2386 | 4.70 | 99% |
| White Birch | .604 | .3649 | 6.32 | 99% |
| Elm | .645 | .4163 | 6.13 | 99% |
| Ironwood | .685 | .4693 | 6.19 | 99% |
| Red Oak | .704 | .4959 | 5.76 | 99% |
| American Beech | .716 | .5135 | 5.28 | 99% |
| Larch | .730 | .5332 | 5.33 | 99% |
| Soft Maple | .742 | .5506 | 4.65 | 99% |
| Bass Wood | .751 | .5640 | 4.35 | 99% |
| Red Pine | .757 | .5745 | 4.05 | 99% |
| Age of Stand | .760 | .5790 | 3.70 | 99% |
| Alder | .766 | .5880 | 3.47 | 99% |
| Black Cherry | .771 | .5948 | 3.23 | 99% |
| Hemlock | .778 | .6022 | 3.03 | 99% |
| Black Spruce | .799 | .6073 | 2.81 | 99% |
| Poplar | .782 | .6122 | 2.63 | 99% |
| Cedar | .785 | .6170 | 2.45 | 98% |
| White Spruce | .786 | .6188 | 2.27 | 98% |
| Balsam | .787 | .6198 | 2.09 | 95% |
| Jack Pine | .788 | .6213 | 1.94 | 90% |
| Hard Maple | .792 | .6266 | 1.82 | 90% |
| White Pine | .807 | .6518 | 1.87 | 90% |

Table 6. Regression Variables Used to Predict an Estimate of Lodge Density as a Function of Combined Vegetation Species

| Variable | Regression Value ($b_n$) | Abundance Percentage | Product ($b_n x_n$) |
|---|---|---|---|
| Hard Maple | -.0904 | 16.105 | -1.4558 |
| White Birch | -.1164 | 15.170 | -1.7657 |
| Poplar | -.0942 | 13.091 | -1.2331 |
| Elm | .5112 | 0.296 | .1513 |
| Ash | .0216 | 0.362 | .0078 |
| Soft Maple | -.1685 | 2.666 | -.4492 |
| Alder | -.0414 | 2.740 | -.1134 |
| Red Oak | -.0680 | 0.744 | -.0505 |
| Yellow Birch | -.2549 | 5.124 | -1.3056 |
| Basswood | -.2696 | 0.328 | -.0884 |
| Black Cherry | .0449 | 0.191 | .0084 |
| Balsam | -.0806 | 6.681 | -.5384 |
| White Spruce | -.1176 | 3.566 | -.4193 |
| Black Spruce | -.1023 | 5.423 | -.5547 |
| White Pine | -.0838 | 5.890 | -.4935 |
| Red Pine | -.1730 | 1.661 | -.2873 |
| Jack Pine | -.0917 | 3.060 | -.2806 |
| Cedar | -.1178 | 1.540 | -.1814 |
| Hemlock | -.0599 | 2.367 | -.1417 |
| American Beech | -.0864 | 1.030 | -.0889 |
| Larch | .1960 | 0.097 | .0190 |
| Mixed Hardwood | -.1045 | 1.514 | -.1582 |
| Ironwood | .4065 | 0.266 | .1081 |

Constant (A) = 10.959

Lodge Density (Y) = 1.64 lodges/square mile

observed mean lodge density of 1.52 lodges per square mile for the traplines. The percent deviation represented by these values was 8%.

The Chi-square distribution was calculated to compare the observed beaver lodge density with the predicted value obtained from the multiple regression equation. The Chi-square value obtained from this calculation, based on all 49 traplines, was 31.03 with 48 degrees of freedom. The percentage point distribution of the Chi-square values indicated that the predicted lodge density estimate represented the actual beaver lodge density at the 99% level of accuracy (Fisher and Yates, 1970). The observed and predicted values of beaver lodge density are presented in Table 7.

The regression equation developed to estimate beaver lodge density for the vegetation associations observed in the North Bay Trapping District was used to predict beaver lodge density for the pre-settlement period. The pre-settlement forest conditions which were involved in this determination were derived from the study of reconstructed forest types in the state of Michigan (Veatch, 1959). Based on the results of this pre-settlement vegetation study, three distinct categories were classified to represent the major vegetation types of the Upper Great Lakes Region. These communities were

Table 7. Predicted and Observed Lodge Density Values

| Trapline No. | Observed Density | Predicted Density |
|---|---|---|
| 1 | 1.6 | 1.67 |
| 2 | 1.3 | 1.76 |
| 3 | 2.1 | 1.99 |
| 4 | 2.2 | 2.08 |
| 5 | 1.7 | 1.64 |
| 6 | 0.9 | 1.06 |
| 7 | 0.2 | .80 |
| 8 | 0.8 | 0.91 |
| 9 | 0.8 | 4.01 |
| 10 | 1.0 | 1.59 |
| 11 | 0.7 | 0.95 |
| 12 | 0.4 | 0.72 |
| 13 | 3.1 | 2.73 |
| 14 | 3.6 | 2.43 |
| 15 | 1.7 | 1.06 |
| 16 | 0.8 | 0.43 |
| 17 | 1.1 | 1.70 |
| 18 | 0.7 | 1.55 |
| 19 | 0.8 | 0.66 |
| 20 | 0.5 | 1.01 |
| 21 | 0.8 | 0.96 |
| 22 | 0.5 | 0.02 |
| 23 | 1.2 | 1.46 |
| 24 | 0.5 | 1.83 |
| 25 | 1.7 | 6.58 |
| 26 | 1.6 | 1.42 |
| 27 | 2.0 | 2.14 |
| 28 | 1.8 | 1.48 |
| 29 | 1.2 | 0.58 |
| 30 | 2.1 | 1.74 |
| 31 | 0.8 | 1.88 |
| 32 | 3.4 | 2.73 |
| 33 | 0.5 | 0.54 |
| 34 | 0.6 | 0.69 |
| 35 | 0.5 | 1.02 |
| 36 | 0.8 | 1.24 |
| 37 | 0.5 | 0.76 |
| 38 | 3.4 | 1.42 |
| 39 | 1.6 | 1.04 |
| 40 | 1.0 | 0.80 |
| 41 | 2.0 | 2.15 |
| 42 | 4.0 | 3.49 |
| 43 | 3.1 | 3.29 |
| 44 | 2.1 | 2.20 |
| 45 | 2.6 | 2.44 |
| 46 | 2.1 | 1.79 |
| 47 | 2.2 | 2.45 |
| 48 | 1.5 | 1.13 |
| 49 | 2.4 | 2.39 |

described as: 1) dominant deciduous for those vegetation associations where the dominant vegetation species were broadleaved trees, 2) dominant coniferous for those vegetation associations where the dominant vegetation species were evergreen, and 3) mixed coniferous-deciduous for those vegetation associations where evergreen and broadleaved species were equally represented.

Correlation coefficients and mean abundance values were obtained from the multiple regression analysis and trapline data of the North Bay District to calculate beaver lodge density based on the species composition of pre-settlement Upper Great Lakes forests. Using the prediction equation, it was determined that beaver lodge density in dominant deciduous vegetation associations was 1.45 lodges per square mile. The data for this association were collected in Table 8. Dominant coniferous vegetation association data are summarized in Table 9. The prediction equation for this association was used to arrive at an estimate of .84 beaver lodges per square mile for the density of lodges in coniferous vegetation associations. Mixed coniferous-deciduous vegetation associations were estimated to support 1.95 beaver lodges per square mile. The data used for this category of vegetation are summarized in Table 10.

