THE UNIVERSITY OF ALBERTA

ECOLOGY OF THE MUSKRAT
(ONDATRA ZIBETHICUS SPATULATUS)
ON THE PEACE-ATHABASCA DELTA, WOOD BUFFALO NATIONAL PARK

DAVID ARTHUR WESTWORTH

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1974

ABSTRACT

Ecology and population dynamics of a muskrat population were studied for two years on a 890 ha marsh on the Peace-Athabasca Delta. The study coincided with a period of declining water levels and emphasis was placed on determining the effect of resulting environmental changes on the muskrat population. A livetrap, tag and recapture program, in which 610 muskrats were marked, provided information on population size, structure, survival, movements and social relationships.

Muskrats made year-round use of houses built in dense stands of offshore emergents. There were seasonal trends in location of new houses, with regard to water depth and cover type. Use of bank burrows declined as receding water levels reduced the availability of suitable den sites.

Sedge *(Carex vesicaria)* was the most abundant emergent species (85% of emergent cover) and also the most extensively eaten food plant, however, clear preferences were shown for sweetflag *(Acorus calamus)* and burreed *(Sparganium eurycarpum)*. Animal matter was not an important part of the diet. A correlation was detected between observed preference and nutrient content of food plants. In winter muskrats relied more on submerged aquatics and the rootstocks of emergents, with houses apparently serving as an important source of stored food.

Muskrats were monogamous and territorial, with family groups occupying mutually exclusive home ranges. Members of each family group remained together within the home range until the beginning of the next mating period. Minimum length of family home ranges averaged 130 m in 1971. A marked "shuffle" of home ranges occurred during spring mating, however, no dispersal of established residents was observed during fall.

Breeding began between April 23-27 and was correlated with the appearance of open water. The last known litter birth occurred on

August 21. Juveniles did not begin breeding in the calendar year of their birth. Adult females produced an average of 2.4 litters with an average size of approximately 7.5.

Juvenile sex ratios were heavily overbalanced in favor of males, however, adult sex ratios were nearly even during the breeding season. Natural mortality factors during mating or spring dispersal are thought to be responsible for removing excess males from the population.

Density of breeding pairs increased from one per 4.8 ha in 1970 to one pair per 4.0 ha in 1971. Fall population densities were approximately 2.8 muskrats per ha in 1970 and 3.5 in 1971.

Recapture of tagged muskrats provided minimum survival rates for the population. Disappearance during the first year of life amounted to approximately 87%. Approximately 70% of all tagged nestlings survived until October, with at least 65% of these surviving over winter. Similar survival rates were observed for adults with approximately 89% disappearing during their second year of life.

Fur trapping was a principal mortality factor, accounting for about 50% of the annual production in areas trapped. The effects of predation, disease and parasitic infection were not considered significant. Some losses through intraspecific strife were noted, mainly as a result of cannabalism on nestlings.

Declining water levels reduced the amount of available habitat and predisposed muskrats in shallow areas to increased mortality. Movements toward deeper water resulted in increased crowding and territorial interactions. In winter high rates of house abandonment were associated with shallow water, thin snow cover and small house sizes. Behavioral adjustments by muskrats are thought to be important in assuring winter survival during periods of low water.

ACKNOWLEDGEMENTS

I would like to express my appreciation to the Department of Energy Mines and Resources for financially supporting this study.

I wish to thank my supervisor, Dr. W.A. Fuller for making the study possible and critically reviewing this manuscript. Similarly, thanks are due to my committee members Dr. W.M. Samuel and Dr. G.H. LaRoi for reviewing this manuscript and its previous draft. Dr. Samuel also provided guidance with the parasitological portion of the study.

A number of other people assisted in various ways and their help is gratefully acknowledged. Mr. G. Douglas, kindly identified all of my plant material. Dr. B. Chernick provided helpful advice concerning statistical analysis of data. Mr. P.J. Martin of the Alberta Soil and Feed Testing Lab provided nutrient analysis of forage and helped interpret the results. Mr. J. Chesterman took great effort producing the photographic plates.

To Mr. E. Atwell, I extend sincere thanks for his tireless and enthusiastic field assistance in the first year of this study.

I owe special thanks to Mr. Horace Wylie for his valuable assistance throughout the study and for making his home and trapline cabin available to me during all of my visits. I have relied heavily upon his experience and knowledge of past conditions on the study area.

I also would like to thank my parents, Mr. and Mrs. Arthur Westworth, who offered encouragement and assisted in various ways during final preparation of this thesis.

Above all, I owe thanks to my wife Marilyn for her assistance and encouragement in all phases of the study.

TABLE OF CONTENTS

ABSTRACT.......... iv

ACKNOWLEDGEMENTS.......... vi

LIST OF TABLES.......... xi

LIST OF FIGURES.......... xii

LIST OF PHOTOGRAPHS.......... xiv

INTRODUCTION.......... 1

DESCRIPTION OF THE AREA.......... 3

The Peace-Athatbasca Delta.......... 3

Physiography.......... 3

Vegetation.......... 5

Climate.......... 6

The Study Area.......... 8

METHODS.......... 14

Livetrapping and Tagging.......... 14

Reproduction.......... 15

Food Habits.......... 16

Habitat Selection and Composition.......... 17

Necropsies.......... 17

Statistical Analysis.......... 17

DWELLING HABITS.......... 18

Summer Houses and Nest Houses.......... 19

Fall or Winter Houses.......... 21

Selection of House Building Sites.......... 21

Composition of Houses.......... 26

Use of Bank Burrows.......... 26

Use of Pushups.......... 28

FOOD HABITS.. 30
Use of Animal Food.. 35
Winter Food Habits.. 36
Nutrient Content of Food Plants.......................... 37
Relationship between Food Preference and Nutrient Content... 39
HOME RANGE, TERRITORIALITY AND MOVEMENTS........................ 42
Home Range.. 42
Territoriality.. 46
Summer Movement Patterns.. 48
Winter Movements.. 52
Emergency Movements.. 53
Dispersal Movements.. 54
Spring Dispersal.. 54
Fall Dispersal.. 57
REPRODUCTION.. 60
Mating Habits.. 60
Pairing.. 60
Minimum Breeding Age.. 61
Breeding Season.. 62
Temporal Distribution of Muskrat Births.................... 63
Number of Litters Per Female.. 67
Interval between Consecutive Litters...................... 68
Litter Size.. 70
Average Production Per Female.. 70
SEX AND AGE STRUCTURE.. 73
Sex Ratios.. 73
Age Ratios.. 78

POPULATION SIZE AND DENSITY 82

Breeding Population 82

Fall Population 82

SURVIVAL AND MORTALITY 84

Adult Survival and Mortality 84

Juvenile Survival and Mortality 85

Summer and Early Fall 85

Nestling Mortality 86

Post-weaning Summer Mortality 86

Effect of Litter Size on Survival 86

Winter Mortality 88

Effect of Litter Order on Juvenile Survival 89

Longevity 91

MORTALITY FACTORS 92

Intraspecific Strife 92

Predation 93

Disease and Parasites 96

Fur Harvest 99

Livetrapping and Disturbance during the Study 101

RELATIONSHIPS WITH OTHER WILDLIFE 102

Waterfowl 102

Bison 103

Other Wildlife 105

WATER LEVEL AND HABITAT RELATIONSHIPS 106

A Review of Delta Successional Patterns 106

Water Levels Since 1968 109

Changes in Vegetation on the Study Area 110

Effect of Low Water on Summer Activity and Survival of Muskrats.... 112

Effect of Low Water on Winter Activity and Survival of Muskrats.... 114

Factors Affecting Winter Use of Muskrat Houses.... 118

Water Depth.... 118

Snow Depth.... 118

Cover Type.... 120

House Size.... 122

Disturbance.... 124

Adjustments for Survival during Low Water.... 126

(1) *Selection of House Building Sites*.... 126

(2) *House Size*.... 127

(3) *Number of Houses per Home Range*.... 127

(4) *Intraspecific Relationships*.... 128

CONCLUDING DISCUSSION.... 129

Factors Controlling the Egg Lake Population from 1970-72.... 129

Factors Determining Long-Term Population Levels on the Delta.... 132

LITERATURE CITED.... 134

APPENDIX I Summary of climatic data for Fort Chipewyan provided by the Atmospheric Environment Service, Edmonton.... 139

APPENDIX II Plant species found on the study area.... 140

APPENDIX III Evaluation of the fluting length technique for determining the age of muskrats.... 142

APPENDIX IV Bird species associated with Egg Lake.... 145

APPENDIX V Change in Egg Lake water level during 1971.... 147

LIST OF TABLES

Table 1.	Composition of 50 summer and fall muskrat houses at Egg Lake in 1971	27
Table 2.	Utilization and availabilty of principal muskrat food plants on and around 208 feeding platforms	31
Table 3.	Parts of plants eaten by muskrats	34
Table 4.	Nutrient content of principal muskrat food plants	38
Table 5.	Relative nutritive value of muskrat food plants	41
Table 6.	Summary of livetrapping data for 25 family home ranges in 1971	45
Table 7.	Time intervals between births of consecutive litters of muskrats	69
Table 8.	Size of complete muskrat litters in 1970 and 1971	71
Table 9.	Sex ratios of nestlings	74
Table 10.	A comparison of nestling sex ratios in relation to age of litter	75
Table 11.	Age ratios of muskrats in 1971 and 1972 spring harvests (March 15 to May 10)	79
Table 12.	Comparison of muskrat age ratios with several other areas	80
Table 13.	Helminths from 40 Egg Lake muskrats taken during 1971 and 1972 spring harvests	97
Table 14.	Recovery of tagged muskrats in spring harvests	100
Table 15.	Cover types of winter muskrat houses in relation to condition of use, water depth and snow cover	121

LIST OF FIGURES

Figure 1.	Map of the Peace-Athabasca Delta	4
Figure 2.	Schematic profile of major biotic communities on the Peace-Athabasca Delta	7
Figure 3.	Egg Lake study area showing distribution of emergent vegetation	10
Figure 4.	A portion of the study area showing the distribution of major vegetation types	13a
Figure 5.	Number of active muskrat houses in a 100 ha portion of Egg Lake during 1971	22
Figure 6.	Distribution of summer and fall built muskrat houses in relation to water depth in October 1971	23
Figure 7.	Frequency of occurrence of cover types around summer and winter muskrat houses in 1971 compared with relative availability of each emergent species	25
Figure 8.	Family home ranges (HR) of muskrats during 1971	44a
Figure 9.	Relationship between number of recaptures and longest distance between captures in 1970 and 1971 combined	50
Figure 10.	Average distance between successive captures and longest distance between captures during 1970 and 1971 combined	51
Figure 11.	Intramarsh movements associated with spring dispersal	56
Figure 12	Distribution of muskrat births during 1970 and 1971	64
Figure 13.	Birthdates of muskrat litters in 1971 according to litter order	66
Figure 14.	Sex ratios of livetrapped (Summer, Fall) and killtrapped (Spring) muskrats	76
Figure 15.	Relationship between size and age of complete litters	87

Figure 16. Relative contribution of 1st, 2nd and 3rd litters to total production of nestlings and to juvenile population in October 1971 and 1972 spring harvest... 90

Figure 17. Condition of muskrat houses in April 1972 in relation to fall water depth........................... 119

Figure 18. Condition of muskrat houses in April 1972 in relation to house height.............................. 123

Figure 19. Diagramatic summary of the interrelationships and relative importance of muskrat mortality factors..... 130

Figure 20. Frequency distribution of fluting lengths for muskrats taken during the 1971 and 1972 spring harvests.. 143

LIST OF PHOTOGRAPHS

Photograph 1. An aerial view of the west end of Egg Lake, looking north across the study area.............. 11 a

Photograph 2. Extensive offshore stands of sedge, typical of muskrat habitat on the west end of Egg Lake.. 11 a

Photograph 3. An aerial view looking west over the study area.. 11 a

Photograph 4. A typical nest house............................ 20 a

Photograph 5. Top of nest house opened to show nest containing a 2-week old litter...................... 20 a

Photograph 6. A winter house built in a clump of bulrush....... 20 a

Photograph 7. Vegetation utilization around a winter house..... 20 a

Photograph 8. An adult muskrat on a predominantly sweetflag feeding platform.......................... 33 a

Photograph 9. Heavy utilization of sweetflag.................. 33 a

Photograph 10. A muskrat feeding on submerged aquatic vegetation... 33 a

Photograph 11. Bison on the north side of Egg Lake.............. 104 a

Photograph 12. Heavy grazing and trampling by bison on the west side of the study area..................... 104 a

Photograph 13. Winter muskrat houses partially eaten by bison... 104 a

Photograph 14. Pre-Cambrian granite outcropping near the center of Egg Lake showing previous high water line, October 1971......................... 111 a

Photograph 15. Recently exposed mudflats along the north side of the study area, July 27, 1971............. 111 a

Photograph 16. Looking toward the north side of the study area from a point well out on the marsh, July 27, 1971...................................... 111 a

INTRODUCTION

Through most of its long history, Fort Chipewyan has served as an important center of the fur industry in Canada's northwest. Part of its eminence has been due to the abundant biological resources of the Peace-Athabasca delta. The shallow lakes and marshes of the delta annually produce tens of thousands of muskrats, the trapping of which has been the mainstay of the local economy. Soper (1942) noted that in good years between 70,000 and 90,000 muskrat pelts, obtained mostly from the Peace-Athabasca delta, were traded at Fort Chipewyan alone. Fuller (1951) reported that muskrats accounted for about 70% of the total value of fur taken by delta trappers.

To maintain their levels, the delta lakes and marshes depend on periodic flooding brought about by the combined peak flows of the Peace and Athabasca Rivers. Historically, the frequency of flooding and hence delta water levels have been highly variable. Early records contain references to periods of drastically low water which must have markedly reduced the extent and suitability of muskrat habitat on the delta.

Muskrat populations on the delta have historically undergone wide fluctuations in abundance. It is not known to what extent disease or intrinsic cyclic tendencies were responsible; however, it is probable that water level fluctuations were a major factor. William Brown, a Hudson's Bay Company trader at Fort Chipewyan, made early reference to muskrats and water levels in his annual report for 1820-21 (Simpson's Journal, 1938; cited in Wuetherick, 1973):

> The Musquashes are a species of animals whose numbers depend entirely upon the state of the lakes and rivers - for when the water is high for a few years they become very numerous but when low they entirely disappear.

Fuller (1951) also reported that very low muskrat populations coincided with a period of low water levels from about 1945-47.

In spite of short term deficits of water and periodic reductions in the muskrat population, the recurring nature of spring floods has combined with e high productivity of this species to create a high, long-term level of muskrat production on the delta. The W.A.C. Bennett Dam, built about 1100 km (700 mi) upstream on the Peace River, began retaining water in 1968 which resulted in reduced spring and summer flows and a disruption of the normal hydrologic regime on the downstream delta (Bennett, 1971). A number of scientists voiced concern that this would cause permanent ecological damage to the delta and cause hardship for the people who still depended on its biological resources (Peace-Athabasca Delta Committee, 1970).

In 1970, I began this investigation with the overall objective of studying the ecology and population dynamics of muskrats on the Delta. Specific objectives were to:

(a) examine the demography of the population

(b) determine the factors responsible for annual mortality

(c) evaluate habitat utilization

(d) determine the response of the population to declining water levels

This study provides a base for evaluating long term effects of the Bennett Dam and for planning future muskrat management on the Delta.

DESCRIPTION OF THE AREA

The Peace-Athabasca Delta

The Peace-Athabasca delta is situated at the west end of Lake Athabasca at the confluence of the Peace, Slave and Athabasca river drainage basins (Fig 1). It covers an area of approximately 3900 sq km (1500 sq mi), about three-quarters of which lies within Wood Buffalo National Park.

Physiography

The delta lies within the Mackenzie Lowlands subdivision of the Western Plains physiographic region and is bordered by the Canadian Shield to the northeast (Green and Laycock, 1967). According to Bayrock and Root (1971) the delta came into existence following deglaciatio about 10,000 years ago.

The topography of the delta reflects its glacial and fluvial development. Most of the delta is very flat and only slightly higher than Lake Athabasca which has an average level of 209 m (685 ft) asl (Bennett, 1971). On the northeastern side the flat landscape is broken by outcroppings of pre-Cambrian bedrock. Elsewhere, the only variations in relief are river terraces and levees which often enclose large areas of contiguous wetlands.

The most prominent landscape features on the delta are its many rivers, streams, lakes and marshes. The Athabasca River, which arises in the mountains of west-central Alberta, enters the delta from the south and presently is responsible for nearly all of the active sedimentation. The Peace River, which originates in the mountains of northeastern British Columbia, only flows into the delta during flood periods.

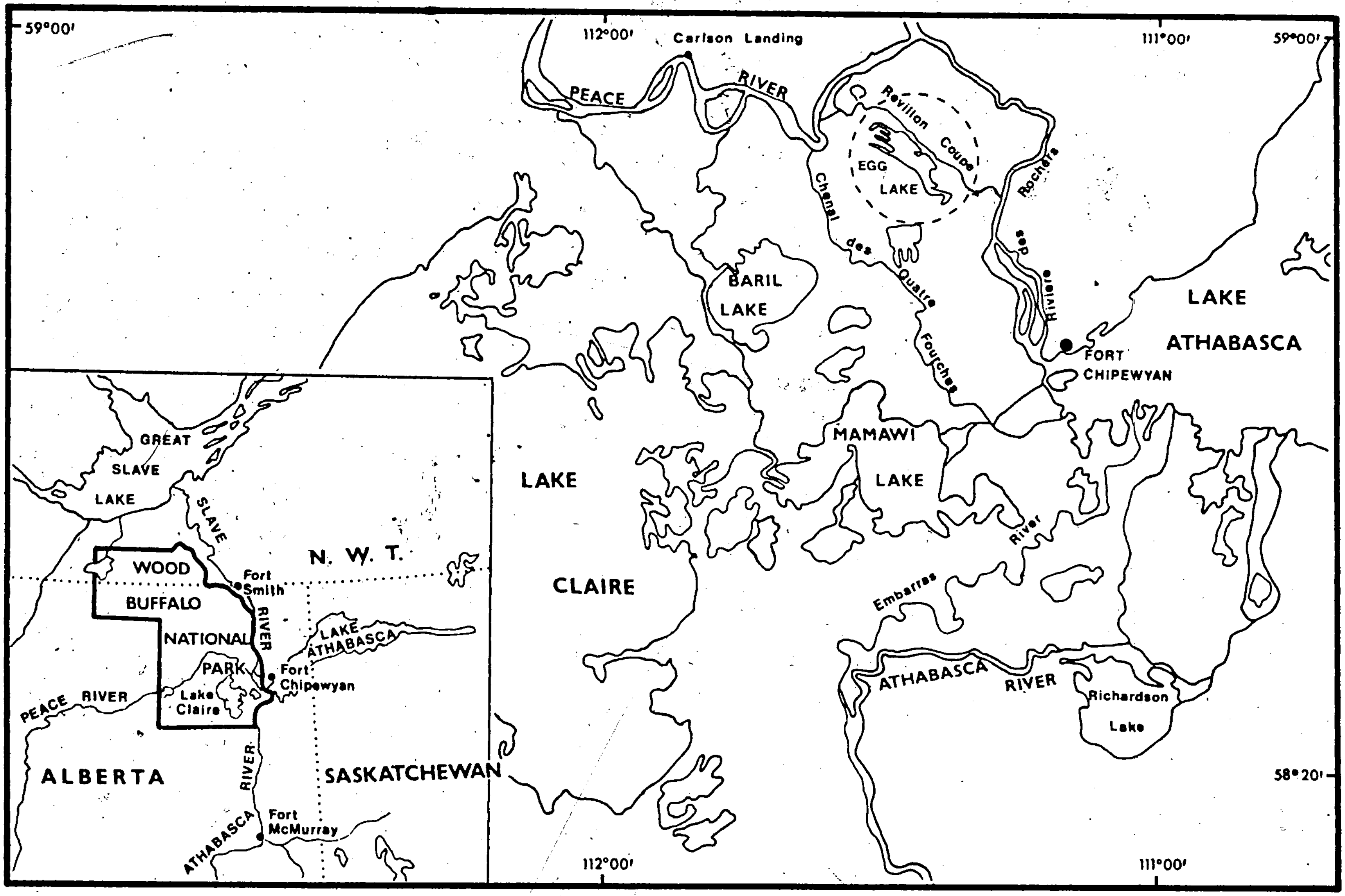


Figure 1. Map of the Peace-Athabasca Delta showing location of the study area.

For most of the year it enters the Slave River, bypassing the delta to the north. Water also enters the delta from the much smaller Birch River, which arises in the Birch Mountains and flows into Lake Claire from the west. The delta is drained by the Slave River through its outlet channels, the Riviere des Rochers, the Revillon Coupe and the Chenal des Quatre Fourches.

The largest delta lakes (Claire, Mamawi and Baril) remain connected to Lake Athabasca and together cover over half of the delta's surface. Of smaller size but greater importance with respect to muskrat and waterfowl production are the numerous, shallow, perched lakes and marshes. These occupy inter-levee depressions and receive source water only when it flows over the levees at times of flood.

The normal hydrologic cycle of the delta was described by Bennett (1971): Peak flows of the Peace and Athabasca Rivers occur in spring or early summer. At this time the higher level of the Peace River causes water to enter Lake Athabasca. This results in a damming effect which raises the level of Lake Athabasca enough to flood much of the delta. Additional flooding frequently results from the formation of ice jams along rivers during breakup which raise water levels above the levees. From 1968 to 1971, peak flows of the Peace River were substantially lower than normal. Consequently, extensive flooding did not occur and delta water levels declined.

Vegetation

The Peace-Athabasca delta lies in the Boreal-Subarctic Alluvial Lowlands section of the Northern Taiga zone (La Roi, 1967). Within the delta the distribution of plant communities reflects local variations in moisture and relief. Raup (1935) gave the following description of the delta vegetation (using current nomenclature given by Fuller and La Roi, 1971):

> "Although the differences in the elevation of the plain above the water table are slight, they are enough to determine the arrangement of the plant cover. Lands subject to inundations, or at most only a few inches above the water-table, have an herbaceous vegetation ranging from semi-floating aquatic plants to sedges and grasses. Large areas in the lower deltas have nearly pure stands of the [marsh] sedge *Carex atherodes* or blue-joint grass *Calamagrostis canadensis*. On the margins of stream channels, abandoned or otherwise, are long lines of willows *Salix* spp., which are limited to the slightly elevated ridges peculiar to such areas. The farther toward the margins of the basin the more land is covered by shrub and tree growth, so that the upper deltas and the banks of the larger channels support a forest of [white] spruce and balsam poplar. Forest growth extends farthest into the lowlands along the actual margins of the streams. The granite hills have a scrubby timber of [white] spruce *Picea glauca*, Jackpine *Pinus banksiana*, and canoe birch *Betula papyrifera* var. *neoalaskana*. Not only are the positions of these major types of vegetation determined topographically, but also most of the lesser plant associations within them."