Table 8. Regression Variables Used to Estimate Lodge Density as a Function of Dominant-Deciduous Vegetation Species.

| Variable | Regression Value ($b_n$) | Abundance Value($x_n$) | Product ($b_n x_n$) |
|---|---|---|---|
| White Birch | -.1164 | 9.53 | -1.1092 |
| Hard Maple | -.0904 | 34.32 | -3.1025 |
| Poplar | -.0942 | 4.56 | -0.4295 |
| Yellow Birch | -.2549 | 11.87 | -3.0256 |
| Ash | .0216 | 2.48 | 0.0535 |
| White Pine | -.0838 | 4.46 | -0.3737 |
| Hemlock | .0599 | 3.34 | 0.2000 |
| American Beech | -.0864 | 5.49 | -0.4743 |
| Elm | .5112 | 3.48 | 1.7789 |
| Balsam | -.0806 | 3.02 | -0.2434 |
| Spruce White | -.1176 | 2.62 | -0.3081 |
| Red Oak | -.0680 | 3.29 | -0.2237 |
| Cedar | -.1178 | 1.90 | -0.2238 |
| Soft Maple | -.1685 | 5.62 | -0.9469 |
| Basswood | -.2696 | 4.02 | -1.0837 |

Constant (A) = 10.959

Lodge Density (Y) = 1.45 lodges/square mile

Table 9. Regression Variables Used to Estimate Lodge Density as a Function of Dominant-Coniferous Vegetation Species.

| Variable | Regression Value ($b_n$) | Abundance Value ($x_n$) | Product ($b_n x_n$) |
|---|---|---|---|
| White Pine | -.1164 | 13.50 | -1.5714 |
| Black Spruce | -.1023 | 12.16 | -1.2439 |
| White Spruce | -.1176 | 6.40 | -0.7526 |
| Balsam | -.0806 | 8.51 | -0.6859 |
| Jack Pine | -.0917 | 6.78 | -0.6217 |
| Hemlock | -.0599 | 7.25 | 0.4342 |
| Cedar | -.1178 | 6.45 | -0.7598 |
| Larch | .1960 | 4.51 | 0.6879 |
| Red Pine | -.1730 | 9.07 | -1.5691 |
| Poplar | -.0942 | 1.55 | -0.1460 |
| Alder | -.0414 | 3.81 | -0.1577 |
| Mixed Hardwood | -.1045 | 3.48 | -0.3636 |
| White Birch | -.1164 | 3.09 | -0.3596 |
| Basswood | -.2696 | 2.45 | -0.6605 |
| Elm | -.5112 | 2.78 | -1.4211 |
| Ash | .0216 | 3.41 | 0.0736 |
| Soft Maple | -.1685 | 2.56 | -0.4313 |
| Yellow Birch | -.2549 | 2.24 | -0.5709 |

Constant (A) = 10.959

Lodge Density (Y) = 0.84 lodges/square mile

Table 10. Regression Variables Used to Estimate Lodge Density as a Function of Mixed Coniferous-Deciduous Vegetation Species.

| Variable | Regression Value ($b_n$) | Abundance Value ($x_n$) | Product ($b_n x_n$) |
|---|---|---|---|
| Hard Maple | -.0904 | 9.67 | -0.8741 |
| Soft Maple | -.1685 | 4.48 | -0.7548 |
| Poplar | -.0942 | 4.45 | -0.4191 |
| Mixed Hardwood | -.1045 | 3.90 | -0.4075 |
| White Pine | -.0838 | 8.85 | -0.7416 |
| Black Spruce | -.1023 | 10.95 | -1.1201 |
| Jack Pine | -.0917 | 3.76 | -0.3447 |
| Hemlock | .0599 | 2.97 | 0.1779 |
| Red Pine | -.1730 | 4.89 | -0.8459 |
| Cedar | -.1178 | 8.02 | -0.9447 |
| Balsam | -.0806 | 10.13 | -0.8164 |
| Elm | .5112 | 2.84 | 1.4518 |
| Larch | .1960 | 1.90 | 0.3724 |
| Basswood | -.2696 | 5.02 | -1.3533 |
| Ash | .0216 | 2.61 | 0.0563 |
| White Birch | -.1164 | 4.35 | -0.5063 |
| Yellow Birch | -.2549 | 6.92 | -1.7639 |
| Alder | -.0414 | 4.29 | -0.1776 |

Constant (A) = 10.959

Lodge Density (y) = 1.95 lodges/square mile

To apply the results of the above calculations to historic beaver lodge density it was necessary to determine the extent of forest cover for the Great Lakes drainage basin. The Upper Peninsula of Michigan was used to estimate the area represented by each of the forest classifications identified in this study. The total area of the Upper Peninsula of Michigan was found to be 16,500 square miles; however, the forested regions of this area are represented by 15,851 square miles when coastal and other unforested regions are eliminated (Winters, 1976; Veatch, 1959). Based upon Veatch's (1959) vegetation reconstruction, the ration of the area represented by each of the vegetation classifications examined in this study was determined. It was found that dominant deciduous vegetation represented 6379 square miles, dominant coniferous vegetation 6960 square miles, and mixed coniferous-deciduous 2512 square miles, in the Upper Peninsula of Michigan.

The total drainage area for the Upper Great Lakes Region was determined to be 288,770 square miles with approximately 12,000 square miles of coastal and unforested area (Hilborn and Fawcett, 1972). The total forested area of the region when these areas were taken into consideration was 276,770 square miles. The area represented by the identified vegetation classifications in the Upper Great Lakes Region based on the ratio established for the upper peninsula are as follows: dominant deciduous 111,382 square miles, dominant coniferous 121,527 square miles, and mixed coniferous-deciduous 43,861 square miles. Using the values for beaver lodge density arrived at through the previous analysis, the total number of beaver lodges which could have occurred in these vegetation associations during the pre-settlement period were: 1) dominant deciduous: 161,504 lodges 2) dominant coniferous: 102,083 lodges 3) mixed coniferous-deciduous: 185,528 lodges or an estimated total equal to 349,115 lodges for the Great Lakes drainage basin.

Novak (1977) concluded that an estimate of 5.42 individuals per colony accurately represented the number of beaver present in lodges in north central Ontario. Using the expected value for beaver lodge density in the Upper Great Lakes Region and Novak's (1977) density of beaver per lodge, it was possible to calculate an estimate for the number of beaver which were present in the drainage areas of the Upper Great Lakes Region. The estimate was determined to be 1,892,203 beaver in the region during the pre-settlement period, ca. 1600.

# DISCUSSION

The purpose of this study was to develop a reliable method to estimate pre-settlement beaver population density. To accomplish this objective, it was necessary to isolate a set of ecological factors which could be incorporated into an index of beaver density for contemporary and historic environmental conditions. Numerous studies have demonstrated the ecological relationship between beaver colonies and environmental parameters such as stream flow, valley width and gradient, soil conditions and vegetation associations (Gill, 1972; Novakowski, 1967; Retzer, 1955; Brandt, 1947). However, to date there has not been an attempt to correlate beaver population density with specific environmental conditions so as to predict beaver population density based on these conditions.

Essentially the problem was to study the relationship between an extinct animal and the physical and biotic environments which influenced the population dynamics of the species. For this assessment it was imperative that the ecological conditions prevalent before the extirpation of the species be established.

This information was obtained from habitat reconstructions which were based on contemporary ecological associations and other data relevant to the biological requirements of the beaver in the Upper Great Lakes Region.

Reconstruction of the paleoecology of ancient forms by reference to the ecology of recent representatives has been shown to be an accurate method of reconstructing the historic environment conditions with which extinct fauna and flora were associated. This has been especially true in studies of recent and ancient taxa not widely separated in time (Laporte, 1977; McAlester, 1968).

Ecological reconstructions of postglacial environmental conditions have been attempted using a variety of techniques (McAlester, 1968). Vegetation associations have been successfully reconstructed for the Upper Great Lakes Region using pollen analysis of bogs and other sedimentary sources and studies of Bryophyte (Diatome) distribution in Michigan (Farrand and Eschman, 1974; Dillon, 1956). Potter (1947) analyzed the pollen content of postglacial bogs in the Southern Great Lakes Region and found a sequence of dominant tree genera which examined include _Picea_, _Abies_, _Pinus_, _Betula_, _Quercus_, _Tsuga_, _Carya_, and _Fagus_. Specific forest cover types have been reconstructed for the State of Michigan based on soil mapping and subsequent correlations with the known ecological relationships between plant species and soil conditions (Veatch, 1959). This study established that correlations could be obtained between soil type and vegetational units, and demonstrated the utility of such information in the establishment of historic ecological relationships.

The ecological requirements of wildlife species are usually associated with biotic rather than abiotic factors and ecological reconstruction of faunal associations present complex problems which cannot always be resolved due to the large set of unknown factors influencing the population (Laporte, 1977). However, the ecological requirements of beaver represent an important exception to this general rule in that the presence of beaver colonies has been shown to be correlated with specific ecological conditions because of the dietary selectivity of the species and the physical limitations of beaver dam and lodge site construction (Hay, 1958; Retzer, 1955; Ives, 1942; Brandt, 1938).

The ecological requirements for continuous beaver occupancy, has been considered to be more restricted than for many other wildlife species (Gill, 1972; Smith, 1950). The specific habitat characteristics which have been shown to limit the presence of beaver colonies can be segregated into two distinct categories: 1) vegetation suitability for dietary and construction purposes and 2) geomorphology of terrain and stream availability.

Vegetation associations required for successful beaver occupancy were found to be an essential factor association with the presence or absence of beaver colonies throughout the animal's range. The presence of specific vegetation species were found to be essential to meet the nutritional requirements of the animal and provide suitable construction materials for lodges and dams (Novakowski, 1967; Hall, 1960). Beaver food utilization studies have consistently demonstrated that various species of the genus *Populus* (Cottonwood, Aspen, Poplar, etc.) constitute an extensively utilized dietary component whenever it is available in the environment (Novakowski, 1967; Hammond, 1943). Other woody vegetation found by Nixon and Ely (1969) to be of major importance in the beaver diet were Common Alder (*Alnus serrulata*), Buttonbush (*Cephalanthus occidentalis*), Red Elm (*Ulmus rubra*), Maple (*Acer rubrum*, *A. saccharinum*), and Ash (*Fraxinus americana*, *F. pennsylvanica*). Hall (1960) found that Willow (*Salix spp.*) and Quaking Aspen (*Populus tremuloides*) constituted important forage species for beaver while some evidence for the use of coniferous species was also indicated.

Herbaceous vegetation has been shown to be important in the summer and fall diet (Northcott, 1972; Nixon and Ely, 1969; Aldous, 1938). Nixon and Ely (1969) found that herbaceous species in the beaver diet include Water Lillies (Nuphar variegatum, N. microphyllum), Queen-of-the-Meadow (Filipendula ulmaria), and grasses (Gramineae). Under normal summer conditions, beaver feed on grasses, forbs, and aquatic plants whenever possible and consume woody plants during this season only when the former are unavailable (Brenner, 1967; Rutherford, 1964; Brandt, 1938). However, woody plants constitute the bulk of the winter diet and were considered to be an important limiting factor throughout the animal's distribution in northern latitudes (Novakowski, 1967).

The geomorphology of terrain and stream availability have also been found to influence the site suitability for beaver dam construction and lodge occupancy. Retzer (1955) studied the physical environmental effects of beavers in the Colorado Rockies and determined that beaver occupancy was dependent upon valley grade, valley width and bedrock geology. It was concluded that valleys with less than six percent grade were most suitable for successful beaver occupancy. Streams which had a greater than 11% grade were considered questionable to unsuitable for permanent occupancy by beaver (Retzer, 1955). Other ecological studies have not shown stream gradient to be of major importance for the establishment of beaver colonies in northern latitudes and mountainous areas (Hay, 1958; Smith, 1950). Beaver dam construction appeared to have no correlation with either stream gradient or stream flow according to Smith (1950). All new and rebuilt dams observed in Smith's study were constructed on streams with less than 4.0% slope. Based on the data collected by Hay (1958), it was evident that no significant relationship existed between stream gradient, width of floodplain and beaver colony density. Hay concluded that further study of the role of physical environmental features on beaver populations has no direct utility other than the possible effect on the type and amount of food available.

Beaver populations have been shown to demonstrate a positive association with the type of vegetation available in the environment. In northern habitats, such as in the Upper Great Lakes Region where topographic relief is not extreme, they may represent the most important limiting factor for beaver site selection (Gill, 1972; Smith, 1950; Brandt, 1947). A statistical correlation between beaver lodge density and specific habitat characteristics which influence beaver site selection and occupancy was completed in the present study based on vegetation profiles developed from North Bay, Ontario, traplines records.

The initial bivariate regression analysis of the trapline data resulted in a significant correlation between lodge density and ten dominant vegetation types. A majority of these species demonstrated a high positive correlation with lodge density and were also found to be associated with beaver diet. The remaining species demonstrated a significant negative correlation with lodge density. Two of these were hardwood species, White and Yellow Birch, which are generally associated with beaver habitat but occur predominantly on upland sites and are therefore not directly important to beaver as resources for food or construction materials. The harvest of beaver was found to have a statistically significant association with lodge density. This appears to be an indication of a direct and positive relationship between lodge density and trapping success; as lodge density increased, there was a corresponding increase in trapping success. These data however, did not involve an expression of the effort associated with a given harvest statistic and was therefore not a measure of actual harvest intensity.

The bivariate analysis provided a preliminary description of the association between each of the independent variables and the dependent variable, lodge density. The coefficient of determination represented the amount of variation accounted for by each of the selected variables considered independently. The explained variation expressed by this statistic ranged from 9.30% for White Ash (*Fraxinus americana*) to 4.13% for American Elm (*Ulmus americana*). A large degree of variation remained unexplained when only the bivariate analysis technique was used.

A second analysis was used to further clarify the variation in lodge density and the dominant vegetation species. The multivariate regression analysis was chosen to regress lodge density with habitat characteristics. This technique provided a method to quantify the contribution of the set of independent variables to the dependent variable. The effect of the combined set of vegetation species on lodge density was found to be significant at the 90% level of confidence indicating a high degree of accuracy. It was considered that the remaining variation not accounted for with this analysis could possibly be further clarified if all of the ecological determinants of lodge density could be introduced into the analysis. The data required for such an analysis however, were not available for this study.

A third statistical approach was undertaken to determine which combinations of vegetation species have the greatest influence on the dependent variable. The step-wise multiple regression analysis was employed for this determination because it was designed specifically to estimate the contribution of each independent variable toward explaining the variation of the dependent variable. The application of this regression technique provided a hierarchical list of vegetation combinations which have varying degrees of association with lodge density. The program illustrated that many of the negatively associated independent variables encountered during the bivariate analysis were of importance, and could be used to more clearly explain the variation in lodge density. A number of inverse relationships were found to be important for this purpose. For example, Yellow and White Birch were found to have a negative association with lodge density in the bivariate analysis; however, both species were ranked in the first five variables selected for analysis by the step-wise program. This ranking was directly related to the contribution of the variable to the explained variance and thus indicated the usefulness of these variables in accounting for the variation in the dependent variable. Independent variables positively associated with lodge density according to the bivariate analysis was a major component of the variables selected in the first ten steps of the step-wise program. Ash, Mixed Hardwood, American Elm, Red Oak and American Beech were found to contribute most significantly to an explanation for the variation of the dependent variable.

The value of the step-wise analysis was that the influence of any vegetation species on lodge density was identified in the hierarchical list of vegetation combinations generated from step 1 to step 24. Thus each vegetation species was examined independently to determine the influence it exerted on lodge density. The ability to isolate each vegetation species became increasingly important when lodge density was predicted as a function of specific vegetation associations.

The strongest association and greatest amount of explained variation, as measured by the correlation coefficient and coefficient of determination, were obtained from the step-wise multiple regression program. The data derived from this regression analysis were used to predict lodge density by substituting into the appropriate regression equation. The mean abundance values and corresponding regression coefficients for the 23 independent variables representing vegetation species were regressed to determine a predicted value for lodge density using these vegetation parameters (see Table 6). When the predicted and observed lodge density values were compared using the Chi-square test for dispersion it was concluded that the predicted value for lodge density was sufficiently close to the actual value observed to demonstrate the accuracy of the prediction techniques and extend the analysis.

The determination of an accurate method to estimate beaver population density has been the object of numerous investigations (Novak, 1977; Aleksiuk, 1968; Hay, 1955; Brandt, 1947). As early as 1868, Morgan arrived at an estimate of beaver density in the Lake Superior Region which indicated 7.0 beaver per colony. More recent studies of beaver population densities in the Great Lakes Region have shown this value to be an overestimate. Brandt (1947) using lodge counts in the state of Michigan determined the average colony size to be 5.1 beaver per lodge. Beaver population density for Ontario beaver colonies was examined by Novak (1977). The average beaver per colony based on the results of his investigation was shown to be 5.4 individuals per lodge when factors such as age and year class ratios were considered.

The use of beaver lodges as an index of beaver population density can not be regarded as a reliable estimate of population density without giving consideration to the wide variety of variables concerning colony size and the distribution of adult beaver within the territory of a colony (Smith, 1950; Warren, 1932; Aleksiuk, 1968). In the Upper Great Lakes Region, many colonies have individuals which do not utilize lodges and live in bank burrows exclusively (Brandt, 1938). Other animals utilize more than one lodge and often occupy bank burrows as well (Hay, 1958). Brandt (1947) conducted an extensive examination of beaver colonies in Michigan and concluded that a reasonable method for estimating beaver population density would utilize an October or November census of all lodges which could be positively associated with beaver activity. Brandt stated that if census were taken during the fall season, estimates would be substantially correct. As stated earlier, Novak (1977) developed a method to determine the number of individuals per colony using lodge counts in the Upper Great Lakes Region. This estimate may be considered high, under some conditions. However, an inflated estimate would be offset by individuals living in bank dens and omitted in the lodge census.