Fuller and LaRoi (1971) noted that periodic interruption of the normal successional process (aquatic ⟶ terrestrial) by flooding has resulted in a zonal sequence of distinct habitat types over much of the delta (Fig 2).

Climate

The climate of the area is influenced by the continental, northern location. Winters are long and cold and summers are short and warm. Average annual precipitation is light (40 cm) with most of it falling during the summer. The average frost-free period is about 3 months. Freeze-up usually begins in late October with break-up beginning in April or early May. Climatological data were provided by the

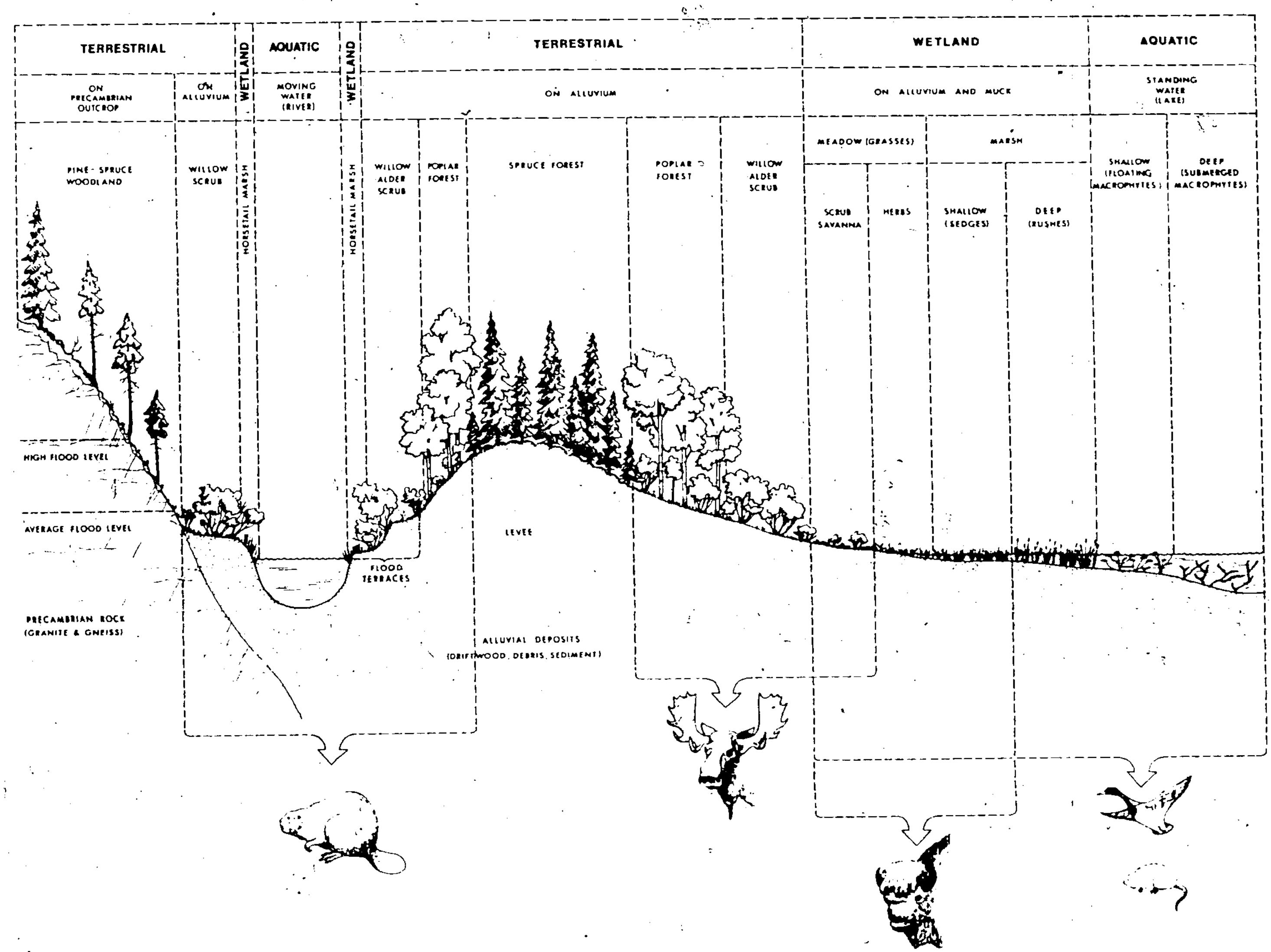


Figure 2. Schematic profile of major biotic communities on the Peace-Athabasca Delta (from Fuller and LaRoi, 1971).

Atmospheric Environment Service, Edmonton. Monthly temperatures, rainfall, and snowfall for the period of study along with means for the period 1963-1972 are shown in Appendix I.

The Study Area

The study area, known locally as Egg Lake, lies within the registered trapping area of Horace Wylie. It is located in the north-east part of the delta approximately 19 km (12 mi) northwest of Fort Chipewyan. Situated along the south side of the Revillon Coupe River in a northwest-southeast orientation, it extends from approximately 58° 51' N to 58° 55' N latitude and 111° 21' W to 111° 28' W longitude. Egg Lake is about 9.7 km (6.0 mi) in length and 1.8 km (1.1 mi) at its greatest width and covers an area of approximately 890 ha (2200 a).

The lake occupies a depression surrounded by natural levees of active and abandoned river channels and low hills and ridges of granite bedrock. It has no present connection with the delta drainage system and is therefore called a backwater or perched slough. It only receives flood water when the Peace River spills over its banks, usually as a result of an ice jam. Flooding did not occur from 1968 to 1971 inclusive. The lake is uniformly shallow over most of its area with gently sloping sides, except where bedrock outcroppings occur. Water depths in 1970 averaged 50-60 cm and generally did not exceed 1 m. Water level and habitat changes during the study period will be described later.

On the sides of the basin the distribution of plant communities closely conforms to the generalized profile in Figure 2. The tops of the levees support a mixed forest of white spruce *(Picea glauca)*, aspen

(Populus tremuloides) and balsam poplar *(Populus balsamifera)*. Jack-pine *(Pinus banksiana)* grows on the rock outcroppings with occassional clusters of birch *(Betula papyrifera)* on the sides. At lower contours poplar is replaced by alder *(Alnus tenuifolia)* and a well-developed zone of willow (*Salix* spp). An ecotonal zone of willow shrub grades into a meadow community dominated by blue-joint grass *(Calamagrostis canadensis)* and sedge *(Carex* spp). These meadows are most extensive along the north and east sides of the lake.

The shoreline marsh community is dominated by sedge *(Carex* spp) and includes a variety of plants such as slough grass *(Beckmannia syzigachne)*, spike rush *(Eleocharis palustris)*, golden dock *(Rumex maritimus)* and marsh ragwort *(Senecio congestus)*. Shallow water areas along the shoreline support emergent species dominated by sedge *(Carex vesicaria)* with frequent stands of sweetflag *(Acorus calamus)* and giant burreed *(Sparganium eurycarpum)* and with occassional patches of horse-tail *(Equisetum fluviatile)*, river bulrush *(Scirpus fluviatilis)* and arrowhead *(Sagittaria cuneata)*. In contrast to many other delta lakes, cattail *(Typha latifolia)* and reed grass *(Phragmites communis)* are quite sparce. Shoreline emergents are fairly extensive along the north side of Egg Lake and generally poorly developed along the south side.

Of particular importance to muskrats are extensive stands of offshore emergents in the west and central parts of the lake. These stands consist of a complex interspersion of clumps of emergent vegetation and open water. They extend over a total area of approximately 450 ha (1100 a) with actual coverage of emergents only amounting to about 20%. My field studies were restricted primarily to the west half of Egg Lake (Fig 3, Photo 1-3).

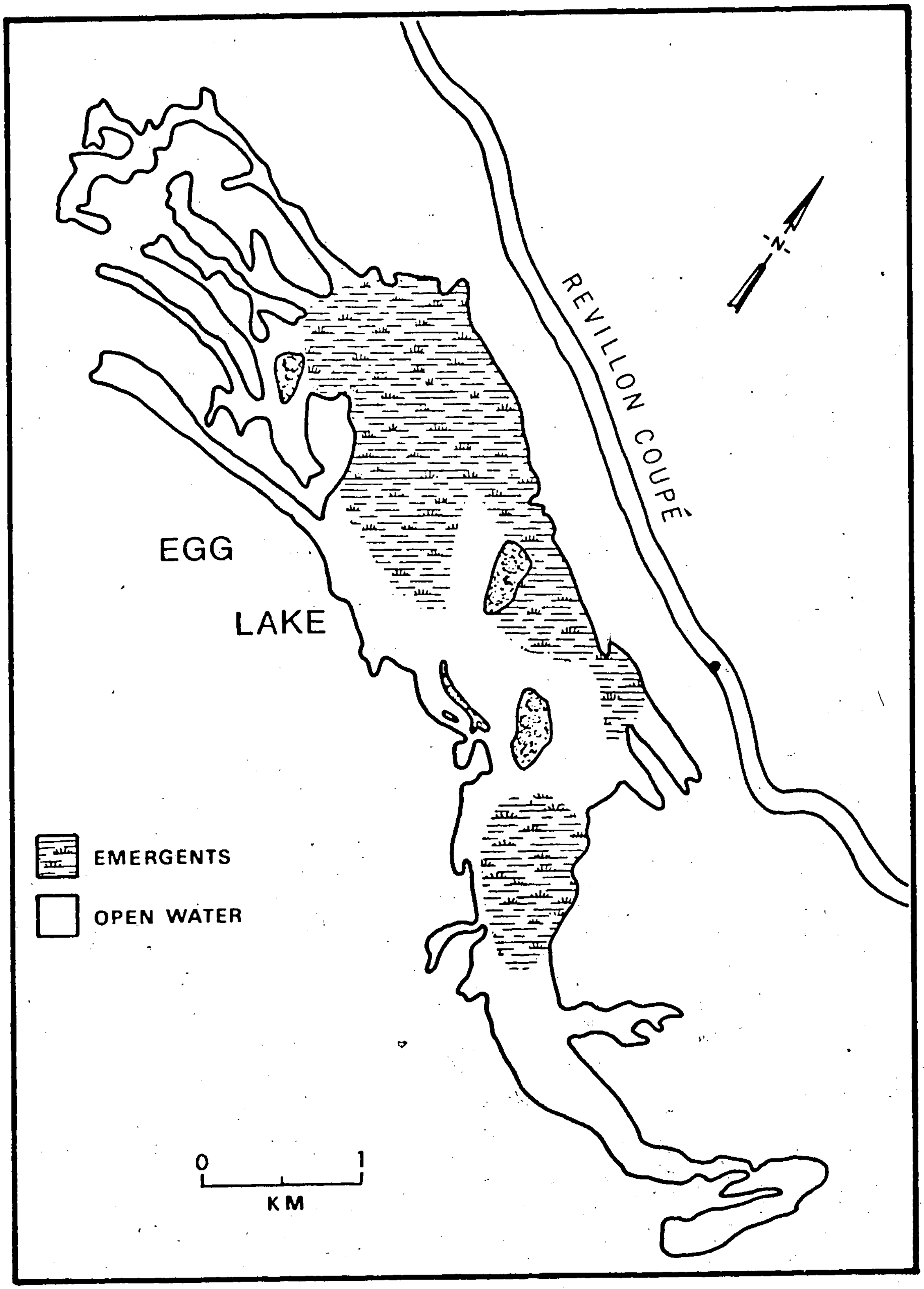


Figure 3. Egg Lake study area showing distribution of emergent vegetation.

Photograph 1. An aerial view of the west end of Egg Lake, looking north across the study area. The Revillon Coupe parallels the lake in the background, September 7, 1971.

Photograph 2. Extensive offshore stands of sedge *(Carex vesicaria)*, typical of muskrat habitat on the west end of Egg Lake, July 1971.

Photograph 3. An aerial view looking west over the study area, September 7, 1971.

A portion of this area, consisting of a transect (approximately 620 m wide) extending across the lake near the center of the study area, is shown in Figure 4. Sedge *(Carex vesicaria)* accounts for approximately 85% of the total emergent coverage in the mapped area. Most of the remainder consists of sweetflag *(Acorus calamus)*, giant burreed *(Sparganium eurycarpum)* and hardstem bulrush *(Scirpus acutus)*. These species usually occur in small, pure stands within the larger stands of sedge. Open water areas contain abundant growths of submerged aquatic vegetation dominated by water milfoil *(Myriophyllum exalbescens)* and pondweeds (principally *Potamogeton zosteriformis* and *P. richardsonii)*. Other open water species, including the floating-leaf types, water smartweed *(Polygonum amphibium)* and yellow pond-lily *(Nuphar variegatum)*, occur only infrequently. Duckweeds *(Lemna trisulca* and *L. minor)* are abundant throughout the marsh. A more complete list of plants found at Egg Lake is given in Appendix II.

Figure 4. A portion of the study area showing the distribution of major vegetation types. Unpatterned areas represent open water (submerged aquatic vegetation).


N
LEGEND
bulrush
burreed
sedge
sweet flag
sweet flag-sedge
horsetail
willow
spruce-poplar
bare mud
rock
grass
500 FEET

METHODS

Livetrapping and Tagging

Livetrap, tag and recapture was the principal method used in this study. It provided information on population size and structure, survival, distribution, movements and social relationships. National brand livetraps and National self-piercing, fish fingerling tags (Size 1, Style 1005) were used throughout the study. In 1970, livetrapping was conducted during July and August over a 140 ha area. In 1971, livetrapping was conducted from June until mid-October with most of the effort restricted to a 100 ha area. This is referred to as the intensive study area. In September and October livetraps were also set on floating platforms in open water areas and along the Revillon Coupe and a nearby slough to sample dispersal within and away from Egg Lake. Additionally, a number of bank runs were livetrapped during 1971 using a multiple capture trap designed by Snead (1950).

Livetraps were baited with pieces of burreed, sweetflag or carrots, and set where capture seemed most likely (houses, feeding-platforms, runways). They were then covered with vegetation to provide shade and extra food for the occupants. Traps were usually set in the evening and checked the following morning. In 1971, traps were checked at about 6 hour intervals if juveniles less than 200 g were believed to be present. After a muskrat was captured it was coaxed into a wire-mesh holding cone fitted with a moveable wooden floor. Slight upward pressure on this floor held the subject relatively immobile for measuring, sexing and tagging. Two sizes of cones held the full range of sizes from newly weaned juveniles to adults.

Data recorded included tag numbers, sex, age (adult or juvenile), weight, total length, tail length, signs of pregnancy, presence of a vaginal membrane, wounds or defects. Muskrats were tagged on both ears and weighed to the nearest 5 g using an Ohaus brand spring scale. To increase uniformity of measurement, tail length was measured from the anus to the tip of the tail. Males were identified by the presence of a penis.

During the study, 610 muskrats were tagged, including 169 in 1970 and 441 in 1971. Livetrapping also resulted in 502 recaptures, including 100 in 1970 and 402 in 1971. Therefore, the total number of captures during the study was 1112.

Reproduction

Information on numbers, sizes and birth dates of litters was obtained by periodically opening houses throughout the breeding season. Houses in each breeding range were checked at about monthly intervals. Best results were obtained when the female was not in the nest, since disturbed females sometimes dragged nestlings into the water. Females were found in the house at all times of the day, however, her presence could often be detected by quietly approaching the house and listening for the sounds made by the suckling young. Fresh construction and preparation of a nest of finely shredded sedge was usually evident several days before the birth of a litter.

When a litter was found, each nestling was sexed, weighed to the nearest gram, measured (total and tail length) and examined for wounds or defects. Females were identified by the presence of nipple scars, a smaller genital sheath and the closer spacing of the genital sheath to the anus than in males. All nestlings over 60 g in weight were tagged -- nestlings smaller than this usually slough-off tags. A litter was recorded as "complete" if the female did not leave the house as it was opened and if nestlings were not found leaving on their own. Following disturbance, the litter was returned to the nest and the house was restored to resemble its original condition. Litters were aged by comparing the average tail length with the tail length regression line of Dorney and Rusch (1953).

Food Habits

A quantitative study of summer food preferences was made in 1971 by comparing utilization of each forage species to its availability within a 30 m radius of the main dwelling or nest house in six randomly-selected home ranges. Utilization was based on the relative abundance of each species on all feeding platforms within this area. Each feeding platform was separated into the component plant types and the relative volume (percentage) of each species was estimated and recorded. Availability was determined on the basis of percent cover of each species within this area. Cover types were recorded on a small scale map of each area. The ratio, % utilization/% availability, was then used as an index of preference for each plant species.

Samples of each food type were collected from several areas in August, air dried and later ground in a Wylie mill, homogenized and submitted to the Alberta Department of Agriculture, Soil and Feed Testing Laboratory for analysis of protein, calcium, phosphorus, fat and fiber. Samples were analyzed separately for the stem, roots and leaves of each species and the results averaged to give a total value for the whole plant.

Habitat Selection and Composition

Each house on the study area was marked nearby with a numbered stake and the location indicated on a map. Plant species around the house (cover type), water depth, size and condition were recorded for each house. Water depth was measured in four places around the house at distances of approximately 2 and 8 m from the house. Ice thicknesses and snow depths were periodically measured each winter.

Cover type selection was related to availability by marking the area covered by each vegetation type on an enlarged outline map produced from aerial photographs. Coverage of each species was then determined by counting dots on an acreage determination grid.

Necropsies

All dead animals found during the study were examined macroscopically in the field for disease, wounds or other causes of death. Weight, length, tag numbers (if present) and reproductive condition were also recorded.

Animals taken during the spring harvests were frozen and later some were examined for helminths. Skulls were cleaned with dermestid beetles and aged using the length of fluting of the first upper molar (Appendix III).

Statistical Analysis

Throughout this report means are presented ± one standard error. The Kolmogorov-Smirnoff test was used to determine normality of data. Means were compared using Student's t-test and most other comparisons utilized Chi square tests. Levels of $P < 0.05$ were considered statistically significant.

DWELLING HABITS

The three types of dwellings referred to most frequently in muskrat literature are houses, bank-burrows and pushups. Relative use of each of these structures by muskrats varies according to local conditions and climate. On the Mackenzie delta, Stevens (1955) reported that muskrats occupied bank-burrows throughout the year due to thickness of the winter ice cover and absence of sufficient emergent vegetation for house building; consequently, they relied on extensive use of pushups to sustain them during winter. In sloughs on the upper Athabasca delta, Fuller (1951) found that summer use of bank-burrows was followed by movement to houses in the fall. This is the pattern reported at Big Island Lake, Alberta by Schmitke (1971). On the other hand, more southerly races often tend to be house dwellers throughout the year (Olsen, 1957; Sather, 1958; Dorney and Rusch, 1953). On the Peace-Athabasca delta, variable use of these structures occurs with different types of water bodies. Muskrats occupying streams, ponded meanders and muskegs predominantly use bank-burrows during the summer, while those in shallow marshes with offshore emergent vegetation make greater use of houses. During the period of study at Egg Lake, muskrats depended almost entirely on houses for shelter throughout the year. This was likely the result of several factors including: (a) an abundance of offshore emergent vegetation suitable for house construction, (b) decreased use of bankburrows during the period of low water levels, and (c) a reduced incidence of destructive ice action due to the absence of spring floods.

Summer Houses and Nest Houses

Houses examined in this study were similar in size and structure to those described in other areas. They typically had from one to three chambers with two or three underwater entrances or "plunge-holes". A distinction is frequently made between "dwelling" houses and smaller, single-chambered "feeding" houses; however, this was not very evident at Egg Lake. Feeding sign was found in most of the houses examined although some small houses were clearly used only for feeding or resting by a single muskrat. Maintenance of old houses and construction of new ones proceeded continuously throughout the summer, increasing in intensity as the population size increased.

Litters were born in old houses, freshly-constructed houses or small open nests. The latter were built in dense emergent vegetation and were similar to nests of some diving ducks. The female entered these structures from the top and covered the nest when she was away from it. The birth of a litter in an old house was preceded by a period of fresh construction. A dry nest lined with fine sedge was normally prepared 2 to 3 days before a litter was born (Photos 4 and 5). In many cases females with litters were apparently tolerant of older juveniles using other parts of the same house; in other cases, new houses or nests were built some distance away from existing houses.

In 1971, 71% (12) of the first litters observed were born in houses used the previous winter. The other 29% (5) were born in newly constructed houses close to a winter house. Of 16 second litters observed, 62% were born in the same house as the first litter, while 38% were born in newly constructed houses or nests built within 40 m of the

Photograph 4. A typical nest house.

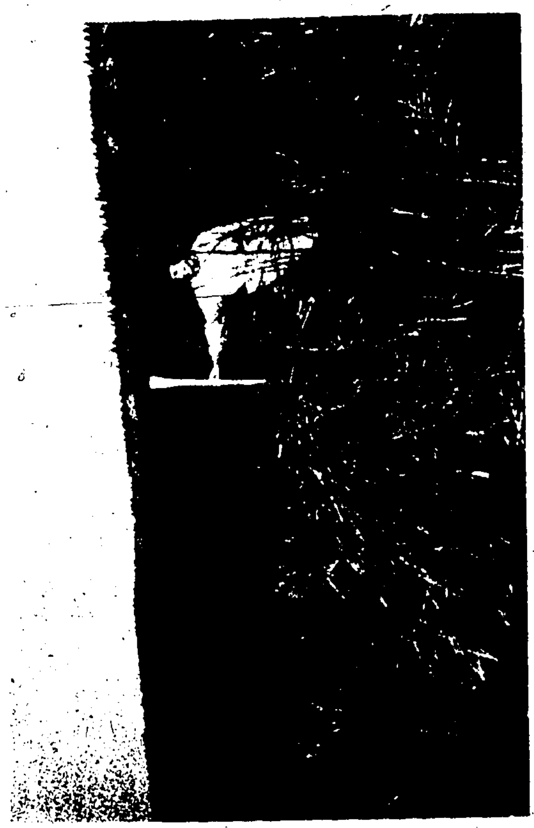
Photograph 5. Top of nest house opened to show nest containing a 2-week old litter.