# CONCLUSION

The results of this investigation have demonstrated a reliable method to quantitatively assess the population density of beaver (Castor canadensis Kuhl) in the Upper Great Lakes Region during the pre-settlement period prior to the fur trade, ca. 1600. The methodology developed in this study involved the use of regression analysis techniques to demonstrate the relationship between beaver lodge density and specific habitat characteristics. This correlation was extended to reconstructed vegetation associations during the historic period to estimate the historic population density of beaver during this period.

Historic beaver population density in the Upper Great Lakes Region was estimated based on the contemporary correlation between beaver abundance and habitat associations combined with historic vegetation reconstructions. Contemporary beaver populations were surveyed to collect precise lodge density and habitat data. Beaver lodge density counts were obtained from active traplines where the dominant tree species abundance was known. These data were correlated using bivariate analysis to characterize the relationship between lodge density and habitat associations. The predictive value of this correlation was established based on a step-wise multiple regression program for each of 23 tree species examined. Reconstructions of historic vegetation associations for the Upper Great Lakes Region were than used to describe pre-settlement forest conditions in the Great Lakes watershed. The vegetation reconstructions were entered into the multiple regression program to arrive at the estimated beaver lodge density. The actual population density estimate was calculated on the basis of the number of individuals known to occur in active lodges in the Great Lakes Region.

It was determined that approximately two million beaver represented a reasonably accurate assessment of beaver density in the drainage area of the Great Lakes during the pre-European settlement period, ca. 1600.

The statistical analysis used to correlate beaver lodge density with vegetation species indicated that deciduous trees such as Ash (Fraxinus sp.), Poplar (Populus sp.), Oak (Quercus sp.), Beech (Fagus sp.), Elm (Ulmus sp.), and other mixed hardwoods were important indicators for predicting lodge density. Coniferous trees, for example, Balsam (Abies balsamea) and Cedar (Thuja occidentalis), were also correlated with suitable sites for beaver occupancy, but to a lesser extent than broadleaved trees. Other ecological factors relating to beaver habitat characteristics such as stream availability and topographic relief did not exhibit high correlations with lodge density due to the relative homogeneity of these conditions in the Upper Great Lakes Region.

Based on the results of this study, it can be shown that some of the important ecological relationships between wildlife species and their environmental conditions can be examined systematically in situations where the species in question are no longer living. This method of study has potential utility for examining the biological relationships among species in the past by combining present knowledge of ecological interactions with reconstructions of historic and pre-historic habitat conditions.

The utility of examining beaver population density in an historic context has important implications for historians, sociologists and anthropologists concerned with the dynamics of the fur trade in the Upper Great Lakes Region and other areas of North America where the fur trade was an important factor in the exploration and settlement of the continent. Previous studies of the fur trade and interactions between fur companies and Native people have been limited to data based on fur company returns and harvest statistics. Fur trade interactions and competition were dependent in many cases on the abundance and distribution of beaver; however, at the present time there exists a paucity of data relating to this important factor in the development and expansion of the trade throughout the beaver's range. This study has shown that it is possible to systematically examine the population density of extinct beaver populations and provide a technique to further develop our understanding of the complexities of the early history and development of North America.

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APPENDICES

# APPENDIX A

Table A1. Vegetation Data for Trapline #1

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| White Birch | 32.18 | 1171.0 |
| Balsam Fir | 15.80 | 575.0 |
| White Pine | 13.37 | 484.0 |
| Poplar | 8.62 | 313.8 |
| White Spruce | 8.26 | 300.8 |
| Hard Maple | 6.32 | 230.4 |
| Black Spruce | 6.26 | 228.0 |
| White Cedar | 3.08 | 112.2 |
| Red Pine | 2.83 | 103.2 |
| Jack Pine | 1.64 | 60.0 |
| Soft Maple | 1.29 | 47.0 |
| Elm | 0.23 | 8.4 |
| Ash | 0.12 | 4.2 |

Table A2. Vegetation Data for Trapline #2

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| White Birch | 25.14 | 544.0 |
| Poplar | 20.75 | 659.0 |
| White Pine | 9.57 | 250.8 |
| Black Spruce | 8.23 | 215.6 |
| Hard Maple | 7.41 | 189.0 |
| Balsam Fir | 7.02 | 184.8 |
| Soft Maple | 6.63 | 174.0 |
| White Spruce | 5.53 | 145.8 |
| Red Oak | 5.53 | 145.2 |
| Alder | 3.62 | 95.0 |
| Jack Pine | 0.68 | 16.0 |
| Red Pine | 0.06 | 1.8 |

Table A3. Vegetation Data for Trapline #3

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Jack Pine | 40.67 | 1719.0 |
| White Birch | 21.89 | 921.0 |
| Black Spruce | 15.64 | 658.3 |
| Poplar | 8.58 | 361.0 |
| White Pine | 5.81 | 246.6 |
| Mixed Hardwood | 2.26 | 95.0 |
| Balsam Fir | 2.05 | 86.2 |
| Alder | 1.21 | 51.0 |
| Red Pine | 0.85 | 35.6 |
| Red Oak | 0.77 | 32.2 |

Table A4. Vegetation Data for Trapline #4

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| White Birch | 35.80 | 988.0 |
| Poplar | 29.04 | 801.4 |
| Black Spruce | 14.16 | 390.8 |
| Jack Pine | 7.66 | 211.4 |
| Red Pine | 3.35 | 92.8 |
| White Pine | 2.49 | 68.6 |
| Alder | 2.36 | 65.0 |
| Balsam Fir | 2.29 | 63.2 |
| Hard Maple | 1.95 | 54.0 |
| White Spruce | 0.72 | 19.8 |
| Larch | 0.18 | 5.0 |

Table A5. Vegetation Data for Trapline #5

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| White Birch | 25.38 | 706.4 |
| White Pine | 23.92 | 665.7 |
| White Cedar | 16.67 | 463.8 |
| Balsam Fir | 16.39 | 456.3 |
| Black Spruce | 5.17 | 143.8 |
| White Spruce | 4.07 | 113.3 |
| Red Pine | 2.85 | 79.3 |
| Soft Maple | 2.07 | 57.6 |
| Yellow Birch | 2.00 | 55.7 |
| Poplar | 0.76 | 21.1 |
| Alder | 0.72 | 20.0 |

Table A6. Vegetation Data for Trapline #6

| Species | Percentage Abundance | Total Acreage |
| --- | --- | --- |
| White Birch | 48.40 | 1789.4 |
| Poplar | 19.43 | 718.2 |
| Hard Maple | 7.41 | 274.0 |
| Balsam Fir | 5.32 | 196.6 |
| Soft Maple | 4.51 | 166.4 |
| Black Spruce | 4.25 | 157.2 |
| White Pine | 3.77 | 139.6 |
| White Spruce | 3.72 | 137.6 |
| White Cedar | 1.56 | 57.8 |
| Red Oak | 0.82 | 30.2 |
| Alder | 0.68 | 25.0 |
| Ash | 0.14 | 4.8 |

Table A7. Vegetation Data for Trapline #7

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Poplar | 28.13 | 458.0 |
| White Birch | 27.70 | 451.0 |
| Jack Pine | 16.50 | 268.6 |
| White Spruce | 7.29 | 118.8 |
| Yellow Birch | 5.46 | 88.6 |
| White Pine | 5.43 | 88.4 |
| Hard Maple | 3.26 | 53.2 |
| Balsam Fir | 2.90 | 47.2 |
| Black Spruce | 1.71 | 27.8 |
| Red Pine | 1.62 | 26.4 |

Table A8. Vegetation Data for Trapline #8

| Species | Percentage Abundance | Total Acreage |
| --- | --- | --- |
| White Birch | 54.50 | 844.8 |
| Poplar | 23.86 | 369.8 |
| White Pine | 9.15 | 141.8 |
| White Spruce | 4.01 | 62.2 |
| Jack Pine | 3.15 | 48.8 |
| Red Pine | 3.07 | 47.6 |
| Balsam Fir | 1.61 | 25.0 |
| Soft Maple | 0.48 | 7.4 |
| Hard Maple | 0.17 | 2.6 |