Photograph 6. A winter house built in a clump of [illegible]sh.

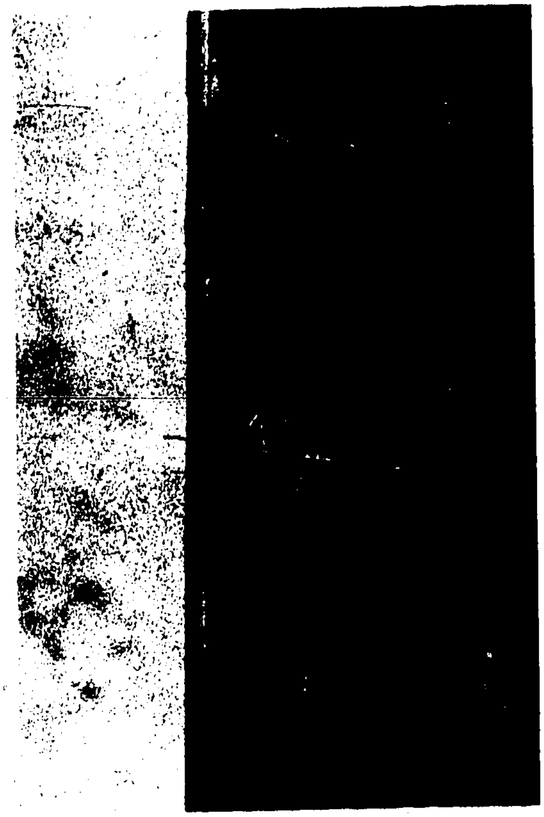
Photograph 7. Vegetation utilization around a winter house, October 19, 1971. Muskrat activity has kept water from freezing in the immediate vicinity of the house.

4

5



6



7

previous house. All eight of the litters known to be third litters were born in new houses.

Fall or Winter Houses

While many of the summer houses continued to be used during winter, a resurgence of house building began in late August and continued until freeze-up (Fig 5, Photo 6). House building was the major activity during this period and seemed to be intensified by weather factors. In 1971, ice skims began forming on the sides of the marsh in mid-September. The first significant snowfall (about 2 cm) occurred on October 16. In my field notes for that date I noted that "for the first time muskrats were frequently seen on houses during the day". The lake completely froze on October 19, although the activity of muskrats kept the water from freezing around houses (Photo 7). House building continued throughout the day and muskrats were frequently seen sitting or moving around on the ice. Muskrats appeared to begin establishing pushups as soon as the lake froze.

Fall or winter houses were generally larger than summer houses; 135 houses measured in October 1971 had an average height of 49.3 ± 1.3 cm and an average diameter of 2.4 ± 0.1 m. Analysis of house size data indicates a single, normally-distributed peak with no suggestion of more than one size class.

Selection of House Building Sites

There was a seasonal trend in location of new houses with respect to water depth (Fig 6). During the period of fall house building there was a definite tendency to select deeper water, while in summer

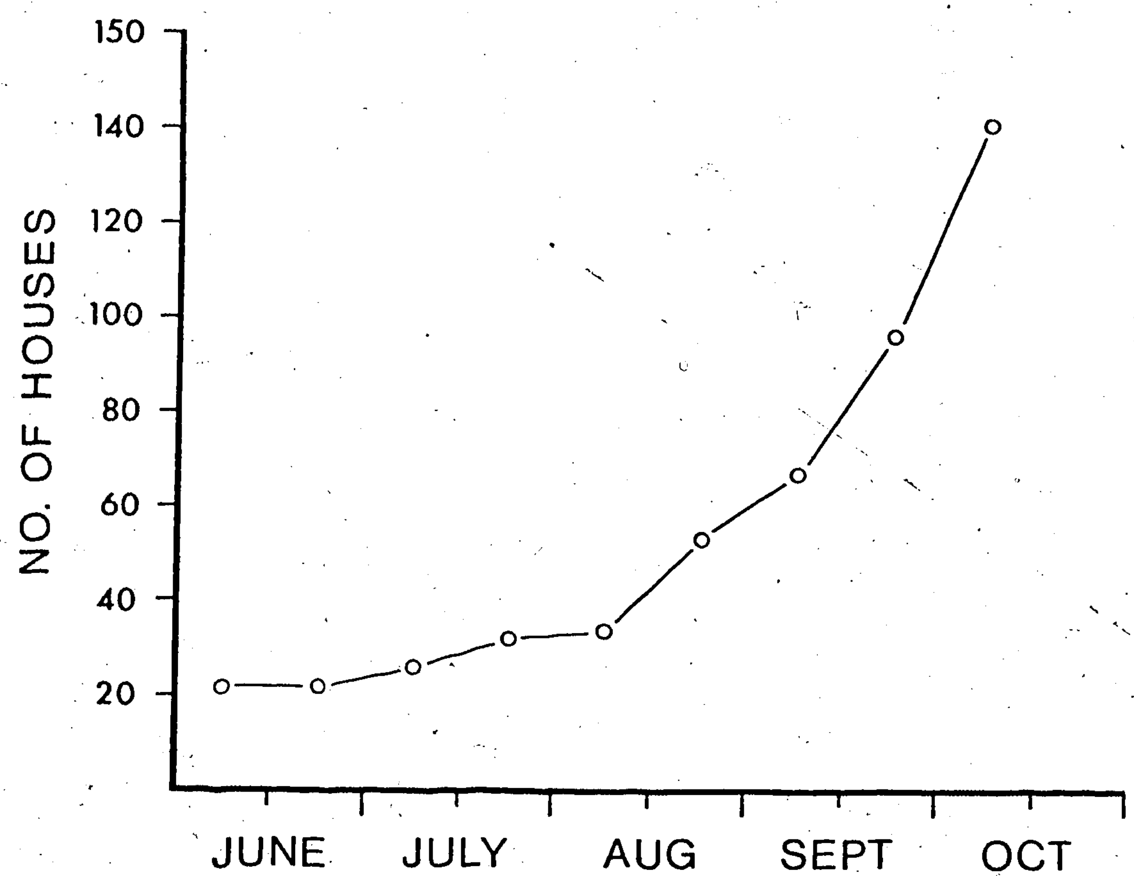


Figure 5. Number of active muskrat houses in a 100 ha portion of Egg Lake during 1971.

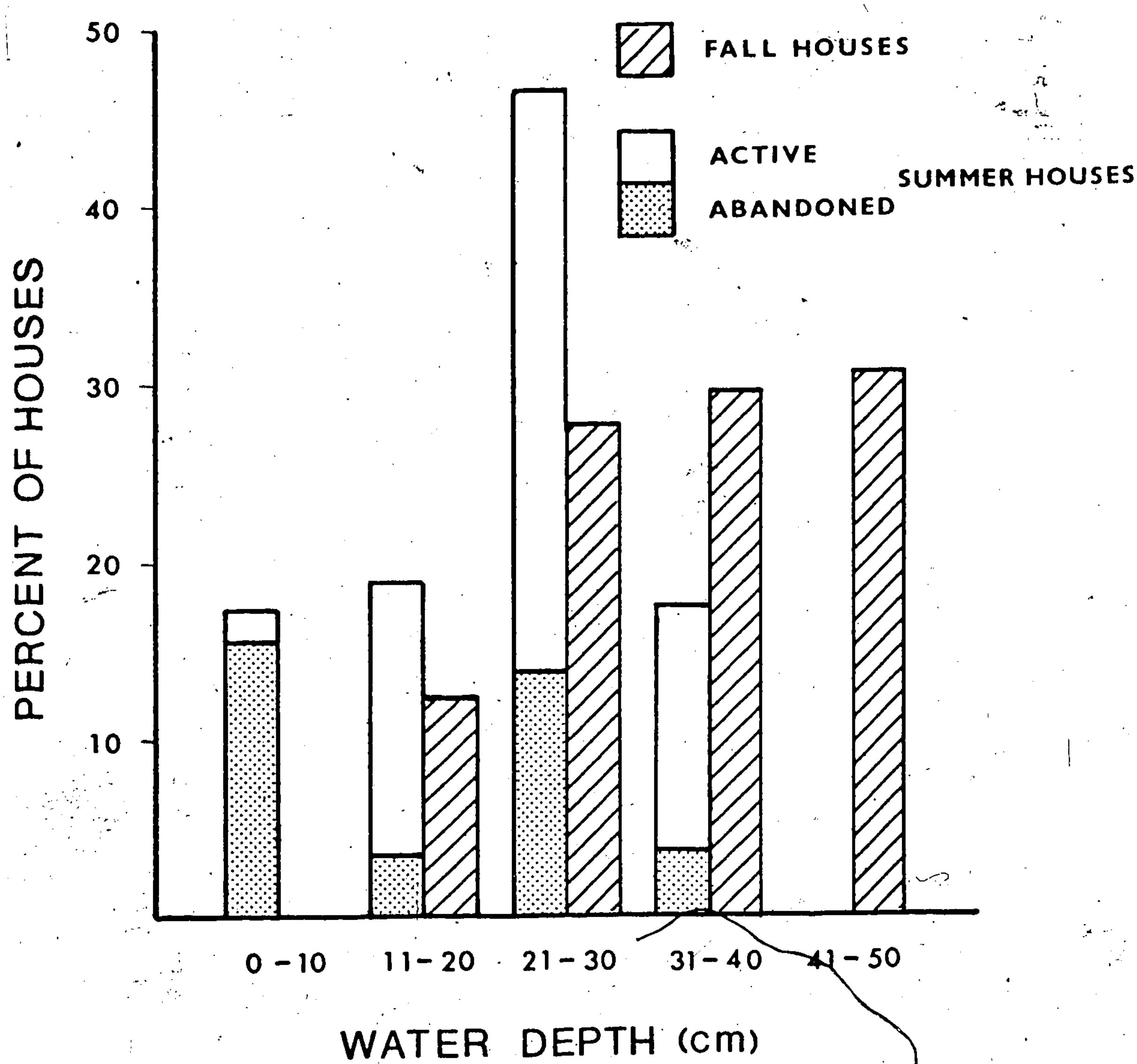


Figure 6. Distribution of summer and fall built muskrat houses in relation to water depth in October 1971.

there was a greater tendency to construct houses on former feeding platforms without regard to water depth. The proportion of summer houses maintained for winter use was lower in shallow water. This partly reflects movements that occurred as the water level declined on the study area. Water deeper than 50 cm was generally not available since muskrats require a base of emergent vegetation to build a house on and 50 cm is near the maximum depth tolerance for most emergent species (Bellrose, 1950; Harris and Marshall, 1963).

There were also seasonal differences in location of houses with regard to cover type (Fig 7). In this study, cover type refers to the kind of emergent plants in the immediate vicinity of the house; in addition, open water (submerged aquatic vegetation) is included as a cover type. Differences between the proportion of summer and winter houses in each cover type were not significant for sedge, burreed or bulrush but were highly significant for sweetflag ($X^2 = 12.37$, $P < 0.01$, 1 df) and open water ($X^2 = 11.64$, $P < 0.01$, 1 df). These differences appear to be associated with selection of deeper water in fall. Sweetflag, which was a preferred food and building site during summer, grew in somewhat shallower water than sedge, burreed and bulrush. Similarly, there was a tendency to build winter houses on the outer edge of vegetation 'islands', adjacent to deeper water.

While the increased frequency of bulrush around winter houses was not significant, it appears to provide the most secure building sites. There are several reasons for this: (1) it tolerates deeper water than do most of the other emergents, (2) the sturdy stems, meshed together with dead stalks, provide a strong matrix for house attachment and (3) during winter it traps a deeper cover of insulating snow than

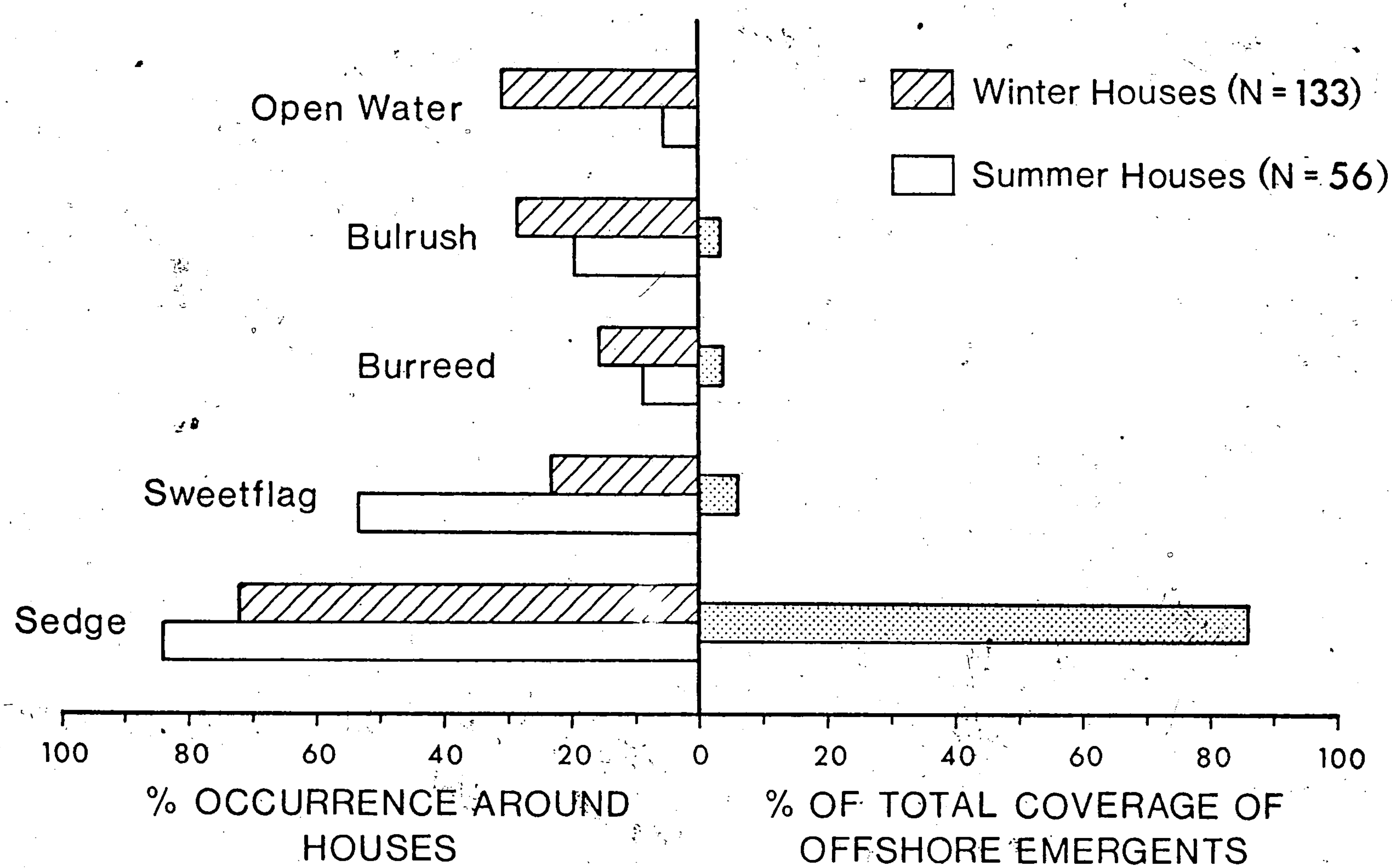


Figure 7. Frequency of occurrence of cover types around summer and winter muskrat houses in 1971 compared with relative availability of each emergent species.

do the others. Almost every available clone of bulrush was utilized as a building site.

While sedge was utilized in about equal proportion to its availability, sweetflag, burreed, and bulrush were distinctly over-represented as cover types. This reflects a tendency to build houses where more than one type of emergent is available. Two or more emergent species were represented at 57% of the summer houses and 32% of the winter houses. In other words, an interspersion of emergent plant types was important in selection of house building sites. The difference between summer and winter houses results from the increase in open water as a cover type during fall.

Composition of Houses

The composition of 50 houses was determined during the summer and fall of 1971 (Table 1). Composition was determined by: (a) separating a portion of each house into component plant types and (b) estimating the percent of the total volume contributed by each species.

In general, houses were constructed from materials that were most available. This was particularly apparent during the period of fall house building. In many cases, all emergent and submergent plant growth was cleared away in a 3 to 7 m radius around part of the house (Photo 5). During summer there was probably a greater tendency for unused food remains to become incorporated into dwellings.

Use of Bank Burrows

There is evidence that use of bank burrows declined as water levels in the marsh receded from levee banks and islands. Shrinkage

Table 1. Composition of 50 summer and fall muskrat houses at Egg Lake in 1971.

Plant	Frequency of Occurrence	Percent Occurrence	Average Percent Composition
sedge	46	92	38 (tr-90)
sweetflag	26	52	22 (tr-80)
burreed	20	40	5 (tr-15)
bulrush	16	32	28 (tr-60)
milfoil	40	80	23 (tr-50)
pondweeds	12	24	tr
willow	5	10	tr
organic bottom material	15	30	30 (5-90)
duckweed	50	100	

of shoreline was proceeding fairly rapidly due to the shallow gradient of the lake basin. In early summer of 1970 the number of active bank-runs around the west end of the lake was approximately 2.5 per km of shoreline; this decreased to 1.7 by June of 1971 and 1.0 in September of that year. This trend was confirmed by Horace Wylie (pers comm).

Many of these were no longer typical bank burrows, since they consisted of a house constructed in the branches or roots of willows and connected to the lake with a long tunnel or open runway. The den itself was sometimes 15 m or more from the water line. This exposed the runways to trampling by bison and increased the vulnerability of the occupants to predation. Bank burrows were usually abandoned when muskrats were no longer able to keep a few centimeters of water in the runway.

Use of Pushups

Pushups are small, single-chambered structures built over a hole in the ice. They serve as shelters for breathing holes and as resting or feeding sites which allow muskrats to forage over an extended area. The structure and function of pushups is described more fully by Fuller (1951) and Stevens (1955). At Egg Lake, pushup construction began immediately after freeze-up, but pushups did not appear to receive extensive use until mid-winter when snow depths were adequate to insulate them and forage supplies became reduced in the vicinity of houses. They were composed almost entirely of submerged aquatics, notably water millfoil *(Myriophyllum exalbescens)* and pondweeds *(Potamogeton* spp). In some cases, particularly where the snow cover was deep, pushups consisted only of a snow cavity above the breathing hole.

Muskrats made less use of pushups in the study area than they did in some of the other delta lakes. In spring of 1971, Canadian Wildlife Service personnel conducted a survey of muskrat houses and pushups on Egg Lake and lakes in two other parts of the delta. They found a ratio of 1.2 pushups/house at Egg Lake compared to 2.5 and 4.5 pushups/house in the other two areas (Surrendi and Jorgenson, 1971). This is probably due to the abundance of offshore emergent vegetation and a greater tendency to construct houses at Egg Lake. Use of pushups is apparently more closely linked with the winter survival of muskrats occupying bank burrows (Stevens, 1955). There is also some indication that use of pushups declined on the study area during the period of low water levels. H. Wylie (pers comm) noted that pushups were more numerous prior to 1970 and that more pushups and fewer houses were evident the winter following the spring flood of 1972.

FOOD HABITS

Widespread studies in North America and Europe have shown muskrats to be highly versatile in their ability to adapt to diverse food sources. While they are primarily herbivorous, local populations may feed extensively on animal material (Errington, 1939, 1941; Sather, 1958; Dilworth, 1966). Some populations show a tendency toward indiscriminate feeding while others demonstrate marked preferences (Errington, 1941; Takos, 1947; Bellrose, 1950; Dilworth, 1966). Only a few of the many studies on muskrat food habits have attempted to relate forage utilization to availability.

Observations of feeding and forage utilization were made throughout the study. These were supplemented by a semi-quantitative determination of food preferences during August 1971. This was accomplished by: (a) determining the availability of major forage species around a number of dwelling houses and, (b) determining the relative abundance of each species on feeding platforms in each of these areas. A ratio of the percent of each species utilized to the percent available in the feeding radius can then be used as an index of preference. Thus an index of 1.0 would indicate that a plant was being utilized in exact proportion to its abundance in the feeding radius of the muskrat. An index of < 1.0 indicates selection against and > 1.0 indicates preference for.

Twelve species of plants were found on 208 feeding platforms examined, of which only seven were abundant enough to be considered important (Table 2). A clear preference exists only for sweetflag with a lesser preference for burreed. Sedge was eaten in slightly greater proportion than it occurred and bulrush was eaten slightly less. This

Table 2. Utilization and availability of principal muskrat food plants on and around 208 feeding platforms.

Plant	Frequency of Occurrence on Feed Plat. (%)	Utilization (%)	Availability (%)	Preference Index
A. calamus	33.7	19.9	4.0	4.97
S. eurycarpum	13.5	5.7	2.1	2.71
C. vesicaria	88.9	63.0	41.9	1.50
P. zosteriformes	33.7	6.8	12.0	0.56
S. validus	6.7	1.4	4.2	0.33
M. exalbescens	40.9	2.7	29.2	0.09
P. richardsonii	6.7	0.6	6.7	0.08
Lemna spp	100.0			

agreed with numerous observations in which sweetflag was being heavily utilized while more abundant species around it were virtually neglected (Photo 9). Similarly new growth of burreed often received heavy local-ized use.

Use of submerged aquatic plants may have been underestimated by this method. Muskrats were frequently observed feeding on the surface of open water areas, where they consumed millfoil and pondweeds without first carrying them to feeding platforms (Photo 10). Duckweed was found on all platforms examined and was profusely abundant throughout the marsh. Muskrats were not observed feeding on this plant by itself, although substantial amounts of it are probably ingested along with other vegetation.

Muskrats also exhibited preferences for certain parts of plants (Table 3). Order of preference was subjectively determined on the basis of observations made throughout the study. For example on July 12, 1971, I recorded the following observation of an adult female muskrat feeding on bulrushes: "She made a shallow dive (about 6 in.) pulling a bulrush stem loose from the roots. She then rested several feet away where she ate all of the white basal portion before discarding the green top." The leaves of sweetflag, on the other hand, were usually cut off 10 to 15 cm above the base.

A notable difference between this and most other studies is the virtual absence of cattail within the study area. While nearby parts of the delta contained heavy growths of cattail, only a few insignificant stands were found at Egg Lake. This may constitute the absence of a valuable food plant. Errington (1963) stated that cattails are the most important native food of muskrats in northern United States.

Photograph 8. An adult muskrat on a predominantly sweetflag feeding platform.

Photograph 9. Heavy utilization of sweetflag.

Photograph 10. A muskrat feeding on submerged aquatic vegetation.

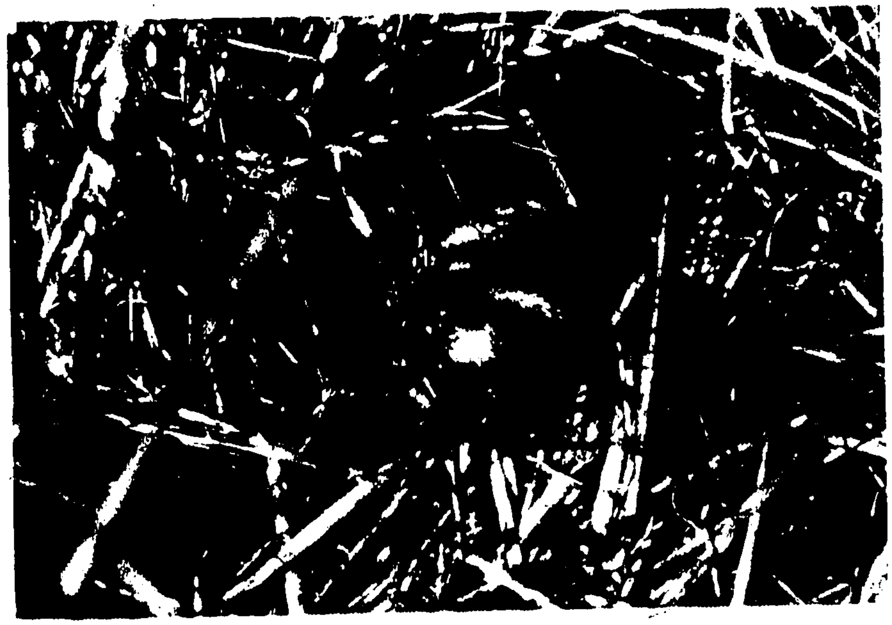


Table 3. Parts of plants eaten by muskrats.

Plant	Parts Eaten in Order of Preference
C. vesicaria	base of stem, leaves, rhizomes
A. calamus	leaves, base of leaves, rhizomes
S. eurycarpum	leaves, rhizomes, base of leaves
S. validus	base of stem, upper stem, rhizomes
M. exalbescens	leaves, stem and fruit
P. zosteriformes	leaves, stem and fruit
P. richardsonii	leaves, stem and fruit
E. fluviatile	stems
S. congestus	stem and leaves
S. cuneata	leaves and petioles
Lemna spp.	entire plant

Use of Animal Food

Several instances of feeding on animal matter were detected during the study. Empty shells of snails were occasionally seen on feeding platforms. Remains of aquatic arthropods were found in the digestive tract of several animals; however, these are probably consumed incidentally while the muskrat is feeding on submerged aquatic vegetation. The partially devoured body of a coot *(Fulica americana)* was found inside a dwelling house on June 13, 1971.

Three incidents of cannibalism were discovered during the two summers. On August 22, 1970 the partially eaten bodies of two nestlings were found, one in the nest and one in a passageway close to the nest of a house which I had not previously visited. Three more 4- to 5-day old nestlings were alive and apparently healthy in the nest. The house was restored and livetraps were set on it. On the morning of August 23, the traps yielded both adults and two large juveniles. The right hind leg of the adult male was completely missing with the resulting wound not yet healed. He had also previously lost one of his upper incisors and the remaining one protruded at an angle. When the house was reopened, one of the remaining nestlings was found dead but uneaten with tooth marks on the neck and foreleg. The pattern of the tooth marks matched the abnormal bite of the adult male. On September 4, 1970 the remains of an older nestling, believed to have been eaten by a muskrat, were found in another previously unvisited house. The third case was found on July 17, 1971 in a recently abandoned house. A 1-week old nestling was found with flesh removed from the head and neck. It apparently had died soon after the litter was captured and measured on July 11. At that time the adult male was livetrapped and broke both of his upper incisors fighting the trap. H. Wylie (pers comm) has also noted occasional incidents of other muskrats feeding on kill-trap victims. Although the first case in 1970 clearly indicates predation by an adult on live young, cannibalism is usually the result of scavenging by starving muskrats and was not a widespread occurrence during the study. This evidence suggests that animal matter is not an important component of the diet of Egg Lake muskrats.

Winter Food Habits

Winter food habits were not studied, although indirect signs of this activity were evident when the ice left the lake. As expected, muskrats apparently relied on greater use of submerged aquatics and the roots and rhizomes of emergents for sustenance during winter than during summer. Runways up to 1 m lower than the floor of the lake were found leading from houses to deeper water. Along one such runway, followed for about 25 m, millfoil and pondweeds had been cleared away for about 0.5 m on either side. The root stocks of sweetflag, sedge and bulrush were often eaten to such an extent that the undermined vegetation was floating in the vicinity of houses.

Little evidence was found of food storage as such, however, this was not looked for in bank burrows or after freeze-up. In October 1971, a recently constructed house (No. 61), almost 1 m in height, was opened to find that the recently chewed-out chambers and passageways were crammed with pondweed (prob. *P. zosteriformes*). H. Wylie (pers comm) has noted that muskrat houses are appreciably larger in years of low water levels. While this differs from the purposeful storage of choice food plants, it undoubtedly constitutes an important winter food supply under those conditions.

Nutrient Content of Food Plants

The nutrient requirements of wild animals in general and musk-rats in particular are not known. It is useful, however, to examine the nutrient content of muskrat forage and extrapolate from the better known requirements of domestic herbivores. Such information also serves as a nutritive baseline for this species. That is, it can be said that this level of nutrients is capable of supporting the observed rate of growth, reproduction and maintenance.

Samples of several of the most important muskrat food plants were submitted to the Alberta Department of Agriculture, Soil and Feed Testing Laboratory for determination of protein, fat, fiber, calcium and phosphorus. The importance of protein for body maintenance, growth, reproduction and lactation is well known to animal nutritionists. Calcium and phosphorus play important roles in skeletal development and reproduction. In domestic animals phosphorus deficiencies are known to cause retarded growth, loss of estrus, embryo resorption and decreased lactation. Fat represents an efficient energy source for the animal. Crude fiber, on the other hand, constitutes the least digestible part of the forage; the level of fiber is usually inversely proportional to the level of digestible energy. If enough low fiber food is not available an animal may not be able to consume enough to satisfy its nutrient requirements.

The nutrient content of the plants analysed appears to fall within the range acceptable to most domestic herbivores (Table 4). Protein requirements for cattle range from 7.5% in a maintenance ration to 11% in a production ration (P.J. Martin, Animal Nutritionist, pers comm). Domestic rabbits require 12% protein for maintenance, 15% for normal

Table 4. Nutrient content of principal muskrat food plants.

Plant	Protein	Calcium	Phosphorus	Fat	Fiber
C. vesicaria					
rhizomes	6.4	0.44	0.21	1.4	32.3
base of stem	3.4	0.12	0.11	1.5	38.5
leaves	7.4	0.29	0.13	1.9	32.9
Mean	5.7	0.28	0.15	1.6	34.6
A. calamus					
rhizomes	7.3	0.68	0.19	7.3	29.3
base of leaves	7.6	0.58	0.19	3.0	40.1
leaves	9.5	0.88	0.14	2.1	37.7
Mean	8.1	0.71	0.17	4.1	35.7
S. eurycarpum					
rhizomes	8.4	0.44	0.24	0.9	31.7
base of leaves	3.6	0.88	0.09	2.0	34.5
leaves	6.2	1.42	0.11	0.7	
Mean	6.1	0.91	0.15	1.2	33.1
S. validus					
rhizomes	7.6	0.58	0.17	0.9	36.4
base of stem	2.2	0.14	0.08	2.1	
stem	8.2	0.56	0.14	1.3	37.3
Mean	6.0	0.43	0.13	1.4	36.9
M. exalbescens					
Whole Plant	17.5	3.20	0.24	0.4	27.2
Potamogeton spp					
Whole Plant	15.0	2.32	0.26	1.2	28.4

growth and 17% for lactating females (NAS-NRC, 1966). Fat levels of 1% to 5.5% were recommended by the U.S. Rabbit Experimental Station (NAS-NRC, 1966). Optimum calcium:phosphorus ratios are generally believed to be in the range of 1:1 to 2:1, although ratios as high as 7:1 may be acceptable to ruminants (P.J. Martin, pers comm). For cattle, 0.18% calcium and phosphorus are required for maintenance. A phosphorus level of approximately 0.22% is required by domestic rabbits.

In general, the leaves are higher in protein and calcium and the roots are higher in phosphorus. The non-green, basal part of the stem and leaves is relatively low in nutrients and high in fiber. The submerged aquatics (*M. exalbesens* and *Potamogeton* spp) are substantially higher in protein, calcium and phosphorus and lower in fiber than are the emergents. These plants are probably an important and efficient nutrient source in winter with considerable survival value. Similarly, the high fat content in the rootstocks of sweetflag may be an important winter energy source. While the level of nutrients can be expected to show seasonal change, the vegetation analysis was done near the end of the growing season and probably reflects winter values.

An important point is that all of these plants are available to most of the muskrats in Egg Lake. This gives them the opportunity of selecting those plants or parts of plants that are high in required nutrients. Consequently, there are no indications that this population faced either a quantitative or qualitative food shortage.

Relationship between Food Preference and Nutrient Content

It is also of interest to determine whether there is a correlation between the observed preference for certain plants and their nutrient content. Table 5 compares the relative nutrient value of six muskrat foods with their degree of preference. Th relative nutrient value of these plants was determined by:

(1) ranking the six plants according to levels of protein, calcium, phosphorus and fat (the plant with the highest nutrient level is given a rank of 6 and the lowest a rank of 1),

(2) summing the ranks for each plant type, and

(3) subtracting the rank for fiber from each sum.

The plant with the highest, total nutrient ranking is considered the most nutritious and so on.

If the four emergent species are considered first, there appears to be a high positive correlation between preference index and total nutrient rank. Unfortunately, the significance of this correlation cannot be properly tested with only four pairs of variables (Spearmans' coefficient). There is also agreement between preference and nutrient content in the two submerged aquatics. The submerged aquatics have a higher nutrient rank than do the emergents but do not have a correspondingly high preference rank. However, I suggested previously that the method of determining forage utilization underestimated the use and therefore the preference rank of millfoil and pondweeds.

Such a correlation between forage selection and nutrient content has been demonstrated frequently for domestic animals (Stelfox, 1971). Palatability is generally directly proportional to protein content and inversely proportional to fiber content (P.J. Martin, pers comm). Muskrats, therefore, appear to be selecting forage both on the basis of palatability and nutritive value.

Table 5. Relative nutritive value of muskrat food plants.

Plant	Preference Index	Nutrient Rank					Total Nutrient Rank
		Protein	Ca	P	Fat	Fiber	
Emergents							
A. calamus	4.97	4	3	4	6	5	12
S. eurycarpum	2.71	3	4	2.5	2.5	3	9
C. vesicaria	1.50	1	1	2.5	5	4	5.5
S. validus	0.33	2	2	1	4	6	3
Submerged aquatics							
Potamogeton spp	0.56	5	5	6	2.5	2	16.5
M. exalbescens	0.09	6	6	5	1	1	16

HOME RANGE, TERRITORIALITY AND MOVEMENTS

Home Range

The classic definition of home range as given by Burt (1940) is "that area about its established home which is traversed by the animal in its normal activities of food gathering, mating, and caring for young". This definition excludes movements associated with migration or dispersal. Most current definitions are essentially unchanged; however, there is widespread disagreement with regard to measurement of home range.

I did not consider the usual method of grid trapping applicable in this study. Muskrats are notably attracted to floating traps in open water. This could have resulted in gross errors in interpretation since the habitat was discontinuous and the proportion of emergent cover was small in relation to the amount of open water. Also, telemetry techniques were beyond the scope of this part of the study. Traps were set where capture seemed most likely (on houses, feeding platforms and along runways) and the locations were marked on a map of the study area. This method gave an insight into the movement patterns of the population but did not permit quantitative comparisons of individual home ranges.

Early in the study it became evident that pairs of adults were occupying fixed areas and that members of each pair could be trapped repeatedly in close proximity to each other, frequently on the same house or feeding platform. In early summer, each pair occupied a fairly limited area within about 50 m of a nest house. Following weaning of the first litter and birth of the second, this area was increased to include additional feeding areas. There was a high degree of cohesion within each family group, with families remaining together until the beginning of the next breeding season. During that period, a muskrat's home range corresponded closely with those of its nearest relatives. They shared dwelling houses and feeding areas and if a move to a more favorable habitat became necessary it was made by the entire family group. Consequently, I found it useful to refer to the area occupied by a family group as a "family home range".

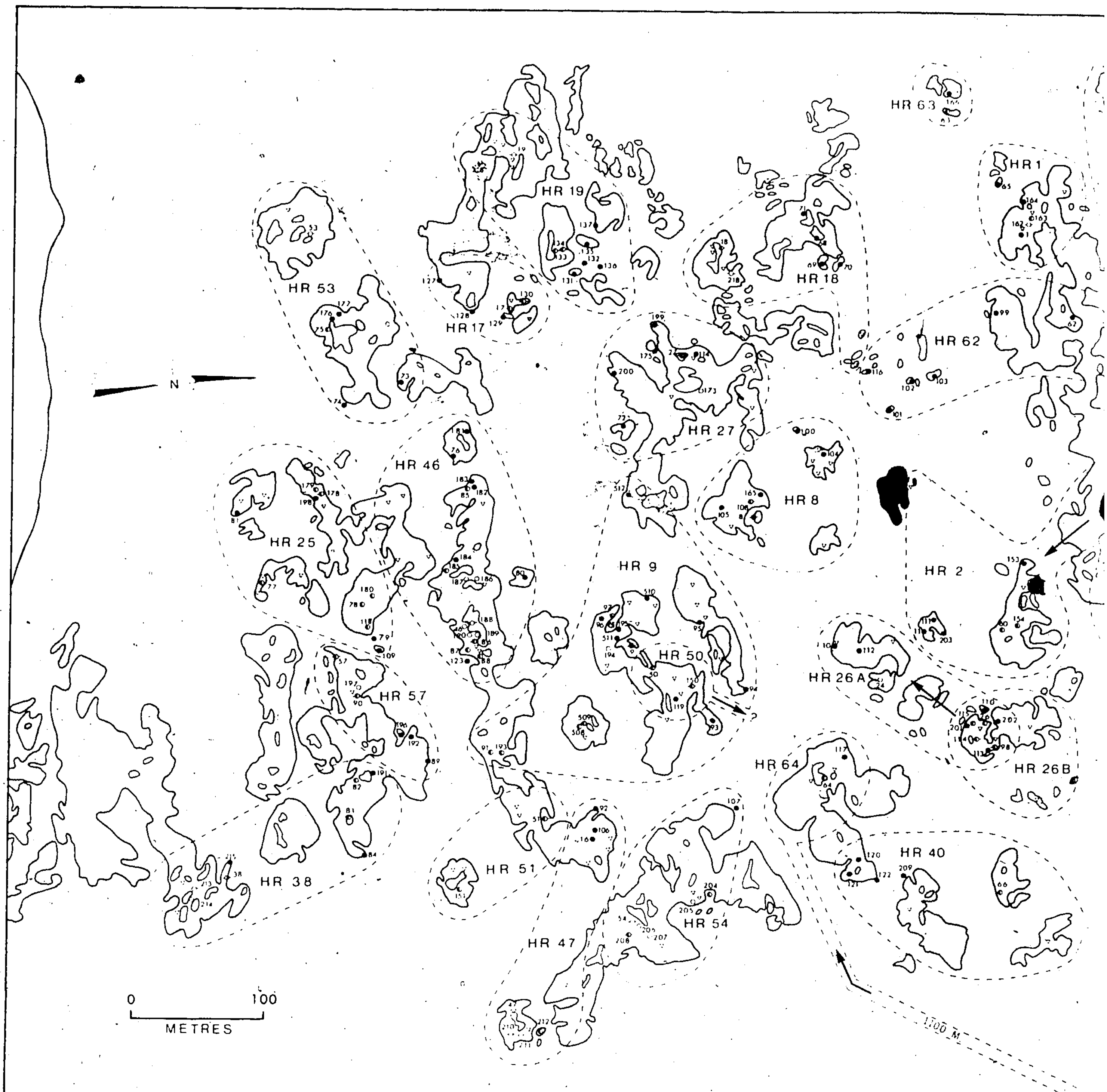
Family home ranges (HR) for a portion of the study area, as revealed by livetrapping in 1971, are shown in Figure 8 with associated data in Table 6. Houses and feeding platforms used by members of the same family group are enclosed by dotted lines. The location of these lines is subjective and no particular significance is attached to size or shape of the enclosed ranges. They were extended to include the area which I felt, on the basis of field experience, likely fell within the home range. Observed differences in home range size and shape may in fact be related to a number of factors including availability of food and cover, family group size, and dominance relationships as well as to the sampling technique. Only home ranges for 1971 are given here as data were more complete for that year than for 1970. There was actually a high degree of similarity between family home ranges in both years, possibly due to the large number of 1970 houses that continued to be used during 1971.

The area of intensive use shifted within each home range during the summer. Houses used early in the summer were sometimes abandoned and new ones constructed near new feeding areas. The area of most extensive use occurred in the fall, just prior to freeze-up. Family home

Figure 8. Family home ranges (HR) of muskrats on the study area during 1971.

-○-	nest houses
○	summer houses
●	winter houses
-◐- ◐	summer and winter houses
▽	feeding platforms
◀——	indicates permanent shift in home range.

[redacted]



N
HR 63
HR 1
HR 19
HR 53
HR 18
HR 17
HR 62
HR 27
HR 8
HR 46
HR 25
HR 2
HR 9
HR 50
HR 26 A
HR 57
HR 26 B
HR 64
HR 40
HR 38
HR 51
HR 54
HR 47
0
100
METRES
1700 M

[redacted]

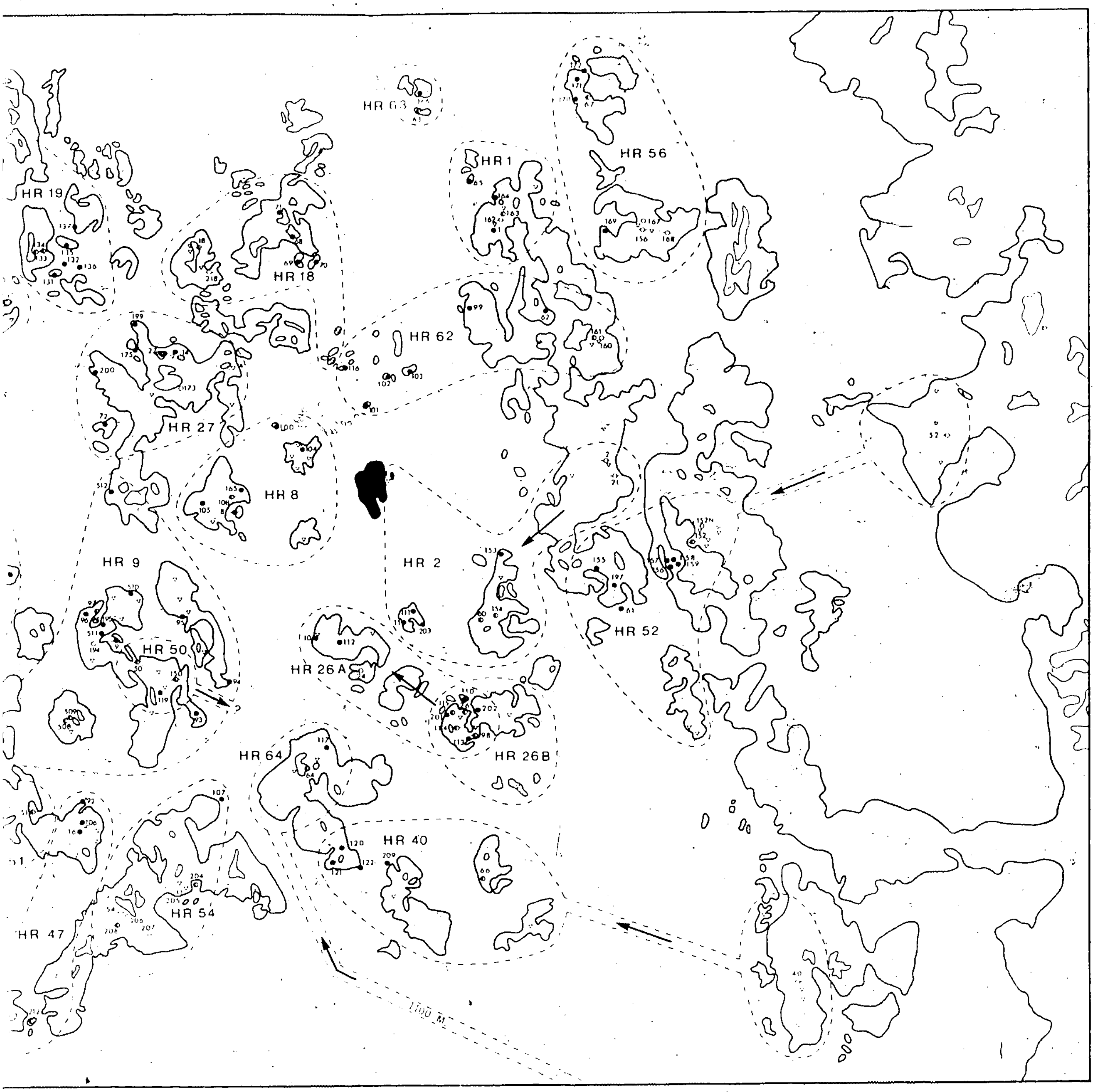

HR 63
HR 1
HR 56
HR 19
HR 18
HR 62
HR 27
HR 8
HR 2
HR 52
HR 9
HR 50
HR 26 A
HR 26 B
HR 64
HR 40
HR 54
HR 47

Table 6. Summary of livetrapping data for 25 family home ranges in 1971.