Table A9. Vegetation Data for Trapline #9

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Jack Pine | 33.69 | 855.0 |
| Poplar | 30.76 | 780.8 |
| White Birch | 22.34 | 566.9 |
| Red Pine | 4.09 | 103.8 |
| Black Spruce | 3.38 | 85.8 |
| White Pine | 1.98 | 50.4 |
| Soft Maple | 1.78 | 45.3 |
| Hard Maple | 1.48 | 37.2 |
| White Spruce | 0.50 | 12.8 |

Table A10. Vegetation Data for Trapline #10

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Black Spruce | 26.65 | 827.9 |
| Balsam Fir | 24.15 | 750.4 |
| White Pine | 15.56 | 483.6 |
| Red Pine | 12.19 | 378.8 |
| White Spruce | 7.94 | 246.8 |
| White Birch | 7.73 | 240.2 |
| White Cedar | 2.56 | 79.4 |
| Alder | 1.13 | 35.0 |
| Mixed Hardwood | 0.97 | 30.0 |
| Soft Maple | 0.49 | 15.2 |
| Poplar | 0.44 | 13.7 |
| Ash | 0.19 | 6.0 |

Table All. Vegetation Data for Trapline #11

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| White Birch | 37.56 | 871.1 |
| Poplar | 27.83 | 645.6 |
| Jack Pine | 7.33 | 170.0 |
| Red Pine | 5.23 | 121.2 |
| White Spruce | 4.50 | 104.4 |
| Black Spruce | 3.58 | 83.0 |
| Soft Maple | 3.12 | 72.4 |
| Hard Maple | 2.90 | 67.2 |
| Balsam Fir | 2.41 | 56.0 |
| White Pine | 2.17 | 50.4 |
| Alder | 2.16 | 50.0 |
| Yellow Birch | 0.81 | 18.8 |
| White Cedar | 0.41 | 9.4 |

Table A12. Vegetation Data for Trapline #12

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| White Birch | 31.29 | 811.2 |
| Poplar | 24.17 | 627.0 |
| Hard Maple | 17.33 | 449.6 |
| White Cedar | 7.50 | 194.6 |
| Yellow Birch | 6.92 | 179.6 |
| White Spruce | 5.02 | 130.2 |
| Black Spruce | 3.30 | 85.8 |
| Balsam Fir | 2.55 | 66.2 |
| White Pine | 0.99 | 25.6 |
| Soft Maple | 0.93 | 24.2 |

Table A13. Vegetation Data for Trapline #13

| Species | Percentage Abundance | Total Acreage |
| --- | --- | --- |
| Poplar | 29.28 | 717.1 |
| Jack Pine | 16.46 | 403.1 |
| White Birch | 15.89 | 389.2 |
| Black Spruce | 12.23 | 299.6 |
| Balsam Fir | 9.65 | 236.3 |
| Alder | 6.45 | 158.0 |
| White Spruce | 4.59 | 112.3 |
| White Pine | 2.85 | 69.8 |
| Larch | 0.85 | 21.6 |
| Red Oak | 0.78 | 19.0 |
| White Cedar | 0.74 | 18.2 |
| Red Pine | 0.20 | 4.8 |

Table A14. Vegetation Data for Trapline #14

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Poplar | 26.00 | 496.0 |
| Balsam Fir | 15.97 | 304.8 |
| White Birch | 13.16 | 251.0 |
| Alder | 13.10 | 250.0 |
| White Spruce | 12.69 | 242.2 |
| Black Spruce | 10.50 | 200.4 |
| Jack Pine | 2.80 | 53.4 |
| Mixed Hardwood | 2.63 | 50.0 |
| White Pine | 1.99 | 38.0 |
| Soft Maple | 0.70 | 13.4 |
| Red Pine | 0.46 | 8.8 |

Table A15. Vegetation Data for Trapline #15

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| White Birch | 37.21 | 968.2 |
| Black Spruce | 32.86 | 854.8 |
| Hard Maple | 8.31 | 216.2 |
| Balsam Fir | 6.23 | 162.2 |
| Soft Maple | 4.81 | 125.2 |
| Poplar | 3.81 | 99.2 |
| Alder | 1.92 | 50.0 |
| White Pine | 1.62 | 42.2 |
| Yellow Birch | 1.58 | 41.2 |
| White Cedar | 1.23 | 31.4 |
| White Spruce | 0.42 | 11.0 |

Table A16. Vegetation Data for Trapline #16

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 39.58 | 1086.8 |
| White Birch | 17.07 | 468.6 |
| Yellow Birch | 12.06 | 331.0 |
| Black Spruce | 8.77 | 240.0 |
| Poplar | 7.93 | 217.8 |
| Mixed Hardwood | 5.46 | 150.0 |
| White Cedar | 2.95 | 81.0 |
| White Spruce | 2.60 | 71.4 |
| White Pine | 1.32 | 36.2 |
| Soft Maple | 0.98 | 26.8 |
| Balsam Fir | 0.89 | 24.4 |
| Hemlock | 0.39 | 10.8 |

Table A17. Vegetation Data for Trapline #17

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| White Birch | 26.62 | 656.0 |
| Hard Maple | 19.27 | 474.8 |
| Black Spruce | 16.60 | 409.1 |
| White Spruce | 8.67 | 213.5 |
| Poplar | 7.13 | 175.8 |
| Alder | 5.07 | 125.0 |
| Yellow Birch | 4.71 | 116.0 |
| Mixed Hardwood | 4.22 | 104.0 |
| Soft Maple | 2.40 | 59.2 |
| Hemlock | 2.06 | 50.8 |
| Balsam Fir | 1.59 | 39.0 |
| White Spruce | 1.18 | 29.2 |
| White Cedar | 0.48 | 12.0 |

Table A18. Vegetation Data for Trapline #18

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| White Birch | 37.19 | 1380.2 |
| Poplar | 26.40 | 930.0 |
| Hard Maple | 16.61 | 584.8 |
| Yellow Birch | 4.29 | 151.2 |
| White Spruce | 3.94 | 138.8 |
| Balsam Fir | 1.98 | 69.8 |
| Ironwood | 1.30 | 45.8 |
| Hemlock | 1.25 | 42.8 |
| Black Spruce | 1.11 | 39.2 |
| White Cedar | 1.08 | 38.2 |
| Soft Maple | 0.98 | 34.6 |
| Mixed Hardwood | 0.71 | 25.0 |
| Red Oak | 0.68 | 24.0 |
| White Pine | 0.48 | 16.8 |

Table A19. Vegetation Data for Trapline #19

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 39.59 | 982.6 |
| Soft Maple | 16.15 | 400.4 |
| White Birch | 16.08 | 399.2 |
| Black Spruce | 11.27 | 279.8 |
| Alder | 5.03 | 125.0 |
| Yellow Birch | 4.31 | 107.0 |
| Poplar | 4.16 | 103.2 |
| White Spruce | 1.94 | 48.2 |
| Jack Pine | 1.47 | 36.6 |

Table A20. Vegetation Data for Trapline #20

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 53.09 | 1291.8 |
| Yellow Birch | 17.93 | 436.2 |
| Alder | 8.22 | 200.0 |
| Poplar | 7.21 | 175.4 |
| White Birch | 4.19 | 102.0 |
| Black Spruce | 2.33 | 56.8 |
| White Cedar | 1.66 | 40.4 |
| Red Oak | 1.18 | 28.4 |
| Ironwood | 1.17 | 28.4 |
| Hemlock | 1.17 | 28.4 |
| White Spruce | 0.83 | 20.2 |
| Soft Maple | 0.51 | 12.4 |
| Balsam Fir | 0.51 | 12.4 |

Table A21. Vegetation Data for Trapline #21

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 43.94 | 891.2 |
| Yellow Birch | 20.12 | 408.0 |
| Black Spruce | 7.89 | 160.0 |
| Balsam Fir | 5.61 | 113.8 |
| Hemlock | 4.80 | 97.4 |
| White Cedar | 3.53 | 71.6 |
| White Birch | 3.32 | 67.4 |
| Alder | 2.96 | 60.0 |
| Larch | 2.96 | 60.0 |
| Mixed Hardwood | 1.97 | 40.0 |
| White Spruce | 1.50 | 30.4 |
| Red Oak | 0.73 | 14.8 |
| Black Cherry | 0.67 | 13.6 |