HR	No. Tagged		No. Recaptures	No. Litters
	Adults	Juveniles		
1	2	4	2	1
2	2	18	22	2
8	2	9	22	2
9	2	19	62	3
17	2	10	13	1
18	2	12	13	2
19	2	15	16	3
25	2	14	19	3
26A	2	3	6	2
26B	2	15	9	2
27	2	8	8	2
38	2	8	6	3
40	2	18	10	2
46	2	27	46	3
47	2	15	12	3
50	2	9	5	2
51	3	1	8	2
52	2	11	18	3
53	2	8	2	3
54	2	19	8	3
56	2	12	18	3
57	2	13	7	2
62	2	20	18	3
63	2	3	6	2
64	2	4	5	?

ranges observed at that time contained an average of 6.0 active houses with a maximum of 17 (HR 9). Houses abandoned previously were often repaired for winter use and all parts of the home range were frequently in use at once. It might be helpful to give an example: HR 25 was located near the south side of the study area. In June 1971 a pair of adults (the female was tagged as a juvenile on house No. 9 in 1970) occupied two houses (178 and 179) located about 2 m apart in a clump of bulrushes. Litters were born in house No. 178 on approximately June 6 and July 5. Both houses were abandoned in mid-July and a new house (No. 77) was built about 75 m away near a feeding platform used earlier. A third litter was born in this house about August 1 and it continued to [illegible] by the entire family until the end of August when several new [illegible] 118, 180) were built about 75 m north of it. In early October [illegible]al new houses were in use (79, 109, 81, 198) and fresh con[illegible]tion was evident on the houses abandoned earlier in the season (77, 178 and 179).

Territoriality

A territory can be defined as that part of the home range from which trespassers are excluded by residents. Comparatively little is known concerning home range and territoriality of muskrats with available literature on this subject showing disagreement. Errington (1940, 1963) concluded that muskrats are territorial, particularly during the breeding season. Sather (1958) reported that family home ranges did not overlap in his Nebraska study. In contrast, Erickson (1959) found that home ranges of family groups in central New York did overlap. Neal (1968) found no evidence of territoriality in northwestern Iowa with up to nine adults using a single lodge.

The best evidence of territoriality on the study area was indirect. Trapping revealed no overlapping of established family home ranges, in that muskrats from only one family group were caught at a given station. This suggests that each family group actively defended houses and feeding areas within its home range. However, two examples of a shift in home range ownership were observed.

One case involved home ranges 9 and 50 during 1971. HR 9 was occupied by a pair of adults that had been tagged on house No. 9 in 1970. In 1971, their first and second litters were born in house No. 9 on approximately May 23 and June 25 with a third litter born about August 19 in house No. 509. In HR 50 the pair of adults produced an "unsuccessful" litter (i.e. a litter that died prior to weaning) in house No. 50 on approximately May 29 and a second litter in house No. 150 approximately July 12. The adult female had also been tagged on house No. 9 in 1970, at the same time as the pair in HR 9. The initial nest houses in 1971 (9 and 50) for both pairs were approximately 30 m apart -- much closer together than was observed for any other home ranges. Although I witnessed no territorial interactions between these two family groups, repeated livetrapping indicated that no home range overlap occurred. The group in HR 50 left the area about a month after birth of the second litter and were not subsequently recaptured. This home range was later occupied by group 9, which repaired the abandoned houses for winter use. The point is that group 50 first left the area before it was occupied by group 9.

On the other hand, overt aggression appeared to be responsible for expulsion of family 26A from their home range. The original pair gave birth to a litter in house No. 114 approximately August 2. By

August 21, this pair had moved to an island of vegetation about 70 m away and a week old litter belonging to a previously untagged pair (26B) was found in house No. 114. During the interval I heard and observed intraspecific fighting in the area on several occasions. Other incidents of this type may have occurred since the declining water level during summer forced muskrats in peripheral parts of the marsh to move and most of the suitable habitat was already occupied by August. In this case, there was also an urgent need for pair 26B to find a safe homesite for an impending litter.

Other isolated incidents of intraspecific fighting were observed or inferred from wounds throughout the summer. It is not known whether or not these were initiated mainly by adult females as found by Errington (1963); nor is it known how much of the home range is exclusively protected. From my observations it seems doubtful that the protected areas extended far into open water.

Summer Movement Patterns

The following two statistics can be used to compare movement patterns within a population: (1) the distance between successive captures and (2) the longest distance between captures (i.e. the distance between the two most separated points of capture).

Average distance between successive captures was used by Brant (1962) and by Wolfe (1968) who obtained a positive correlation between this statistic and home range area of *Peromyscus leucopus* determined by the minimum area method. While subject to many of the biasis involved in livetrapping, this method has the important advantage that movement data from animals having a small number of recaptures can be included.

The longest distance between captures has frequently been used as an index of home range length (Stickel, 1954; Brant, 1962; Brown, 1966; Tomich, 1969). Davenport (1964) found that the longest distance between captures showed the same trends as did the inclusive boundary strip method of home range determination in *Peromyscus polionotus* populations.

A rule of thumb for interpreting movement data is that the number of observations required to determine size of home range is that point at which additional observations do not result in a significant increase. In this study, average values for the longest distance between captures did not increase after two recaptures (Fig 9); therefore, data from muskrats captured three or more times are thought to provide a valid estimate of minimum home range length. This tends to exclude zero values for animals caught twice at the same station.

No significant differences were found between 1970 and 1971 movements, so data for both years have been combined. These data include movements associated with the "normal" extension of home ranges but do not include movements interpreted as dispersal.

Differences between age and sex classes were not significant with respect to either average distance between successive captures or longest distance between captures (Fig 10). The greatest difference was in longest distance between captures for adult males and adult females. This may indicate a tendency for males to be more widely ranging due perhaps to a more active territorial role. Adult females were more confined by breeding and were recaptured only half as frequently as males during the breeding season.

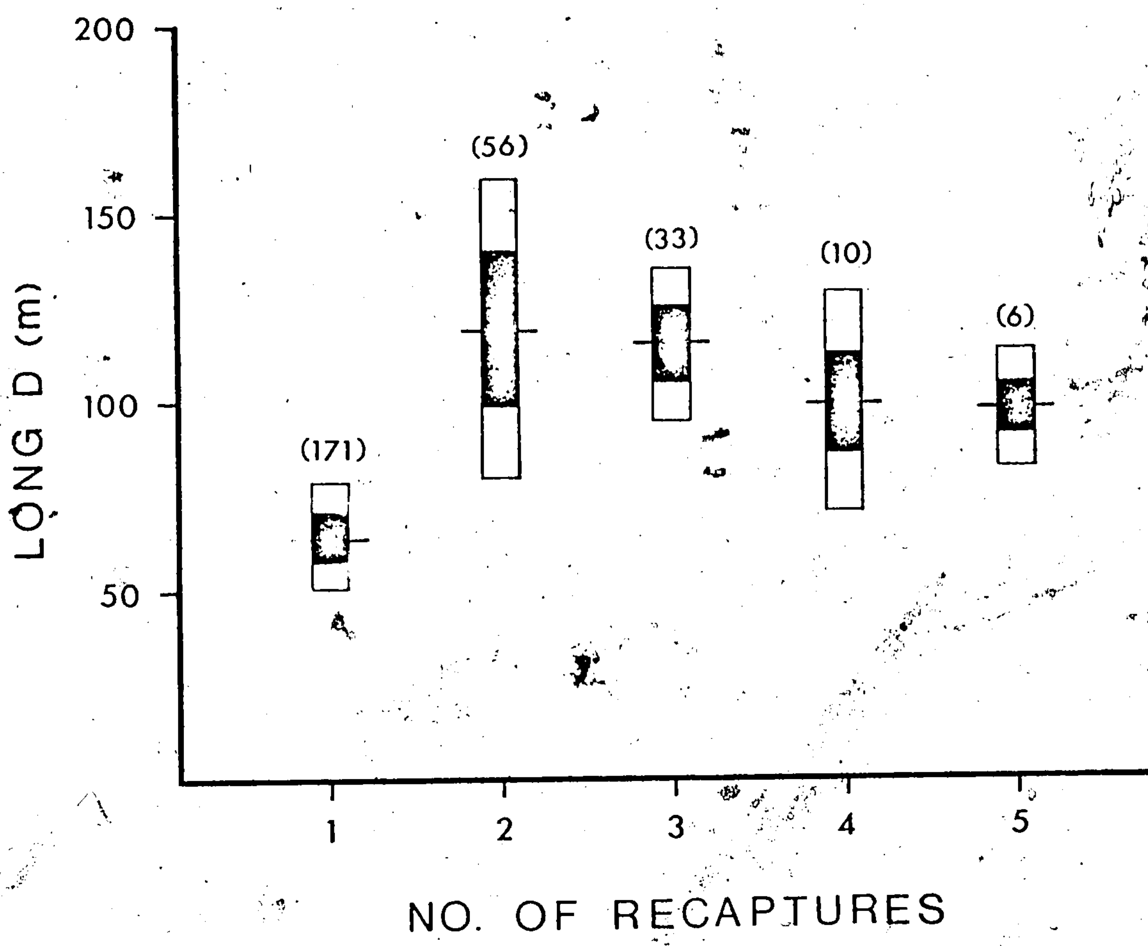


Figure 9. Relationship between number of recaptures and longest distance between captures (Long D) in 1970 and 1971 combined. Means are indicated by horizontal lines. Solid boxes represent one standard error to either side of the mean and open boxes represent 95% confidence intervals for the mean. Number of muskrats are in parentheses.

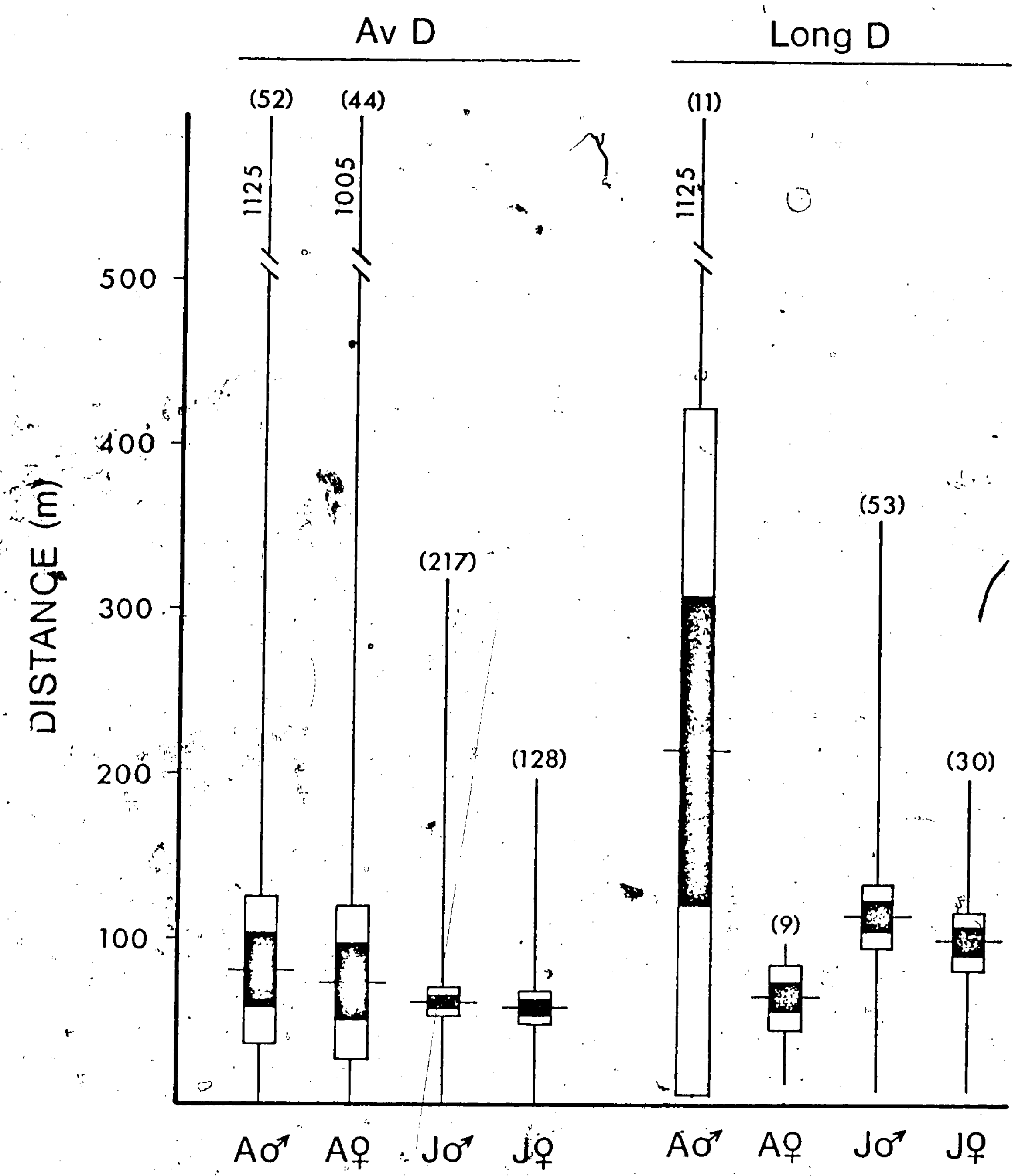


Figure 10. Average distance between successive captures (Av D) and longest distance between captures (Long D) during 1970 and 1971 combined. Means and ranges are indicated by horizontal and vertical lines respectively. Solid boxes represent one standard error to either side of the mean and open boxes represent 95% confidence intervals for the mean. Sample sizes are in parentheses.

There is also no significant difference between the average distance between successive captures and longest distance between captures. This indicates the freedom with thich individual muskrats moved throughout their home ranges. On several occasions muskrats were captured at stations over 100 m apart on successive nights.

Another comparison can be made using the distance between the two most separated capture points in each family home range. This represents the minimum average length of family home ranges and averaged 130 ± 14 m for 25 ranges in 1971. This is not significantly different than the average of the longest distance between captures for individual animals (Fig 10). This means essentially that individual home ranges were similar in size to family home ranges and agrees with the observed high degree of home range overlap between individuals within the family group.

These data indicate that during summer and early fall Egg Lake muskrats occupy a home range of around 100 m in length. Sather (1958) found that muskrats did not move farther than 200 ft (61 m) during summer and early fall. Erickson (1959) also reports average home range sizes of approximately 200 ft (61 m) in diameter. Neal (1968) concluded that "apparently most summer and fall home ranges can be enclosed by a circle 150-200 ft (46-61 m) in diameter". The somewhat larger home range sizes found in this study may reflect a lower population density or a more dispersed food supply on the study area.

Winter Movements

No data were obtained on movements associated with the normal activity of muskrats during winter. One can only suspect that these movements became very restricted when most of the lake became frozen to the bottom in late winter. Evidence from spring fur trapping indicates that muskrats tend to remain within their family home ranges until spring break-up. All of 41 tagged muskrats taken while I was on the study area in April of 1971 were trapped within their fall home ranges. Sather (1958) reported the same tendency in his Nebraska study.

Emergency Movements

As the water level declined during summer and early fall, muskrats in peripheral parts of the marsh were forced to move in the direction of more favorable habitat. In most cases this involved a gradual extension of the home range; whereas, in other cases, movements of over a kilometer were necessary before suitable unclaimed habitat was found. In either case movements caused by drought exposure are considered to be normal home range adjustments rather than part of the dispersal mechanism.

The fates of seven family groups forced to move from drought exposed areas were followed during July and August of 1971. These include home ranges 2, 40, 52 and 64 (Fig 8). All seven remained at their original homesites until water levels approached zero before moving toward deeper water. In each case, the entire family group remained together. Movements into the study area of unmarked muskrats were also observed. In 1971 the number of pairs of adults in the 95 ha area shown in Figure 8 increased from 18 in June to 25 by mid-August.

Information is less complete for drought induced movements in 1970. A home range shift of 240 m was made by a pair with their first litter in late July. In this case the adult female moved at least a few days earlier than did the juveniles. Movement toward deeper water from shallow areas and bank dens during periods of declining water levels has also been reported by other writers (Seabloom and Beer, 1963; Errington, 1939, 1963).

Movements of litters by adults can also be discussed under the heading of "emergency movements". Eight cases were detected in which adults moved litters to a different house. Most instances were probably triggered by my disturbance of the nest house or handling of the litter. The average distance moved was 30 m (3-90 m). The adults carried the nestlings in their mouths to another existing house or constructed a new house before moving them. None of the movements detected in this study resulted in the loss of an entire litter. It is not known to what extent movements of litters occur under normal conditions.

Houses were occasionally disturbed while a litter was being nursed. In such cases the female sometimes left the house with the young still clinging to her nipples. She then either re-entered the house immediately or temporarily deposited the litter in a nearby house or on a feeding platform. Movement of this type was termed "fright movement" by Dorney and Rusch (1953) and was known to have happened seven times in the study area in 1971. In each case at least part of the litter had been returned safely when the house was checked one or more days later.

Dispersal Movements

Spring Dispersal

The many papers which document spring dispersal of muskrats have failed to reach a consensus as to what factors are responsible.

Some workers including Sather (1958) and Erickson (1959) have reported a correlation between break-up of ice and initiation of spring dispersal. Beer and Meyer (1951) correlated spring dispersal with rapid development of reproductive organs and high gonadotropic activity of the pituitary. Errington (1963) concluded that it was a response to "changes in social relationships . . . basically associated with sexual awakening". Mathiak and Linde (1954) also concluded that "breeding season intolerance probably constitutes the prime factor causing the muskrats to move at this time although spring floods may induce some movement". The ecological significance of spring dispersal is more clear. Its importance was stated by Fuller (1951): "Repopulation of areas which have been depopulated through overtrapping, drought, predation, or other causes takes place almost entirely at this time".

Dispersal movements can be broadly divided into those away from the home marsh and those within the home marsh. No information on emigration from the home marsh was obtained as I was not in the study area during the spring dispersal of 1970 or 1971. Although trappers reported seeing muskrats swimming in the rivers during the first week of May each year, following the appearance of open water, no tagged muskrats were reported by trappers in other areas. During this period an increase in intraspecific strife was indicated by an increase in the number of "torn" pelts (H. Wylie pers comm).

Some information regarding movement within the home marsh was yielded by 17 muskrats tagged during 1970 and recaptured during the breeding season of 1971 (Fig 11). These included five males and seven females born in 1970 and one male and four females that were adults in 1970. The average distance between 1970 and 1971 capture sites was

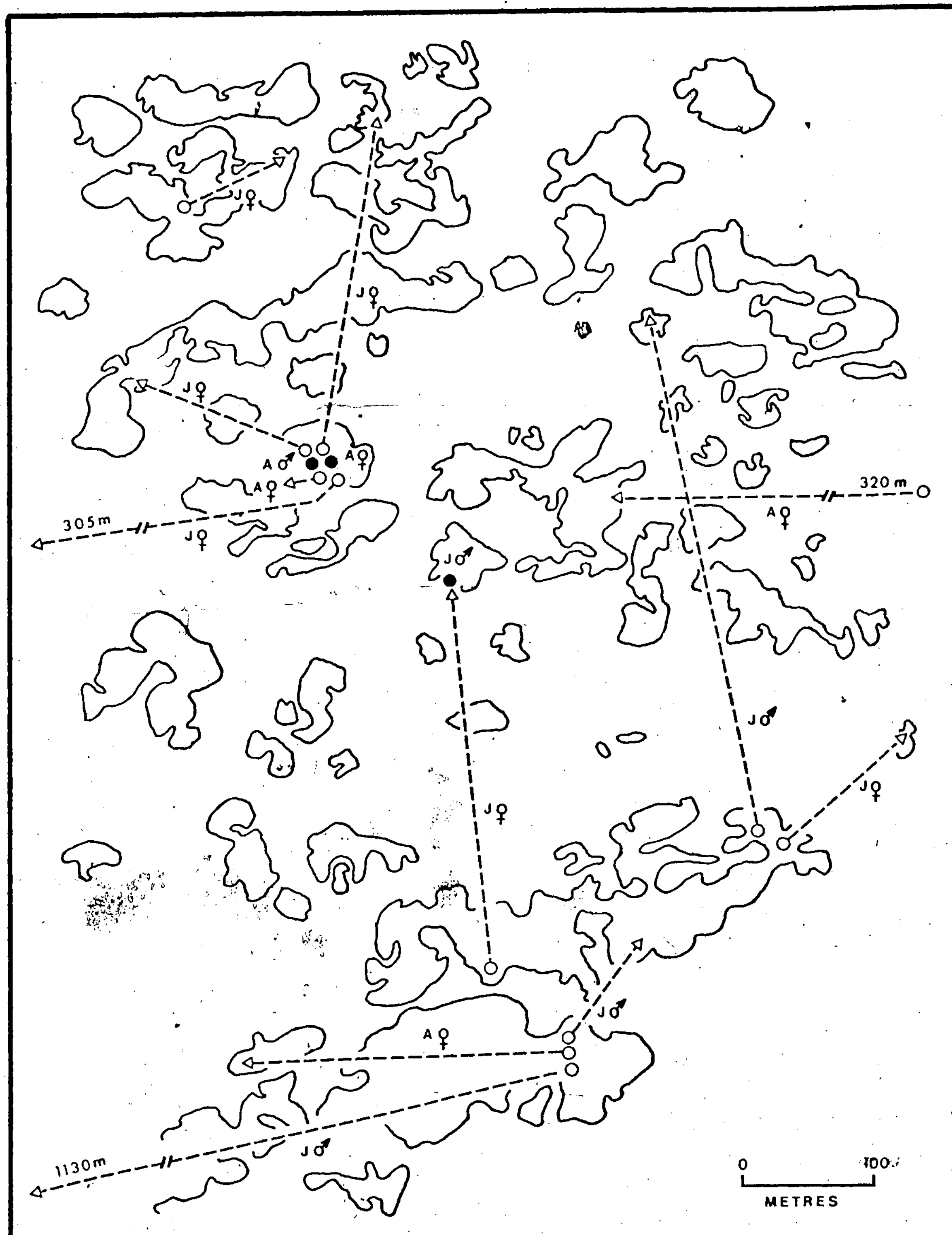


Figure 11. Intramarsh movements associated with spring "shuffle" in a portion of the study area. Open circles denote place of last capture in 1970 and arrows indicate first capture site in 1971. Solid dots indicate muskrats recaptured at the same site the following year.

268 m for the six males and 248 m for the 11 females. These data indicate a fairly complete "shuffle" of home ranges within the marsh during spring dispersal, with only four of the observed muskrats remaining within their former home ranges.

Fall Dispersal

While spring dispersal was associated with break up of family groups and shuffling of home ranges within the marsh, the fall period was marked only by an increasing restlessness among the residents and emigration of a few unsettled individuals.

From the last week of August until freeze-up there was a pronounced increase in the activity of muskrats in open water areas. Floating traps set in the center of large open water areas attracted muskrats from surrounding home ranges as well as a few transients. Two such wanderers captured within the study area on September 17 and 18, 1971, appeared to be victims of intraspecific fighting. One was an adult female that had previously lost most of her tail. The additional loss of use of a hind foot due to a recent slash wound made her almost incapable of diving. Another was an adult male that was later recaptured approximately 1.6 km away on the Revillon Coupe River.

Observations of intraspecific strife increased during this period. On September 12, 1971 four separate incidents of fighting were observed. Another territorial interaction was closely observed just after sunset on September 5. A large juvenile was seen swimming in a circular path around a rock outcropping in the center of the study area. Its movement of 600 m took it through four different home ranges (2, 8, 26A and 62). In one of these (HR 8) it entered a clump of emergent vegetation where it was met with a savage attack and pursued several meters by a resident.

On August 30, 1971 we began seeing muskrats swimming in the Revillon Coupe. During the breeding seasons of 1970 and 1971 no muskrats were sighted in this river. Extreme water level fluctuations in response to wind action on Lake Athabasca make the Coupe unsuitable in terms of muskrat habitat. It does, however, serve as a natural pathway for dispersing muskrats and beaver.

Muskrat activity in the Coupe continued until freeze-up with an apparent peak in intensity in late September. In an attempt to monitor emigration of muskrats from the study area, a series of floating live-traps were set along the river where it runs parallel to Egg Lake. These were checked twice daily from September 21 to October 12. Twelve muskrats were captured during that time of which eight were juveniles (seven males, one female) and four were adults (two males, two females). Both adult males and one juvenile male bore recent slash wounds on the tail. With the exception of the aforementioned adult male, none had been previously tagged on Egg Lake.

Some of these migrants showed a tendency to remain in the area in which they were livetrapped. Five of the 12 were recaptured from 1 to 17 days later, in each case at the same station. Sign along the river indicated that they were using erosion gulleys and driftwood piles for temporary dwellings and that they appeared to be existing entirely on *Equisetum fluviatile*.

No dispersal of resident muskrats was detected during that time, nor were any transients believed to have been successful at establishing home ranges within the study area. This does not preclude the possibility that such movements went undetected. As demonstrated in a later section, known mortality of muskrats during the summer and early fall accounted for all but approximately 5% of the disappearance during that period, indicating that fall dispersal was not a major source of loss of muskrats from the study area.

REPRODUCTION

Mating Habits

Pairing

At Egg Lake there was evidence that the majority of adults form monogamous pair bonds during spring mating that last for at least 1 year. Monogamy was apparent in at least 19 (70.4%) of 27 home ranges studied in 1970 and 28 (93.3%) of 30 in 1971. In these cases the same pairs of adults were repeatedly livetrapped within particular family home ranges and frequently capture of both adults on the same house suggests that males probably had some role in construction of nest houses and care of the young.

Of the eight exceptions in 1970, seven involved an extra female and the other one, an extra male. In 1971, one home range contained two adult females and the other, two adult males.

There are two possible explanations for the greater incidence of apparent polygamy in 1970 compared to 1971. Firstly, livetrapping was less intensive in 1970 than in 1971 and breeding ranges were consequently less well defined, therefore, some of the exceptions may have involved capture of transients or residents of neighbouring home ranges. There were only two instances in which two adult females were captured on the same house. The second possibility is that the population actually was overbalanced in favor of females in 1970. Of 62 adults tagged during July and August of 1970, 34 (55%) were females. These results may agree to some extent with Beer and Meyer (1951) who found that "the females are considerably more tolerant of their own sex than the males". I do not know whether the "extra" females took part in breeding; however the number of juvenile age classes found in "polygamous" home ranges suggested that they usually did not.

Only one pair of muskrats is known to have remained together through two complete breeding seasons. This was at HR 9 where the first and second litters of 1971 were born in the same nest house used in 1970. The number of pair bonds lasting for more than 1 year may be higher in an untrapped population but a duration of 1 year seems to be the general rule. With a couple of exceptions (McLeod and Bondar, 1952; Dozier, 1953), the literature is in general agreement that muskrats are monogamous (Sather, 1958; Erickson, 1959; Schmitke, 1971).

Minimum Breeding Age

No evidence in this study indicates that juveniles begin breeding in the year of their birth. None of the juvenile females examined during fall livetrapping had perforated vaginal membranes or showed signs of pregnancy. Several workers in Canada and the USSR have demonstrated that a marked regression in testis weight and function occurs during August (McLeod et al., 1951; Stevens, 1955; Aspisoff, 1957; Olsen, 1959; and Lavrov, 1960). It seems highly unlikely that the breeding season at the latitude of Wood Buffalo Park is long enough to allow precocial breeding.

Some writers have reported that yearlings begin having litters later in the breeding season than older animals (Stevens, 1955; Lavrov, 1960). In northern USSR, yearlings begin breeding about a month and a half later than adults while in the south they begin to breed at about the same time (Lavrov, 1960). A small amount of data obtained at Egg Lake suggests that breeding of yearlings and older females begins about the same time. In 1971, two females that were known to be at least 2 years old gave birth to litters backdated to May 23 and May 29 while five females born in June of 1970 had their first litters on May 27, June 1, June 6, June 8 and June 18. Data were not obtained for juveniles born later in the summer.

Breeding Season

Observations regarding the onset of breeding were not directly obtained as I was not present on the study area during that period in either 1970 or 1971. In 1970 H. Wylie (pers comm) stopped trapping on May 6, at which time embryos were visible in some of the females. Assuming a period of 10 to 14 days between conception and the time that embryos are visible (Gashwiler, 1950), breeding would have occurred approximately between April 23 and 27.

On May 6, 1971, small embryos were again visible in trapped females. The earliest backdated birth in that year was May 23. Assuming the generally established gestation period of 28 to 30 days, conception of this litter would have occurred about April 23-25. April 20 was an unusually warm day preceded by a period of mild temperatures. In early morning, travel by skidoo was possible on the lake but by evening, open water covered most of the lake and muskrats were active above the ice. Such a correlation between the appearance of open water on lakes and the onset of breeding has also been reported by other investigators (McLeod et al., 1951; Fuller, 1951; Stevens, 1955; Aspisoff, 1957; Erickson, 1959; and Lavrov, 1960). Fuller (1951) agreed that mating begins between April 20 and May 1 in Wood Buffalo Park and is determined by the time of ice break-up. Lavrov (1960) wrote that

". . . mating begins soon after the appearance of patches of open water and emergence of the animals . . ." and noted that "wh[illegible] spring comes late, mating is delayed".

The last known births occurred on August 18 in 1970 and August 21 in 1971. This is apparently associated with the aforementioned decline in sexual activity of the adult males. The proximate factors responsible for the cessation of breeding are not known, although likely factors include photoperiod, increasing density and decreasing quality of forage. The length of the breeding season the[illegible] about 4 months.

Temporal Distribution of Births

The birthdates of 10 litters in 1970 and 40 litters in 1971 were determined by backdating using Dorney and Rusch's (1953) tail length regression. Limited neonatal growth data obtained during this study compared reasonably closely with the above growth curve for Wisconsin muskrats. Since only 10 litters were examined during 1970, these data were supplemented with birth dates determined for livetrapped juveniles. At the end of August it was still relatively easy to distinguish between juveniles of different litters. Measurements of tail length were averaged for juveniles of each litter and age was established using a growth curve for tail length determined from livetrapping data. The earliest livetrapping period was used in each case and only the litter groups less than about 3 months of age (tail length <.235 mm) were included. To reduce the error in backdating, birthdates determined in this way for 1970 and 1971 were [illegible]uped in semi-monthly intervals (Fig 12). This only provides a general picture of the distribution of births but indicates that the period of production was similar each year.

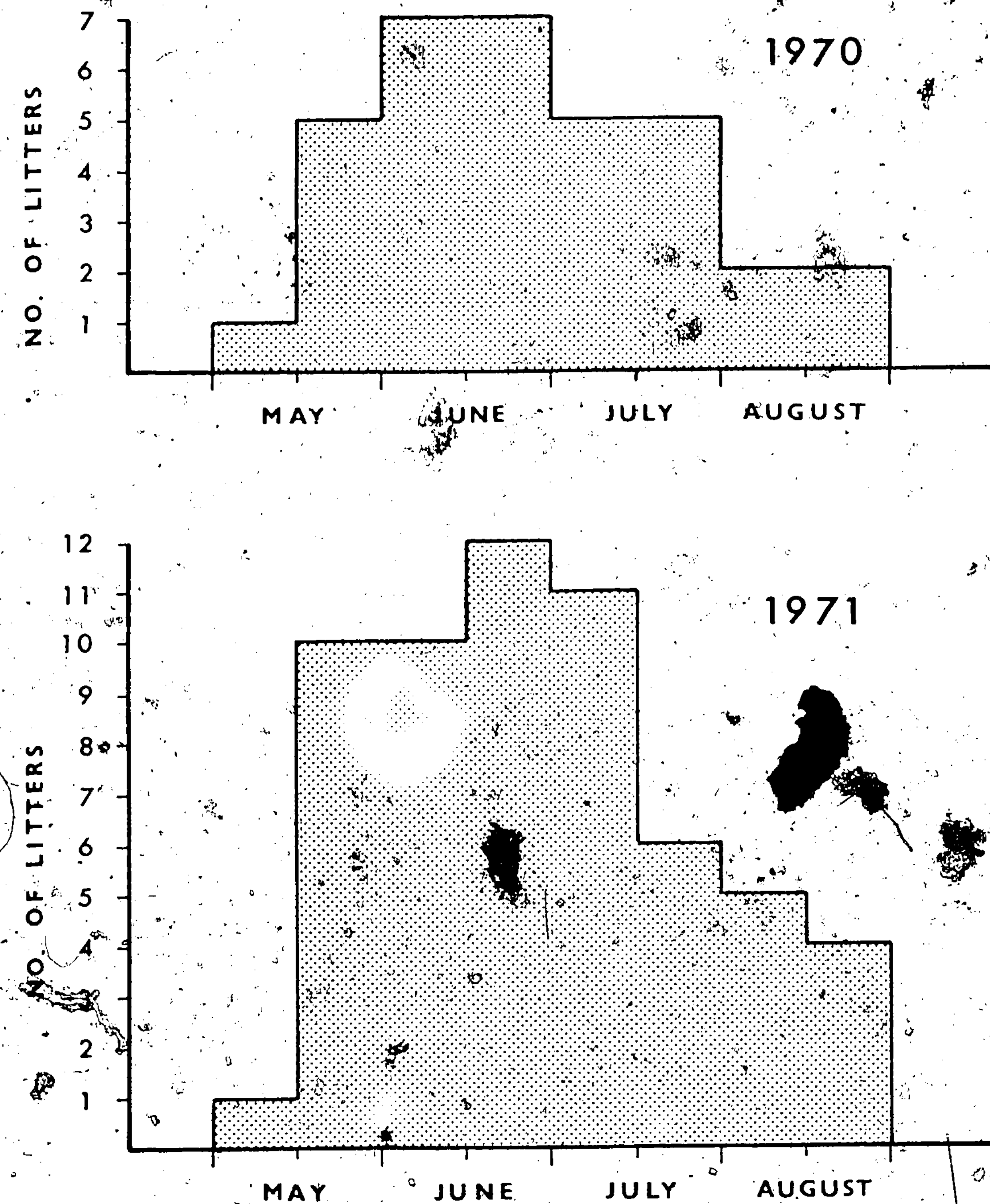


Figure 12. Distribution of muskrat births during 1970 and 1971, grouped in semi-monthly intervals.

In both years parturition appeared to be continuous through the breeding season with June being the month of highest litter production. These findings do not seem to agree with some other workers who have reported a synchronous, well defined peak at the beginning of the breeding period followed by subsequently reduced peaks at approximately monthly intervals (McLeod et al., 1951; Dorney and Rusch, 1953). Olsen (1959) found that early litters on his study area in 1955 were largely unsuccessful due to flooding; in 1956 later breeding, attributed to "an abnormally large proportion of late born young from the preceding year", resulted in a distribution similar to those in Figure 12. In my study, flooding was not a factor but there is some reason to believe that trapping may have effected the temporal distribution of litter production. Open-water trapping following spring break-up is both legal and widely practiced in this area. It is a period when mating behavior and high attraction to bait make muskrats highly vulnerable to hunting (H. Wylie, pers comm). The effect of this on the formation of breeding territories and the synchrony of litter production is not known; however, the fact that pregnant females were being taken at the end of the trapping season indicates that the magnitude of the first period of litter production may have been artificially lowered. This may be important if it results in a lower number of litters produced or lower survival of litters born later in compensatory breeding. An obvious advantage exists if muskrats produce most of their young during the period of most favorable conditions.

In 1974, periods of litter production differed significantly with respect to litter order (Fig 13). Females produced their first litter of the year as late as July 13, however, the period between May

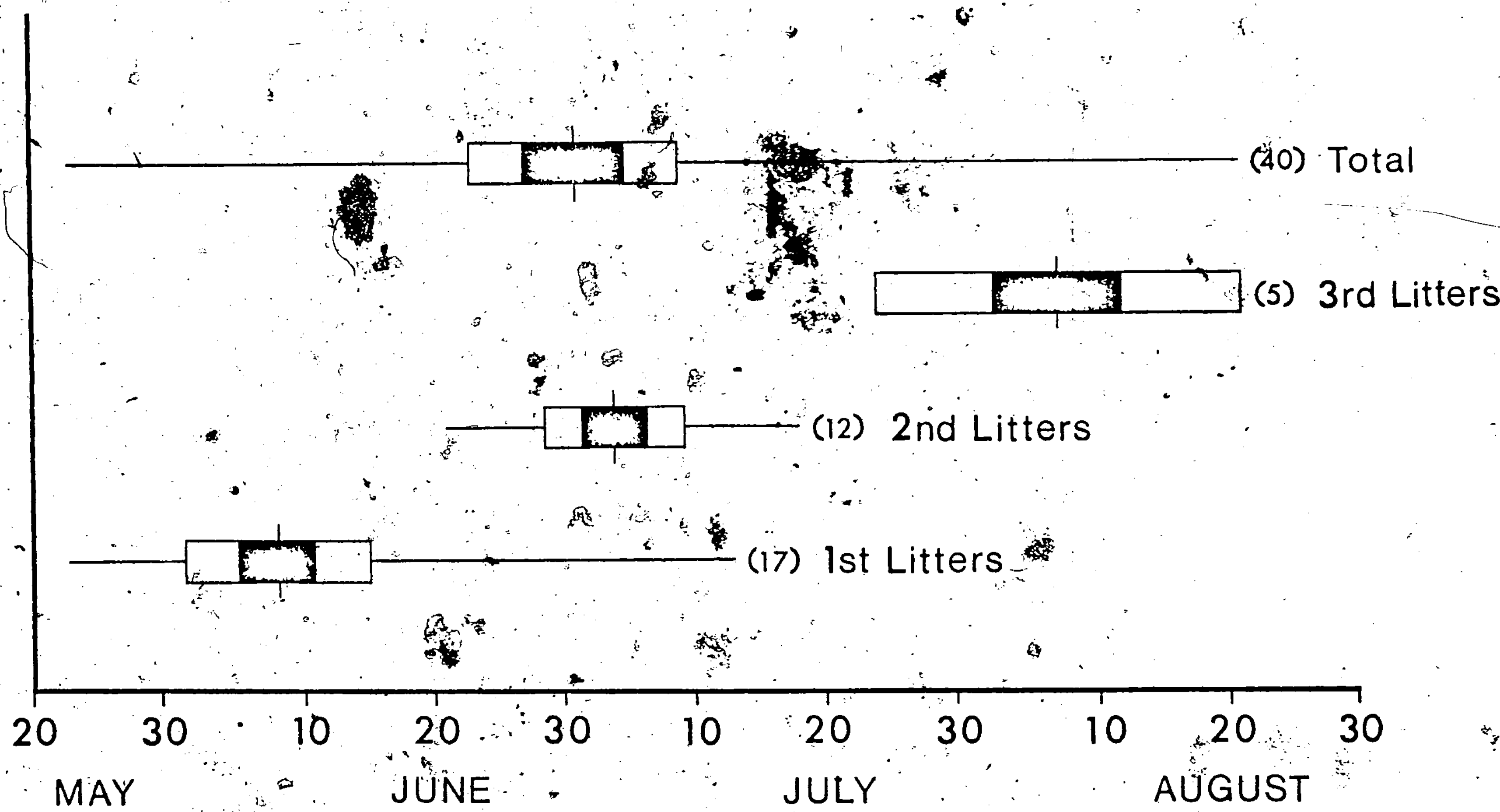


Figure 13. Birthdates of muskrat litters in 1971 according to litter order. Means and ranges are indicated by vertical and horizontal lines respectively. Solid boxes represent one standard error to either side of the mean and open boxes represent 95% confidence intervals for the mean. Number of litters are in parentheses.

23 and June 18 accounted for about 90% of the first litter production. Second litters were born from June 21 to July 18 and birth of third litters began about July 25.

Number of Litters Per Female

The number of litters produced per female during the 1970 breeding season was not determined. Nest checks were not started in earnest until late June and livetrapping was discontinued at the end of August, before many of the late litters were old enough to be livetrapped. Also, because of the low population levels during the study, the usual method of collecting females at the end of the breeding season to count the number of uterine scars was not deemed worthwhile. It did become apparent, however, that most of the females were having two litters and some were having three.

In 1971, periodic nest searching and intensive livetrapping of family groups throughout the breeding season gave productivity data on 18 females. Of these, all bred, with one (5.6%) producing one litter, nine (50.0%) producing two litters and eight (44.4%) producing three litters, for an average of 2.4 litters per females. This figure may be slightly smaller than actual production due to the possibility of an unsuccessful litter going undetected. If data based only on livetrapping of another seven family groups are included, the average number of litters for the combined sample of 25 females is unchanged at 2.4. There was no evidence of a fourth litter being produced.

Again the small amount of data obtained makes it difficult to assess the effect of age on breeding performance. Six females that were known to be yearlings in the summer of 1971 produced an average of

2.2 litters while four muskrats known to be at least two years of age produced an average of 2.5 litters.

Interval between Consecutive Litters

Reliable data on the interval of time between consecutive litters was obtained for 13 females (Table 7). In each case only one adult female was present in the home range and intensive livetrapping verified that it was the same female that was responsible.

The length of time between birth of the first and second litters for 10 females ranged from 28 to 44 days with a mean of 32.9 days. The interval between the second and third litters for five females ranged from 26 to 57 days with a mean of 33.8 days.

Closer examination of this table shows that with three exceptions (43, 44 and 57 days), all of the intervals fall within the range of 26 to 33 days and give an overall mean of 29.5 days. This is probably close to the "normal" interval as is evidenced by an equal mode of 29 and 30 days. The reasons for the longer intervals are not known, although variations in gestation period or time of implantation might occur (Errington, 1963). The 57 day interval is about twice the "normal" period suggesting that an unsuccessful pregnancy may have gone undetected. If this did occur the female involved would have been pregnant four times.

Although only litters less than 3 weeks of age were included, an error may have again been introduced by backdating. These data do indicate, however, that the interval between consecutive litters is about a month and verify that conception usually occurs during post partum estrus.

Table 7. Time interval between births of consecutive litters of muskrats.

Tag Numbers of Female	Interval between Births	
	1st-2nd	2nd-3rd
47		29
160,161	33	
166,167	29	
170,171	44	
172,173	28	
174,175	29	27
270,271		30
325,326	43	
423,424	30	26
623,624	31	
654,655	30	
799,800	32	
939,940		57
	$\bar{x}$=32.9	$\bar{x}$=33.8

Olsen (1959) reported an average interval between successive litters of 27.9 days (18-35) while McLeod et al. (1951) obtained an interval of 28 days and Dorney and Rusch (1953) one of 33 days (29-35).

Litter Size

During this study, litter size was determined for 9 complete litters in 1970 and 23 complete litters in 1971 (Table 8). Litters were judged to be incomplete if the female left the nest as the house was being opened or nestlings were noticed leaving on their own. There is a possibility, however, that error resulted from: (1) incomplete birth of the entire litter, (2) mortality prior to handling or, (3) unnoticed escape by some of the nestlings. The results are therefore minimum estimates of litter size.

There is no significant difference between the mean size of 7.2 in 1970 and 7.5 in 1971. Litter size ranged from 5 to 9 in 1970 with a mode of 8 and from 4 to 11 in 1971 with a mode of 6. In 1971, there was an apparent decline in size of successive litters (Table 8). First litters were significantly larger than second litters ($P < 0.05$). The reason for this is not known, although it might reflect seasonal changes in reproductive physiology of the females.

Average Production Per Female

Average production is the average number of young produced per female during a breeding season. Multiplying the average litter size (7.5) by the number of litters per female (2.4) gives an average production of 18.0 in 1971.

These data fall within the range reported in the literature. Fuller (1951) derived a figure of 17.4 young per female on the basis

Table 8. Size of complete muskrat litters in 1970 and 1971.

Year	No. of Litters	Mean Size (± s.e.)		
1970	9	7.2 ± 0.51		
1971				
1st litters	8	8.9 ± 0.57	t=2.31*	
2nd litters	12	7.2 ± 0.47		t=0.37
3rd litters	3	5.0		
Total 1971	23	7.5 ± 0.41		

*P < .05

of placental scars but found no evidence of the third litter being produced. Ambrock and Allison (1973) also found production to be somewhat lower on the Athabasca delta (about 50 km southeast of Egg Lake) due to smaller litter sizes and production of two litters. At Big Island Lake, Alberta, Schmitke (1971) found average placental scar counts of 16.2 to 22.8 and an average litter size of 8.0. Using the same method, Gunson (1968) placed production at 19.4 in 1966 and 15.3 in 1967 at Cumberland marsh, with average litter sizes of 7.0 and 7.1. Olsen (1959) obtained average scar counts of 19.4 and 20.4 for two years at Delta, Manitoba, with litter sizes of 7.1 and 7.3. Errington's (1963) long-term studies in Iowa yielded an overall average of 2.5 litters per female and 7.5 young per litter for an average production of 18.8 young per female. Variations in reproductive performance are apparently related to location, subspecies and phase of the population cycle (Errington, 1963).