Table A22. Vegetation Data for Trapline #22

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 29.66 | 784.2 |
| Yellow Birch | 23.68 | 626.0 |
| White Cedar | 10.98 | 290.4 |
| Black Spruce | 7.74 | 204.6 |
| Hemlock | 6.32 | 167.0 |
| White Pine | 5.08 | 134.4 |
| Balsam Fir | 4.93 | 130.4 |
| White Spruce | 3.94 | 104.2 |
| White Birch | 3.51 | 92.8 |
| Soft Maple | 1.47 | 38.8 |
| Ironwood | 1.36 | 36.0 |
| Mixed Hardwood | 0.76 | 20.0 |
| American Beech | 0.57 | 15.2 |

Table A23. Vegetation Data for Trapline #23

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Poplar | 37.45 | 669.8 |
| Balsam Fir | 25.65 | 458.8 |
| Alder | 15.10 | 270.0 |
| White Birch | 14.63 | 261.6 |
| Soft Maple | 2.35 | 42.0 |
| Mixed Hardwood | 1.40 | 25.0 |
| Black Spruce | 1.08 | 19.4 |
| White Spruce | 0.86 | 15.4 |
| Ash | 0.74 | 13.2 |
| White Cedar | 0.74 | 13.2 |

Table A24. Vegetation Data for Trapline #24

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Poplar | 37.67 | 815.2 |
| White Birch | 23.97 | 518.8 |
| Alder | 13.86 | 300.0 |
| Balsam Fir | 10.99 | 237.8 |
| Soft Maple | 5.16 | 111.6 |
| White Spruce | 2.85 | 61.6 |
| Black Spruce | 1.30 | 28.2 |
| White Cedar | 1.30 | 28.2 |
| Yellow Birch | 1.01 | 21.8 |
| Hard Maple | 1.01 | 21.8 |
| Red Pine | 0.54 | 11.6 |
| Ash | 0.34 | 7.4 |

Table A25. Vegetation Data for Trapline #25

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 48.92 | 1465.4 |
| Yellow Birch | 20.60 | 617.2 |
| Hemlock | 8.55 | 256.2 |
| Red Oak | 4.93 | 147.8 |
| Black Cherry | 4.56 | 135.8 |
| Poplar | 2.60 | 78.0 |
| Mixed Hardwood | 2.50 | 75.0 |
| Balsam Fir | 2.14 | 64.0 |
| Ironwood | 1.38 | 41.2 |
| White Birch | 1.20 | 36.0 |
| Elm | 0.94 | 28.2 |
| White Spruce | 0.93 | 28.0 |
| White Cedar | 0.75 | 21.6 |

Table A26. Vegetation Data for Trapline #26

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| White Birch | 24.73 | 792.2 |
| Hard Maple | 18.88 | 604.6 |
| Balsam | 17.37 | 556.4 |
| Poplar | 13.22 | 423.4 |
| Alder | 9.37 | 300.0 |
| Mixed Hardwood | 5.59 | 150.0 |
| Soft Maple | 5.01 | 160.6 |
| Basswood | 3.18 | 102.0 |
| Hemlock | 0.87 | 28.0 |
| Red Pine | 0.79 | 25.2 |
| White Spruce | 0.74 | 23.6 |
| White Pine | 0.25 | 8.0 |

Table A27. Vegetation Data for Trapline #27

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 26.90 | 1029.6 |
| Yellow Birch | 18.71 | 716.0 |
| Poplar | 9.87 | 377.8 |
| Balsam Fir | 8.63 | 330.6 |
| Soft Maple | 7.90 | 302.4 |
| Basswood | 7.20 | 275.2 |
| Elm | 7.20 | 275.2 |
| White Cedar | 4.70 | 180.0 |
| Hemlock | 4.01 | 153.4 |
| White Birch | 1.87 | 71.6 |
| White Spruce | 1.00 | 38.2 |
| Black Spruce | 0.90 | 34.2 |
| Red Oak | 0.89 | 34.0 |
| Ash | 0.22 | 8.6 |

Table A28. Vegetation Data for Trapline #28

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 42.85 | 1245.2 |
| Poplar | 22.64 | 644.4 |
| Yellow Birch | 14.45 | 410.4 |
| White Birch | 5.33 | 160.4 |
| Black Cherry | 3.82 | 117.0 |
| White Spruce | 3.08 | 101.8 |
| Balsam | 2.47 | 84.4 |
| Hemlock | 2.02 | 71.6 |
| Elm | 1.37 | 39.0 |
| Black Spruce | 0.88 | 25.0 |
| Red Oak | 0.68 | 19.4 |
| Ash | 0.61 | 17.6 |

Table A29. Vegetation Data for Trapline #29

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 36.72 | 1286.2 |
| Yellow Birch | 19.19 | 671.9 |
| White Birch | 10.73 | 376.6 |
| Hemlock | 6.46 | 225.4 |
| Alder | 5.00 | 175.0 |
| Black Spruce | 4.28 | 149.8 |
| White Cedar | 3.38 | 118.4 |
| Balsam Fir | 2.78 | 97.6 |
| White Spruce | 2.68 | 93.8 |
| Poplar | 2.29 | 80.2 |
| Soft Maple | 2.17 | 76.0 |
| White Pine | 2.08 | 72.8 |
| Red Oak | 1.00 | 35.0 |
| Ironwood | 0.95 | 33.3 |
| Black Cherry | 0.29 | 10.0 |

Table A30. Vegetation Data for Trapline #30

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Poplar | 27.71 | 555.0 |
| White Birch | 20.27 | 406.4 |
| White Pine | 12.98 | 260.0 |
| Jack Pine | 10.03 | 200.6 |
| White Spruce | 7.12 | 142.6 |
| Red Pine | 4.39 | 88.0 |
| Black Spruce | 4.19 | 84.0 |
| Balsam Fir | 4.11 | 82.4 |
| Alder | 3.25 | 65.0 |
| Soft Maple | 2.60 | 52.0 |
| White Cedar | 1.91 | 38.2 |
| Ash | 1.41 | 28.8 |

Table A31. Vegetation Data for Trapline #31

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Poplar | 20.61 | 413.0 |
| Mixed Hardwood | 14.97 | 300.0 |
| White Pine | 12.09 | 242.2 |
| White Birch | 9.48 | 190.0 |
| Balsam Fir | 8.57 | 171.8 |
| Hard Maple | 8.16 | 163.6 |
| Black Spruce | 6.39 | 128.4 |
| White Spruce | 5.92 | 118.6 |
| Soft Maple | 5.19 | 104.0 |
| Alder | 3.49 | 70.0 |
| Yellow Birch | 2.59 | 51.6 |
| Hemlock | 0.86 | 17.2 |
| Red Pine | 0.84 | 16.8 |
| Jack Pine | 0.84 | 16.8 |

Table A32. Vegetation Data for Trapline #32

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Poplar | 49.17 | 1916.3 |
| White Pine | 21.44 | 847.4 |
| Balsam Fir | 6.81 | 265.4 |
| White Spruce | 6.05 | 235.9 |
| Mixed Hardwood | 4.35 | 185.0 |
| Alder | 3.21 | 125.0 |
| White Birch | 2.64 | 102.8 |
| Jack Pine | 1.57 | 61.4 |
| Soft Maple | 1.20 | 49.0 |
| Ash | 1.01 | 39.6 |
| Red Oak | 0.92 | 36.0 |
| Black Spruce | 0.51 | 20.0 |
| White Cedar | 0.34 | 13.2 |

Table A33. Vegetation Data for Trapline #33

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 39.06 | 1301.6 |
| White Birch | 13.93 | 464.4 |
| Yellow Birch | 13.45 | 448.2 |
| Balsam Fir | 11.51 | 383.6 |
| Poplar | 9.66 | 322.0 |
| Hemlock | 4.09 | 136.2 |
| White Spruce | 3.43 | 114.2 |
| White Pine | 3.41 | 113.8 |
| Red Pine | 1.46 | 48.6 |

Table A34. Vegetation Data for Trapline #34

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 35.76 | 1369.4 |
| White Birch | 22.46 | 860.0 |
| Yellow Birch | 10.05 | 385.0 |
| Poplar | 9.81 | 375.6 |
| White Spruce | 7.25 | 277.8 |
| Hemlock | 6.98 | 267.4 |
| White Pine | 2.68 | 102.2 |
| White Cedar | 2.03 | 77.6 |
| Red Pine | 0.96 | 36.6 |
| Black Spruce | 0.76 | 29.2 |
| Mixed Hardwood | 0.65 | 25.0 |
| Red Oak | 0.61 | 23.4 |