SEX AND AGE STRUCTURE

Sex Ratios

In 1970 and 1971, the sex ratio of nestlings was strongly unbalanced in favor of males (Table 9). This agrees with the findings of most other workers (Beer and Truax, 1950; McLeod et al., 1951; Olsen, 1959; Erickson, 1959; Mathiak, 1966). McLeod et al. (1951), Olsen (1959) and Schmitke (1971) found that males predominated in early litters with the sex ratio becoming almost even at the end of the breeding season. This did not appear to be occurring at Egg Lake since the imbalance was greatest in second litters.

Some writers have suggested that the sex ratio is almost even at birth with sex selective mortality in the first few weeks of life causing the preponderance in males (Olsen, 1959; Beer and Truax, 1950). Data obtained in this study are not in agreement on this point (Table 10). It would appear that factors are operating within the reproductive tract of the female that favor an excess production of males. Errington (1963) also reported a preponderance of males (61.2%) among new-born muskrats.

Juvenile males continued to predominate in summer and fall live trapping and samples from the spring harvest (Fig 14). Adult sex ratios, on the other hand, were nearly even during the breeding season. This agrees with most other studies (Fuller, 1951; Stevens, 1955; Errington, 1963; Mathiak, 1966; Gunson, 1968; Schmitke, 1971). Adult females predominated in the spring harvest of 1971 while adult males predominated in the 1972 harvest. These changes probably reflect the small sample sizes for these groups as it seems unlikely that factors would favor female survival one winter and male survival the next.

Table 9. Sex ratio of nestlings

	Sample Size	Males:Female	Probability*
1970 Total	60	1.31	NS
1971			
1st Litters	68	1.27	NS
2nd Litters	86	1.77	< 0.05
3rd Litters	15	1.14	NS
Unknown	59		
Total	228	1.40	< 0.05
TOTAL	288	1.38	< 0.01

*χ^2 test for goodness of fit to a 1:1 ratio.

Table 10. A comparison of nestling sex ratios in relation to age of litters.

Age (days)	Egg Lake Sample Size	Egg Lake Males:Female	Manitoba* Sample Size	Manitoba* Males:Female
0-2	65	1.95	54	0.93
3-7	54	1.70	118	1.15
8-14	111	1.31	183	1.23
15-21	90	1.43	138	2.00

*Olsen (1959)

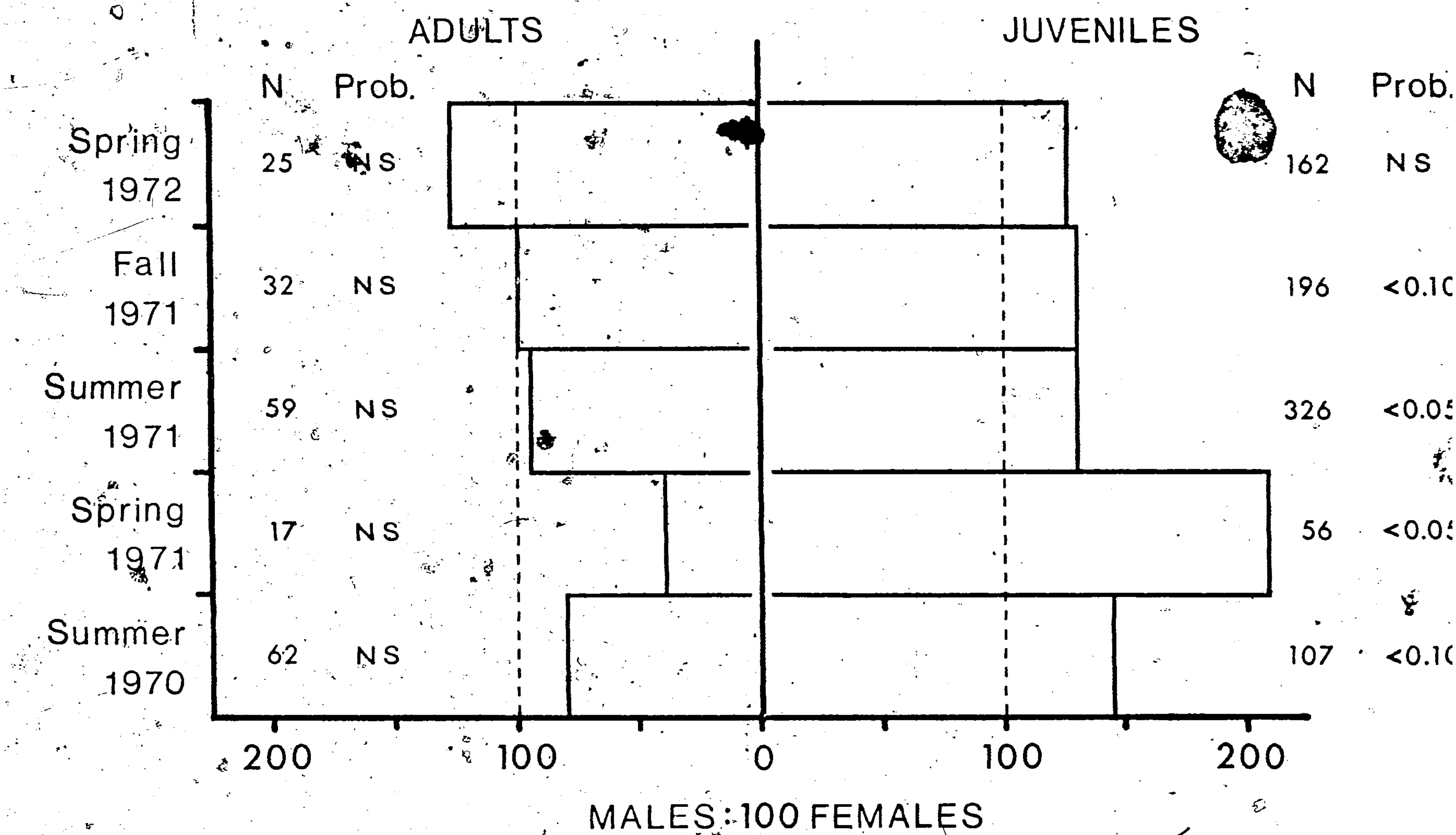


Figure 14. Sex ratios of livetrapped (Summer, Fall) and killtrapped (Spring) muskrats. N = sample size. Probability = significance of X^2 goodness of fit to a 1:1 ratio.

Data in Figure 14 suggest that sex selective mortality or emigration must occur late in the first year of life to even the sex ratio in the next breeding population. One possible source of sex selective mortality is the spring harvest itself. In the spring of 1971 the increased proportion of juvenile males in the kill may have helped equalize the sex ratio of the survivors.

On the Mackenzie delta, Stevens (1955) found that the sex ratio of muskrats shot after the appearance of open water (181 males:100 females) was higher than for muskrats taken earlier (118 males:100 females). This he attributed to the increased activity and belligerence of males at the start of the breeding season. At that time of year males were easily called within rifle range by hunters while females became more secretive. Similar selection of males may occur on the Peace-Athabasca delta where muskrats are also hunted in this way. Fuller (1951) found a similar progression of 96 males:100 females in March to 166 in April and 234 in May. In 1971, the mid-point of the spring harvest on the study area was approximately April 15. The sex ratio of 95 tagged muskrats taken on or before this date was 197 males:100 females, while the ratio of 54 tagged animals taken in the final half of the harvest was 145 males:100 females. Although males may have been more vulnerable in the latter period, the overall effect of fur trapping did little to balance the sex ratio at least in 1971 (Fig 14). This suggests that natural mortality factors during the mating period or spring dispersal are responsible for removing excess males from the population. Fuller (1951) noted that the proportion of pelts torn by fighting was higher among males than among females. Dispersing muskrats become subject to attacks by other muskrats and predation

(Errington, 1937, 1963). While the mechanism is not clear, it is evident that sufficient sex selective mortality must exist to warrant an excess production of males in a species that pairs monogamously.

Age Ratios

In October, adults could still be separated from juveniles on the basis of size and weight. The age ratio determined for 228 house dwelling muskrats in October 1971 was 12.3 juveniles per adult female. I feel this is representative of the fall age structure since adults were no longer reproductively active and litters born in August were old enough to livetrap. A fall age ratio is not available for 1970 since I did not livetrap after the end of August.

Spring age ratios were determined from tag returns and carcasses obtained from the fur harvest. Untagged animals were aged on the basis of length of fluting on the first upper molar (Appendix III). Although the technique is not entirely accurate for this area, age ratios of tagged and untagged samples were similar (Table 11).

The age ratio was higher in 1972 than in 1971, suggesting a relatively higher rate of productivity or survival that year. Use of age ratios in estimating survival will receive further attention in the following section. Age ratios obtained in this study are similar to those reported in other parts of northern North America (Table 12). Mathiak (1966) noted that age ratios varied widely between years and even between adjacent trapping units in Wisconsin.

Age ratios are highly vulnerable to sampling errors since a few adult females one way or the other will cause a significant change in the apparent age ratio. Some writers have reported that fur trapping

Table 11. Age ratios of muskrats in 1971 and 1972 spring harvests (March 15 to May 10).

	Adult		Juvenile			
	M	F	M	F	Juv:Adult	Juv:Adult F
1971 Tagged	0	5	14	8	4.4	4.4
Untagged	5	7	24	11	2.8	5.0
Total	5	12	38	19	3.3	4.8
1972 Tagged	8	9	70	56	7.4	14.0
Untagged	6	2	21	15	4.5	18.0
Total	14	11	91	71	6.5	14.7
TOTAL (1971 & 1972)	19	23	129	90	5.2	9.5

Table 12. Comparison of muskrat age ratios with several other areas.

Location	Source	Period	Sample Size	Juv:Ad	Juv:Ad F
Wood Buffalo Park	This study	October	228	6.2	12.3
		Mar 15 - May 10	260	5.2	9.5
Wood Buffalo Park	Fuller (1951)	Sept 26 - Oct 8	127		14.4
		Mar 1-15	51		11.8
Mackenzie delta	Stevens (1955)	Nov - April	634	4.3	
Alberta	Schmitke (1971)	September	152-296		7.0-15.4
Saskatchewan	Gunson (1968)	October	666	3.4	6.6
		Spring	1736-4055	3.8-8.2	
Wisconsin	Mathiak (1966)	Fall and Winter	56,003		7.1

tends to be age selective towards adults when an area is first trapped (Olsen, 1959; Errington, 1963). At Egg Lake, adults and juveniles appeared to be equally vulnerable throughout the spring harvest. In 1972, adults and juveniles were taken in equal proportions in both halves of the harvest. If actual differences in trapability do occur, the resulting error is minimized by combining data for the entire trapping period.

POPULATION SIZE AND DENSITY

Breeding Population

In 1970, 29 pairs of muskrats were livetrapped in a 140 ha portion of the marsh for a spring breeding density of one pair per 4.8 ha. In 1971, 25 pairs were livetrapped in a 100 ha area for a breeding density of one pair per 4.0 ha.

Approximately 450 ha of the lake consists of habitat similar to the area livetrapped (i.e. an interspersion of offshore emergent vegetation). Using the observed breeding densities, the approximate number of pairs of adults in this area was 94 in 1970 and 113 in 1971. The other half of the lake (450 ha) is entirely open water and was utilized only by bank dwellers. The gently sloping shores with a paucity of emergent cover provided somewhat poor habitat and probably did not contain over two bankruns per kilometer of shoreline. Based on an estimated 20 km of shoreline, this part of the lake may have contained an additional 40 pairs. The breeding population for the whole of Egg Lake then was in the neighbourhood of 130 and 150 pairs for 1970 and 1971 respectively.

Fall Population

Errington (1963) considered the product of the fall age ratio and the number of breeding pairs to be a reliable estimate of the fall population. In 1971, the October age ratio was 12.3 juveniles per adult female. Based on the estimated 150 pairs of adults, the fall population for Egg Lake would be about 1850 muskrats.

The fall population can also be estimated from house counts if the number of muskrats per house is known. Livetrapping of 92 houses during October 1971 resulted in the capture of 226 different muskrats for an average of 2.5 muskrats per fall house. Based on the October age ratio of 12.3 juveniles per adult female and the average of 6.0 houses per family home range, the average number of muskrats per fall house is 2.4. The close agreement between these figures indicates that 2.5 muskrats per house is close to the actual ratio. The density of fall houses in October, 1971 was 1.4 houses per hectare in the 100 ha area, giving a total of approximately 630 houses for the whole lake. Assuming that most of the bank rats were using houses at that time, the estimated fall population in 1971 was 1575 or roughly 1600 muskrats. This agrees fairly well with the previous estimate of 1850.

Fall population data were not obtained in 1970, however, the density of fall houses counted on November 26 was approximately 1.1 houses per hectare. If the number of muskrats per house is assumed to be the same for both years, the fall population in 1970 was around 1240 muskrats. Fall population densities were therefore approximately 2.8 muskrats per ha in 1970 and 3.5 in 1971 for the half of the lake containing emergent habitat.

These data suggest that the population was increasing during the period of study and consequently recovering from a decline apparent in recent years. H. Wylie's fur catches dropped from around 1500 muskrats in 1965 to about 1000 in 1969 and around 700 in 1970. This reflected a decline felt on the delta as a whole (Moncrieff, Montgomery and Assoc. Ltd., 1973). It is not known to what extent these changes represent "cyclic" fluctuations (Elton and Nicholson, 1942) since continuous records of population size or even fur returns for the delta are not available.

SURVIVAL AND MORTALITY

In an animal population exhibiting a high reproductive rate, it is logical to expect correspondingly high rates of mortality. It is of importance in a population study to determine when and to what extent mortality is occurring and which factors are primarily responsible. Reliable estimates are difficult to obtain in a wild population and mortality must often be included under the broader term "disappearance".

This section deals with muskrat survival rates estimated in two ways: (1) from the proportion of tagged animals recovered after a certain time period, and (2) from changes in the age ratio of juveniles to adult females over a time period. The first method does not include an unknown number of survivors that were not trapped or emigrated and thus represents *minimum survival*. The second method is limited by the assumptions that both cohorts are equally trappable and that no mortality of adult females occurred during the interval. Again data were most complete for 1971, and 1970 data are only included where sufficient for meaningful comparison.

Adult Survival and Mortality

Of 40 adults tagged on the intensive study area during the 1971 breeding season, 33 (82.5%) were recaptured after September 30. This includes the recapture of 15 (75%) of 20 adult males and 18 (90%) of 20 adult females. Allowing for the likelihood that several survivors escaped capture, it seems probable that actual mortality during the summer and early fall did not exceed 10%.

Based on tag returns from the spring harvest, 17 (63.0%) of 27 adults known to be alive in October 1971 were still alive in late March

1972. This includes 8 (66.7%) of 12 adult males and 9 (60%) of 15 adult females. Home ranges that were not spring trapped are not included in these calculations. Trapping during the spring harvest was much less intensive than fall livetrapping, accounting to a large extent for the much lower value for minimum overwinter survival. I do not believe that mortality during this period was much greater than during the summer and early fall.

Juvenile Survival and Mortality

Summer and Early Fall

In 1971, 113 (69.8%) of 162 muskrats tagged at less than 3 weeks of age were known to be alive in October. This means that mortality during that period was not over 30.2%. The low level of adult mortality during summer and early fall indicates that the fall age ratio should give a valid estimate of juvenile mortality during that period. Based on the October 1971 livetrapping of 228 house dwelling muskrats, the age ratio just prior to freeze-up was 12.3 juveniles per adult female. This represents a 31.7% loss from the average total production figure of 18.0 juveniles per adult female.

Muskrats livetrapped at bank-runs were not included in these calculations because productivity data were only obtained for house dwelling females. Livetrapping of three bank runs during the fall of 1971 using a multiple capture trap resulted in the capture of 11 individuals of which three were adult females and two adult males. This gives an age ratio of 2.0 juveniles per adult female. Six of these muskrats were recaptured a total of 14 times indicating that most of the occupants had been captured. It is not known whether the low age ratio reflects lower production by bank dwellers or a much heavier rate of mortality. In 1970, livetrapping was not carried out after August, therefore, comparable fall survival estimates are not available.

Nestling Mortality. In 1971, 6 of 38 litters suffered complete mortality. This represents approximately 15.8% of total nestling production. Another 4 litters were only partly successful, resulting in the additional loss of 13 nestlings or 4.6% of total production. Consequently, total neonatal mortality amounted to 20.4%.

There was no significant correlation between number of survivors and age of complete litters in either 1970 or 1971 (Fig 15). Litter size decreased by only about half a nestling during the first three weeks of life. This supports the above evidence that neonatal mortality factors tend to act on the litter as a whole. Dorney and Rusch (1953) found a similar situation in Wisconsin, although overall mortality rates were higher.

Post-weaning Summer Mortality. Since 20.4% of summer juvenile mortality occurs prior to weaning, subsequent losses must amount to slightly less than 10%. This includes additional mortality as well as emigration during the fall dispersal. Eight juveniles or 2.8% of the total production were found dead in the study area during that period, suggesting that losses through dispersal were probably less than 5%.

Effect of Litter Size on Survival. Large litters may place added physiological strain on the female, resulting in a lower chance of survival for the young (Sadleir, 1969). While data from this study are inconclusive, there was no indication that this was occurring.

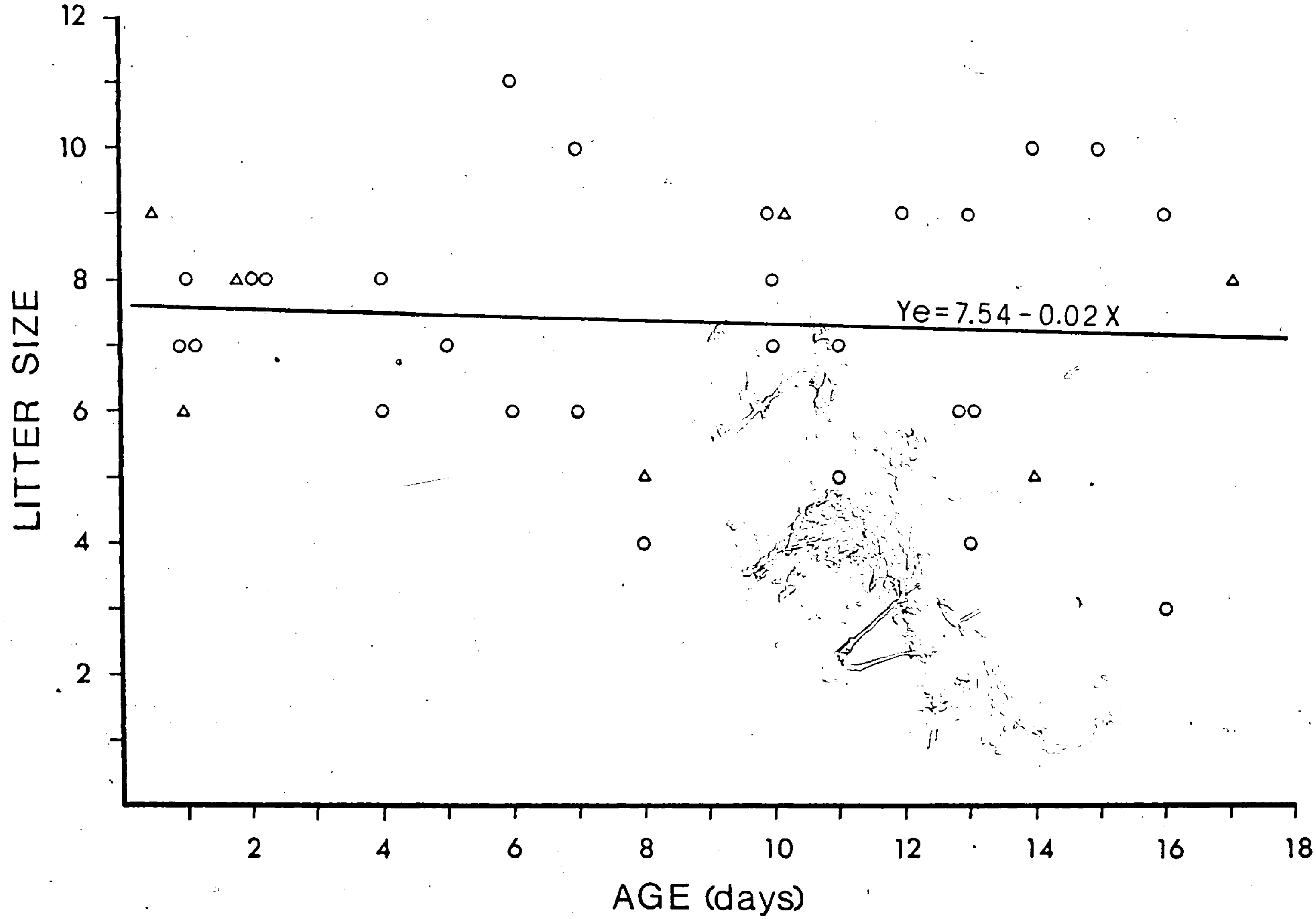


Figure 15. Relationship between size and age of complete litters. Triangles and circles denote 1970 and 1971 litters respectively.

There was no difference in size between litters that were completely successful and ones that were completely unsuccessful. Fifty (68.5%) of 73 nestlings from 9 complete large litters (over seven individuals) survived until October and 41 (68.3%) of 60 nestlings from 10 complete small litters (seven and less) survived that long. Muskrats at Egg Lake were evidently capable of successfully supporting 10 or 11 young.

Winter Mortality

Based on tag returns from the spring harvest, 121 (65.1%) of 186 juveniles known to be alive in October, survived the winter. This means that overwinter mortality did not exceed 35% and was not significantly different from that of adults. Again the recovery rate in spring partly reflects a lower trapping intensity than in fall livetrapping. Recovery rates higher than 65% were obtained in home ranges that were more heavily trapped while I was on the study area in April. There is another way of determining overwinter survival. Considering only home ranges that were spring trapped, 53 (49.1%) of 108 muskrats tagged as nestlings were recovered in the harvest. If 30% were lost prior to freeze-up, the proportion either dying during winter or surviving the winter but not trapped in the spring harvest, was around 20%. Actual mortality during winter was probably closer to 10%.