Table A35. Vegetation Data for Trapline #35

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 28.86 | 1366.0 |
| White Birch | 16.94 | 801.8 |
| White Pine | 12.88 | 609.4 |
| Yellow Birch | 10.15 | 504.2 |
| White Spruce | 9.04 | 453.8 |
| Black Spruce | 5.06 | 239.6 |
| Hemlock | 4.03 | 190.8 |
| Red Pine | 3.36 | 159.0 |
| Poplar | 2.95 | 139.8 |
| Red Oak | 2.53 | 119.6 |
| Alder | 1.06 | 50.0 |
| Balsam Fir | 1.06 | 50.0 |
| White Cedar | 1.05 | 49.8 |
| American Beech | 1.03 | 48.8 |

Table A36. Vegetation Data for Trapline #36

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| White Pine | 25.77 | 929.4 |
| White Birch | 20.75 | 748.4 |
| Poplar | 17.07 | 615.8 |
| Hard Maple | 11.32 | 408.2 |
| Red Pine | 6.00 | 216.5 |
| Yellow Birch | 5.84 | 211.2 |
| White Spruce | 3.62 | 130.6 |
| Black Spruce | 3.13 | 112.8 |
| Alder | 2.22 | 80.0 |
| White Cedar | 1.56 | 56.4 |
| Hemlock | 1.03 | 37.0 |
| American Beech | 1.03 | 37.0 |
| Soft Maple | 0.66 | 23.8 |

Table A37. Vegetation Data for Trapline #37

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| White Birch | 24.39 | 1256.0 |
| Poplar | 16.03 | 825.8 |
| Black Spruce | 14.03 | 722.6 |
| White Pine | 11.49 | 591.6 |
| Hard Maple | 8.23 | 424.0 |
| Balsam Fir | 7.81 | 299.2 |
| White Spruce | 7.41 | 381.6 |
| Yellow Birch | 6.41 | 329.8 |
| Red Pine | 2.82 | 145.4 |
| Hemlock | 2.03 | 104.6 |
| Alder | 0.97 | 50.0 |
| Ash | 0.38 | 19.4 |

Table A38. Vegetation Data for Trapline #38

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| White Birch | 35.01 | 1468.4 |
| Poplar | 25.43 | 1063.6 |
| Hard Maple | 12.28 | 512.0 |
| Mixed Hardwood | 6.10 | 255.0 |
| Balsam Fir | 5.56 | 232.4 |
| Jack Pine | 5.46 | 228.4 |
| Soft Maple | 3.76 | 157.2 |
| Yellow Birch | 2.76 | 113.8 |
| Red Pine | 1.31 | 55.0 |
| Red Oak | 1.31 | 54.8 |
| Ironwood | 0.76 | 31.6 |
| White Spruce | 0.26 | 10.8 |

Table A39. Vegetation Data for Trapline #39

| Species | Percentage Abundance | Total Acreage |
| --- | --- | --- |
| Hard Maple | 27.65 | 1754.0 |
| White Birch | 21.71 | 1376.8 |
| Poplar | 17.69 | 1122.2 |
| White Pine | 7.62 | 483.8 |
| Balsam Fir | 7.40 | 482.0 |
| Red Pine | 5.44 | 345.2 |
| Yellow Birch | 4.29 | 277.0 |
| White Spruce | 2.30 | 145.6 |
| Basswood | 2.03 | 128.8 |
| Black Spruce | 1.95 | 123.8 |
| Hemlock | 0.49 | 30.8 |
| American Beech | 0.38 | 24.2 |
| White Cedar | 0.38 | 24.2 |
| Ash | 0.38 | 24.2 |

Table A40. Vegetation Data for Trapline #40

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 27.73 | 1314.4 |
| White Birch | 19.79 | 937.8 |
| Poplar | 11.56 | 547.8 |
| White Spruce | 10.18 | 482.8 |
| Yellow Birch | 9.65 | 457.2 |
| White Pine | 8.11 | 384.4 |
| Hemlock | 7.31 | 346.2 |
| Balsam Fir | 1.80 | 85.4 |
| Red Oak | 1.42 | 67.2 |
| Red Pine | 1.42 | 67.2 |
| Black Spruce | 1.03 | 48.8 |

Table A41. Vegetation Data for Trapline #41

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 37.98 | 518.0 |
| Poplar | 16.94 | 239.2 |
| White Birch | 12.76 | 180.2 |
| Hemlock | 10.34 | 143.2 |
| Soft Maple | 9.38 | 131.6 |
| Balsam Fir | 5.58 | 57.6 |
| Yellow Birch | 2.58 | 32.2 |
| White Spruce | 1.33 | 18.8 |
| Ash | 1.33 | 18.8 |
| American Beech | 0.79 | 11.2 |
| Ironwood | 0.79 | 11.2 |

Table A42. Vegetation Data for Trapline #42

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| White Pine | 29.89 | 719.2 |
| Poplar | 23.37 | 562.4 |
| Hard Maple | 9.33 | 224.6 |
| White Spruce | 6.99 | 168.2 |
| Red Pine | 5.76 | 138.6 |
| White Birch | 5.33 | 128.2 |
| Red Oak | 3.57 | 86.0 |
| Mixed Hardwood | 2.92 | 70.0 |
| Soft Maple | 2.64 | 63.4 |
| Hemlock | 2.63 | 63.2 |
| Alder | 2.07 | 50.0 |
| Yellow Birch | 1.65 | 39.6 |
| Elm | 1.65 | 39.6 |
| Balsam Fir | 1.33 | 32.0 |
| Ash | 0.87 | 21.0 |

Table A43. Vegetation Data for Trapline #43

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Poplar | 30.22 | 441.8 |
| Hard Maple | 25.31 | 370.0 |
| White Birch | 13.80 | 201.8 |
| Mixed Hardwood | 10.94 | 160.0 |
| Hemlock | 4.62 | 67.6 |
| Ironwood | 3.93 | 57.4 |
| Basswood | 3.65 | 53.4 |
| White Pine | 2.64 | 38.6 |
| Balsam Fir | 2.18 | 31.8 |
| Yellow Birch | 1.63 | 23.8 |
| White Spruce | 0.79 | 11.6 |
| Black Spruce | 0.29 | 4.2 |

Table A44. Vegetation Data for Trapline #44

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 42.99 | 729.4 |
| Yellow Birch | 19.07 | 323.6 |
| Hemlock | 12.66 | 214.8 |
| Red Oak | 5.20 | 88.2 |
| Ash | 4.77 | 81.0 |
| Balsam Fir | 4.02 | 68.2 |
| Soft Maple | 2.40 | 40.8 |
| American Beech | 2.20 | 37.4 |
| White Cedar | 1.95 | 33.0 |
| Elm | 1.65 | 28.0 |
| Black Spruce | 1.30 | 22.0 |
| White Spruce | 1.05 | 17.8 |
| Larch | 0.66 | 11.0 |
| Ironwood | 0.12 | 2.0 |

Table A45. Vegetation Data for Trapline #45

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 40.37 | 905.2 |
| Balsam Fir | 15.68 | 351.6 |
| Yellow Birch | 8.80 | 197.2 |
| Poplar | 8.65 | 194.0 |
| Soft Maple | 5.75 | 129.0 |
| American Beech | 5.04 | 112.8 |
| Mixed Hardwood | 3.79 | 85.0 |
| Hemlock | 3.40 | 76.2 |
| White Spruce | 2.93 | 65.8 |
| Black Spruce | 1.55 | 34.8 |
| Ash | 1.29 | 29.0 |
| Red Oak | 0.99 | 22.2 |
| Larch | 0.78 | 17.4 |
| Ironwood | 0.68 | 14.6 |
| Elm | 0.32 | 7.2 |

Table A46. Vegetation Data for Trapline #46

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 35.29 | 793.4 |
| Hemlock | 18.01 | 393.6 |
| Yellow Birch | 13.07 | 285.8 |
| Soft Maple | 11.88 | 258.6 |
| Balsam Fir | 9.79 | 203.0 |
| American Beech | 6.79 | 137.4 |
| Red Oak | 1.67 | 36.6 |
| White Birch | 0.95 | 20.8 |
| Elm | 0.72 | 15.8 |
| Ironwood | 0.59 | 13.0 |
| Black Spruce | 0.48 | 10.4 |
| White Spruce | 0.42 | 9.2 |
| Poplar | 0.34 | 7.4 |

Table A47. Vegetation Data for Trapline #47

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 34.84 | 705.6 |
| Poplar | 21.33 | 432.0 |
| Balsam Fir | 13.06 | 264.4 |
| Soft Maple | 10.44 | 211.4 |
| American Beech | 8.53 | 172.8 |
| Yellow Birch | 4.82 | 97.6 |
| Ash | 2.73 | 55.2 |
| Mixed Hardwood | 1.98 | 40.0 |
| Hemlock | 1.83 | 37.0 |
| Elm | 0.44 | 9.0 |

Table A48. Vegetation Data for Trapline #48

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| White Birch | 26.75 | 615.6 |
| Alder | 19.77 | 455.0 |
| Poplar | 18.75 | 431.4 |
| Red Pine | 9.52 | 219.0 |
| White Pine | 9.04 | 208.0 |
| Hard Maple | 7.43 | 171.0 |
| Yellow Birch | 4.95 | 114.0 |
| Balsam Fir | 2.48 | 57.0 |
| Soft Maple | 1.04 | 24.0 |
| Red Oak | 0.27 | 6.0 |

Table A49. Vegetation Data for Trapline #49

| Species | Percentage Abundance | Total Acreage |
|---|---|---|
| Hard Maple | 39.85 | 816.6 |
| American Beech | 24.09 | 493.6 |
| Balsam Fir | 18.75 | 384.2 |
| Yellow Birch | 10.18 | 208.6 |
| Soft Maple | 1.79 | 36.6 |
| White Spruce | 1.30 | 26.6 |
| Ash | 1.22 | 25.0 |
| Poplar | 1.22 | 25.0 |
| White Cedar | 0.92 | 18.8 |
| Hemlock | 0.40 | 8.2 |
| Alder | 0.28 | 5.8 |

# APPENDIX B

Table Bl. Beaver Density Data

| Trapline Number | Total Lodges | Total Square Miles | Density Lodges/Square Mile |
|---|---|---|---|
| 1 | 53 | 32.4 | 1.6 |
| 2 | 50 | 39.2 | 1.3 |
| 3 | 73 | 35.6 | 2.1 |
| 4 | 57 | 26.4 | 2.2 |
| 5 | 52 | 31.2 | 1.7 |
| 6 | 39 | 42.4 | 0.9 |
| 7 | 18 | 76.8 | 0.2 |
| 8 | 60 | 72.8 | 0.8 |
| 9 | 70 | 84.4 | 0.8 |
| 10 | 46 | 45.6 | 1.0 |
| 11 | 44 | 61.6 | 0.7 |
| 12 | 41 | 94.8 | 0.4 |
| 13 | 145 | 47.2 | 3.1 |
| 14 | 91 | 25.6 | 3.6 |
| 15 | 68 | 41.2 | 1.7 |
| 16 | 17 | 20.0 | 0.8 |
| 17 | 13 | 12.4 | 1.1 |
| 18 | 48 | 71.2 | 0.7 |
| 19 | 33 | 42.0 | 0.8 |
| 20 | 16 | 33.6 | 0.5 |
| 21 | 44 | 58.0 | 0.8 |
| 22 | 40 | 85.6 | 0.5 |
| 23 | 39 | 34.0 | 1.2 |
| 24 | 8 | 14.8 | 0.5 |
| 25 | 77 | 45.2 | 1.7 |
| 26 | 116 | 73.6 | 1.6 |
| 27 | 78 | 40.0 | 2.0 |
| 28 | 70 | 40.0 | 1.8 |
| 29 | 66 | 56.0 | 1.2 |
| 30 | 280 | 132.8 | 2.1 |
| 31 | 24 | 30.4 | 0.8 |
| 32 | 138 | 40.8 | 3.4 |
| 33 | 49 | 94.4 | 0.5 |
| 34 | 21 | 32.8 | 0.6 |
| 35 | 17 | 32.8 | 0.5 |
| 36 | 42 | 53.6 | 0.8 |
| 37 | 12 | 26.4 | 0.5 |
| 38 | 77 | 22.4 | 3.4 |
| 39 | 26 | 16.4 | 1.6 |
| 40 | 20 | 19.2 | 1.0 |
| 41 | 24 | 12.0 | 2.0 |
| 42 | 56 | 14.0 | 4.0 |
| 43 | 44 | 14.4 | 3.1 |
| 44 | 83 | 40.0 | 2.1 |
| 45 | 96 | 36.4 | 2.6 |
| 46 | 58 | 28.0 | 2.1 |
| 47 | 62 | 28.0 | 2.2 |
| 48 | 22 | 14.8 | 1.5 |
| 49 | 28 | 11.6 | 2.4 |

# APPENDIX C

Table Cl. Vegetation Stand Data

| Trapline Number | Number of Stands | Total Acreage | Mean Acreage | Stand Age |
|---|---|---|---|---|
| 1 | 22 | 3638.0 | 163.4 | 57.2 |
| 2 | 18 | 2621.0 | 145.6 | 55.8 |
| 3 | 22 | 4210.0 | 191.4 | 51.3 |
| 4 | 19 | 2760.0 | 145.3 | 88.5 |
| 5 | 18 | 2783.0 | 154.6 | 83.3 |
| 6 | 25 | 3697.0 | 147.8 | 53.0 |
| 7 | 14 | 1628.0 | 116.3 | 55.1 |
| 8 | 18 | 1550.0 | 86.1 | 53.0 |
| 9 | 18 | 2538.0 | 141.0 | 50.4 |
| 10 | 19 | 3107.0 | 163.5 | 67.4 |
| 11 | 15 | 2319.4 | 154.6 | 58.4 |
| 12 | 16 | 2594.0 | 162.2 | 76.3 |
| 13 | 15 | 2449.0 | 163.3 | 58.5 |
| 14 | 15 | 1908.0 | 127.2 | 45.1 |
| 15 | 14 | 2601.6 | 185.7 | 62.0 |
| 16 | 17 | 2745.6 | 161.5 | 81.0 |
| 17 | 15 | 2464.4 | 164.3 | 83.3 |
| 18 | 15 | 3521.8 | 234.7 | 58.8 |
| 19 | 14 | 2482.0 | 177.3 | 65.5 |
| 20 | 14 | 2432.8 | 173.7 | 75.4 |
| 21 | 15 | 2028.2 | 135.2 | 83.8 |
| 22 | 23 | 2644.0 | 114.9 | 109.2 |
| 23 | 14 | 1788.4 | 127.7 | 35.0 |
| 24 | 14 | 2164.0 | 154.6 | 36.2 |
| 25 | 14 | 2995.4 | 213.9 | 79.4 |
| 26 | 15 | 3203.0 | 213.5 | 39.8 |
| 27 | 13 | 3827.4 | 294.4 | 52.9 |
| 28 | 14 | 2839.6 | 202.8 | 46.0 |
| 29 | 25 | 3502.0 | 140.8 | 88.6 |
| 30 | 17 | 2003.0 | 117.8 | 52.9 |
| 31 | 11 | 2004.0 | 182.1 | 76.6 |
| 32 | 20 | 3897.0 | 194.9 | 50.4 |
| 33 | 13 | 3326.6 | 256.4 | 71.3 |
| 34 | 13 | 3829.2 | 294.6 | 69.6 |
| 35 | 14 | 4732.6 | 338.0 | 90.6 |
| 36 | 15 | 3607.1 | 240.5 | 78.1 |
| 37 | 15 | 5150.0 | 343.3 | 64.2 |
| 38 | 27 | 4183.0 | 154.9 | 60.1 |
| 39 | 12 | 6342.6 | 528.5 | 70.1 |
| 40 | 14 | 4739.2 | 338.5 | 66.7 |
| 41 | 11 | 1412.0 | 128.4 | 53.6 |
| 42 | 21 | 2406.0 | 114.6 | 75.7 |
| 43 | 19 | 1462.0 | 76.9 | 49.2 |
| 44 | 20 | 1715.2 | 84.8 | 90.7 |
| 45 | 19 | 2242.0 | 118.0 | 84.4 |
| 46 | 12 | 2186.0 | 182.1 | 93.6 |
| 47 | 18 | 2025.0 | 112.5 | 88.0 |
| 48 | 16 | 2301.0 | 143.8 | 36.4 |
| 49 | 13 | 2049.0 | 157.6 | 115.0 |