The age ratio of the sample of 143 tagged muskrats taken during the spring harvest was 14.0 juveniles per adult female. This is somewhat higher than the fall age ratio of 12.3. The reasons for this are not known although greater mortality of adult females than juveniles over the winter, or under representation in the trapped sample could account for it.

Trapping was less intense the previous year and survival estimates are considerably lower. Of 107 juveniles tagged during July and August of 1970, 21 (19.6%) were killed during the spring harvest of 1971 and another 14 (13.1%) were either livetrapped in 1971 or killed in spring of 1972. This means a minimum of 32.7% survived until the 1971 spring harvest.

Effect of Litter Order on Juvenile Survival

The relative proportion of first, second and third litter juveniles in the total nestling production was compared to the October 1971 and spring 1972 populations (Fig 16). The contribution of each cohort to the total production was determined by multiplying the litter size by the number of litters of each cohort.

A significant ($P < 0.05$) increase in the proportion of third litter juveniles in the fall population suggests that this cohort suffered less mortality than first and second litter juveniles during summer and early fall. This increase may be the result of a shorter period of exposure to decimating factors. First litter juveniles had been around for up to 5 months by this time while third litter juveniles were only about 2 months old.

The opposite trend occurred in the spring population, with third litter juveniles apparently suffering higher mortality than the other cohorts during winter. This probably reflects a poorer ability by small animals to cope with the environmental stresses of winter. The average weight of each group in October was 788.8 ± 10.5 g for first litter juveniles, 696.2 ± 10.2 g for second litter juveniles and, 533.8 ± 16.4g for third litter juveniles. These means are significantly different

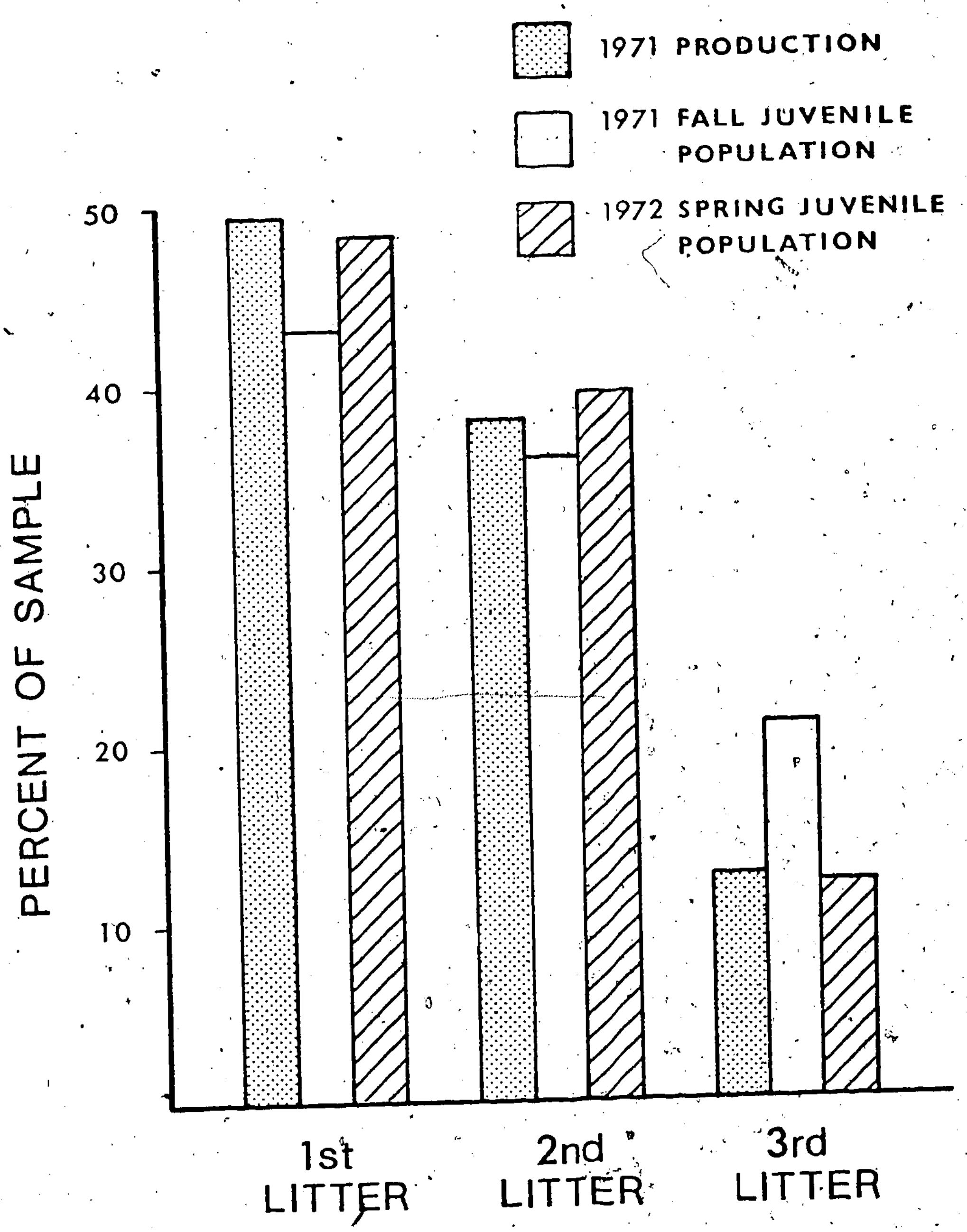


Figure 16. Relative contribution of 1st, 2nd and 3rd litters to total production of nestlings and to juvenile population in October 1971 and 1972 spring harvests.

($P < 0.01$). Early-born litters possess an obvious advantage from the standpoint of size, strength and accumulation of fat reserves. Heat loss problems associated with a smaller body size and a less well developed pelage along with the energy cost of completing molts and a shorter period of exposure to high quality forage, should reduce the chances of winter survival by the youngest animals.

From the population standpoint these differences in summer and winter survival tend to balance each other out. The proportion of first, second and third litter juveniles in the spring harvest was almost the same as the proportion in which they were produced.

Longevity

Since data were obtained from just two summers of livetrapping, only the 1970 cohort provided information on survival after the first spring. Of 107 juveniles tagged in the summer of 1970, 14 (13.1%) were known to be alive in the summer of 1971. This means that disappearance during the first year of life amounted to approximately 87%. Seven of 63 adults tagged in 1970 were also known to be alive in the summer of 1971. If the age of the 1970 adults is assumed to be one year, then 11.1% survived from one to two years of age. Three (4.8%) of 63,1970 adults were recovered in the spring of 1972 at a probable age of 2 3/4 years.

No records of longer survival were obtained. It is probable that less than 5% of the muskrats in this population reach 3 years of age and for practical purposes population turnover takes 2 years. These results agree closely with Mathiak (1966) who also reported a disappearance rate of 87% the first year and complete population turnover in 2 years.

MORTALITY FACTORS

Intraspecific Strife

Errington, who was a principal contributor regarding the role of density-dependant factors in population theory, assigned a regulatory role to intraspecific behavior in muskrats. He concluded that, "on the whole, annual increases and upper levels of maintenance of muskrat populations conformed to mathematical patterns set by the species itself in relation to the supporting capacity of the environment" (Errington, 1963). He found that increased crowding due to high population density or deteriorating habitat usually resulted in increased intraspecific strife.

I have described previously (see: Territoriality) the territorial interactions observed during this study. A small amount of fighting was observed throughout the summer, increasing somewhat during the period of fall dispersal and, based on the number of "torn" pelts, was greatest during the spring mating period. The absence of torn pelts among muskrats taken prior to break-up indicates that widespread fighting did not occur during winter.

There is some evidence that centripetal movements of families from drought exposed areas in 1971 resulted in increased intraspecific strife. Territorial interactions were observed between families 26A and 26B. In this particular case, the disappearance of 26A's second litter may have been a direct consequence. Fighting was also observed in the area between home ranges 26B, 64 and 40. Figure 8 indicates that by the fall of 1971, unclaimed habitat in central (deeper) parts of the marsh was generally not available.

There is little evidence of actual mortality due to wounds inflicted by other muskrats. Dead animals were found only infrequently during the study and in most cases appeared to have died of other causes. A five week old juvenile found on July 4, 1971 may have been a victim of an intraspecific attack. A fresh slash wound had completely severed its tail. On several occasions muskrats with lethal looking wounds were livetrapped. An adult female (HR 17) recaptured on August 5, 1971 had a deep, 10 cm, slash wound on her back and was not subsequently recaptured. Her mate, recaptured a month later, had a prominant scar under his left eye.

Three instances of cannabalism on litters were discovered and have been discussed previously (see: Food Habits). In at least one of these, actual predation appeared to be involved. On several other occasions unsuccessful litters were attributed in part to maternal behavior. Three cases were discovered in which loss of nestlings appeared to be associated with poorly constructed nests -- not lined with dry bedding material. In two cases, young were found that had small scratches or scars on the dorsal side that may have resulted from trampling by older juveniles. Failure of parents to build secure nests and exclude other muskrats from a nest house may predispose litters to greater risk of accidental death or injury. Similarly, young are more vulnerable to predation and rely completely on the ability of the mother to move them quickly and safely.

Predation

This area was well supplied with potential predators of muskrats. Possible mammalian predators included: coyote *(Canis latrans)*, wolf

(Canis lupus), red fox *(Vulpes fulva)*, mink *(Mustela vison)*, black bear *(Euarctos americanus)*, lynx *(Lynx canadensis)*, and fisher *(Martes pennanti)*, while possible avian predators seen were: bald eagle *(Haliaeetus leucocephalus)*, marsh hawk *(Circus cyaneus)*, red-tailed hawk *(Buteo jamaicensis)*, great horned owl *(Bubo virginiansus)* and snowy owl *(Nyctea scandiaca)*. Some evidence on the food habits of these predators was obtained from infrequent observations of kills and partial examination of scats and pellets collected throughout the study. Identifiable muskrat remains were found only in the scats of minks and coyotes.

Mink form a significant part of trappers income on the delta as a whole but do not appear to be abundant at Egg Lake. Ten or 12 mink would be considered a good take by H. Wylie. In 1970, mink occupied several old muskrat bank-burrows on one of the small islands but apparently abandoned this island in 1971. On October 1, 1971 a mink was livetrapped on a muskrat house (#160) about 400 m from the nearest dry land. The only actual mortality attributed to mink during the two summer field seasons was a litter of five found dead on June 21, 1971. The remains of three of these nestlings, which had been eaten almost in their entirety, were scattered on the outside of the house. This differed from suspected cases of cannabalism in which only the soft underparts were usually eaten and the remains were left inside the house. Mink scats collected during the summer were composed almost entirely of the feathers (and occasionally egg shells) of waterfowl and marsh birds. Predation on muskrats may have increased during the winter when these birds were not available. This was reflected in a few scats collected during winter visits. On one occasion (November 1970) a mink trail emerged from a muskrat house and entered a pushup about 10 m away.

Coyotes and foxes were common on the study area throughout the year. H. Wylie (pers comm) considers coyotes the principal muskrat predator at Egg Lake and has observed both coyotes and foxes taking muskrats during the winter. During my infrequent winter visits, I saw several pushups broken into by coyotes and foxes but no evidence of successful predation. Coyotes and foxes habitually visit active muskrat houses during the winter, but Fuller (1951) has suggested that this interest may be primarily directed at smaller microtines which sometimes inhabit these houses. Waterfowl feathers were prominent in summer scats of these species. Wolves were also common on the study area but examination of a few scats and several prey carcasses indicate an almost complete dependence on bison. H. Wylie (pers comm) has never seen evidence of attempted predation on muskrats by wolves.

Bears are not a likely predator of muskrats, although in August 1970 a large black bear was observed in the water several hundred meters from shore. It spent about 10 minutes, plunging around in the emergent vegetation in what appeared to be an attempt to catch flightless ducks. Bee hives, which were occasionally found in old but sometimes active muskrat houses along the shore, could also invite disturbance by bears. Lynx and fisher are uncommon in this area and are not likely predators of muskrats.

There was no evidence of avian predation on muskrats although a pair of bald eagles nested on an island in the marsh and marsh hawks were commonly seen on the study area. Remains around the eagle nest consisted only of waterfowl, marsh birds and fish. Marsh hawks were observed feeding on ducks on three occasions.

These observations suggest that predation was not an important mortality factor at Egg Lake. It may have become more important, however, if water levels had continued to decline. Muskrats in shallow areas must have been more vulnerable to predation and this would have increased if winter freezing forced muskrats to emerge above the ice. This is suggested by other workers. In his extensive Iowa studies, Errington (1963) found that conditions of drought exposure, overcrowding or disease were usually involved when mink or fox predation became significant.

Disease and Parasites

Tularemia and "Errington's (hemorrhagic) disease" are the two diseases generally regarded as capable of significantly affecting muskrat populations (Errington, 1963; Mathiak, 1966). All recently dead animals found during the study were examined macroscopically in the field for symptoms of disease. None appeared to be in a diseased condition, however, none were submitted to a pathologist for closer study. No recent die-offs that might have involved an epizootic, were reported by delta trappers.

Virtually all muskrats examined, including nestlings, were infected with unidentified mites. Viscera of muskrats taken during spring harvests were frozen and later 22 of the 1971 sample and 18 of the 1972 sample were examined for helminths (Table 13). The examination included the entire digestive tract, salivary glands, lungs, trachea, diaphragm, heart, kidneys, mesenteries, liver and bile duct.

All of the muskrats examined were infected with helminths. Trematodes were the most prevalent form (100%) followed by cestodes

Table 13. Helminths from 40 Egg Lake muskrats taken during 1971 and 1972 spring harvests.

Species	Number Infected	Percent Infected	Intensity of Infection	
			Median	Range
TREMATODES				
Plagiorchis sp	40	100	35	1-520
Quinqueserialis quinqueserialis	12	30	4.5	1-23
Notocotylus filamentis	37	93	53	1-261
Wardius zibethicus	34	85	7	1-20
Echinostoma revolutum	4	10	1	1
Schistosomatium douthitti	8	20	2	1-11
CESTODES				
Taenia mustelae	2	5		
Hymenolepis evaginata	35	88	6	1-106
ACANTHOCEPHALAN				
Polymorphus sp	8	20	6	1-155

(88%) and acanthocephalans (20%). Nematodes were not found in any of the muskrats examined. No relationship was apparent between percentage infection and age or sex of host or year collected.

Three of these helminths *(Q. quinqueserialis, N. filamentis* and *H. evaginata)* were previously reported in Wood Buffalo Park (Fuller, 1951). All but two of the helminths found in this study *(W. zibethicus* and *S. douthitti)* have also been recovered in central Alberta studies (Holmes and Zeuge, 1962; Kerr, 1963; Gunson, 1969; Connell and Corner, 1957). *Schistosomatium douthitti* has been found previously in muskrats but has not been reported in Canada (Knight, 1951; Beckett and Gallicchio, 1967).

Final identification has not been completed for all of the worms recovered. While it is not yet clear whether one or two species of *Plagiorchis* were found, the majority appear to be *P. proximus*. Since only a few specimens of *Polymorphus* sp were mature, specific identification could not be made for the majority of the worms recovered (Van Cleave, 1953). The adult specimens appear to constitute an undescribed species of *Polymorphus* (W. Bethel, pers comm). The intermediate hosts for members of this genus are crustaceans and the definitive hosts are waterfowl. Rodent infections with this parasite have been regarded as "accidental" (Van Cleave, 1953), however, central Alberta studies indicate that *P. paradoxus* may be a normal parasite of muskrats in that region (Holmes and Zeuge, 1962; Connell and Corner, 1957). In view of the moderate extensity and intensity of infection of *Polymorphus* sp found here and the presence of crustacean remains in the digestive tract of several of the animals examined, it seems possible that the muskrat is a normal host for this parasite in Wood Buffalo Park as well.

There is no evidence that parasitic infection was contributing directly to mortality of Egg Lake muskrats. Fuller (1951), however, found that the proportion of heavily parasitized muskrats declined in early winter. Lavrov (1960) noted that in the USSR "cysticercosis of the liver was a cause of emaciation" and that death from this had been recorded. Although infections detected in this study were generally light (median = 139 worms per muskrat), parasites may reduce the overall vigor of infected animals and lower their resistance to other forms of stress.

Fur Harvest

Spring trapping accounted for 20.7% of the muskrats tagged in 1970 and 39.7% of those tagged on the study area in 1971 (Table 14). The higher recovery rate in 1971 partly reflects an increase in trapping intensity that year. Trapping was not uniform throughout the study area. Most of the trapping was conducted on the west end of Egg Lake, although not all parts of the area were trapped. For example in 1972 - excluding family home ranges that were not spring trapped - 49.8% of all tagged muskrats (283) or 49.1% of 108 muskrats tagged as nestlings were recovered. In other words, about half of the annual production was harvested in areas that were trapped. This suggests that trapping was a major mortality factor on the study area.

There is also an unknown amount of mortality due to poaching (H. Wylie, pers comm). This mainly occurred after spring break-up and may be significant, partly because of the easy accessibility of Egg Lake from Revillon Coupe and partly because H. Wylie lives in Fort Chipewyan most of the time.

Table 14. Recovery of tagged muskrats in spring harvests.

	No. Tagged*	No. Recovered 1971	1972	1973	Total	Percent
1970	169	27	8		35	20.7
1971	393**		143	3	146	39.7
Total	562				181	32.2

* only includes muskrats tagged on the study area.
** does not include muskrats tagged in 1970 and recaptured in 1971.

There appears to be a relationship between low water levels and mortality caused indirectly by trapping. Since by late winter, most of the houses no longer had water in the plunge-holes, trappers experienced difficulty making "drowning sets". This resulted in an increased number of "wring-offs". Of 55 muskrats taken in traps checked twice daily between April 15-18, 1971, only 16 (29%) were drowned or in the process of drowning. Another five traps contained detached legs or feet and a sixth contained teeth. Muskrats injured in that way should be more vulnerable to predation and intraspecific fighting. As well, a previously described case of cannabalism on nestlings was attributed to a trap-crippled male that evidently experienced difficulty foraging.

Livetrapping and Disturbance during the Study

During the study, eight muskrats died in livetraps or are known to have died as a probable result of being livetrapped. This amounts to 1.4% of the total number tagged on the study area (562) and 0.8% of the total number of captures (1012); therefore, livetrapping is not considered a significant mortality factor.

Other disturbance, particularly checking for litters, probably resulted in additional mortality but this was difficult to determine. There was no loss of an entire litter resulting from a litter being moved during or following disturbance of the nest house. In most instances, dead juveniles found in or near a previously disturbed house were judged (on the basis of size) to be at least a few days older than when last handled. In 1971, 11 young either disappeared or are known to have died shortly after handling. This amounts to approximately 4% of the total production on the study area in 1971. I feel that our disturbance was a minor mortality factor during this study.

RELATIONSHIPS WITH OTHER WILDLIFE

Waterfowl

The study area was used for nesting, brood-rearing, molting and staging by a variety of waterfowl species (Appendix IV). Offshore emergents provided suitable nesting cover for divers and coots, as well as cover for broods and molters. Levees and rocky islands provided upland nesting sites for dabblers, in close proximity to the water. Since the habitat requirements of muskrats and waterfowl are similar in many ways, the possibility of competition arises. However, waterfowl probably feed primarily on submerged aquatics, duckweeds, aquatic invertebrates and seeds of emergent plants (Kadlec, 1962). Vegetative portions of emergents are not extensively eaten by waterfowl. Forage competition with muskrats is therefore unlikely due to the abundance of food available and the dependence of muskrats on emergent vegetation.

The relationship between muskrats and waterfowl appeared to be one of interspecific tolerance with each possessing certain positive benefits for the other. Beard (1953) noted that muskrats have a beneficial effect on waterfowl by thinning emergent cover. Openings created around muskrat houses were highly attractive to dabblers, and muskrat houses were used extensively as loafing sites. This caused some flattening of houses but was probably not a major disturbance. On the other hand, there is reason to believe that waterfowl provided an important "buffer" between muskrats and their natural predators during the ice-free period.

Bison

In recent years the delta has supported 7,000 to 10,000 bison (*Bison bison bison* x *B. b. athabascae*) with the largest proportion occupying the meadows north of Lake Claire (Allison, 1973). Bison use of the study area was seasonal, usually occurring during fall and winter. No bison were observed on the study area earlier than mid-August in 1970 or 1971, however, approximately 100 to 200 bison appeared to winter in the vicinity of Egg Lake.

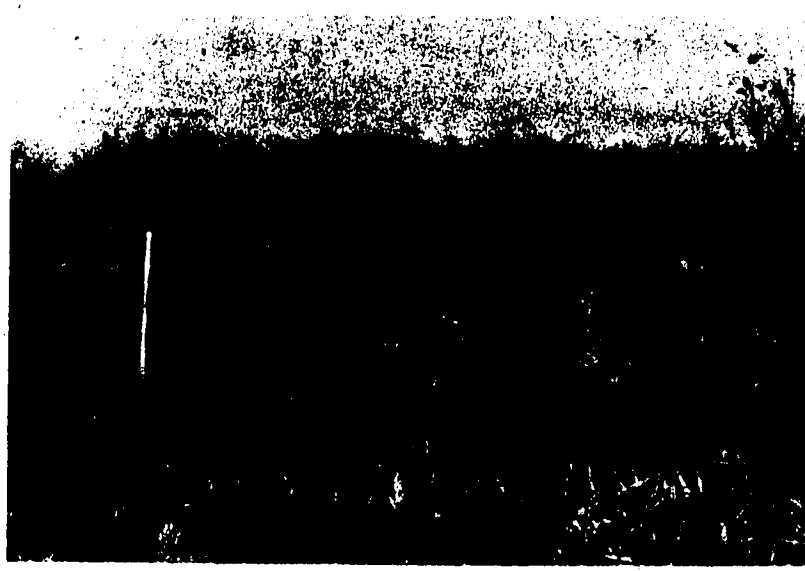
Bison interactions with muskrats were of a disturbance nature with localized instances of direct competition for food. During fall, most bison activity was confined to the *Carex-Calamagrostis* meadow and willow-alder shrub zones although herds were frequently seen grazing in emergent and immature fen communities along the sides of the lake where they utilized new growth of emergents including sedge, burreed, sweetflag, cattail and horsetail (Photos 11 and 12). Feeding areas generally did not overlap with muskrats except around the entrances of a few bank-burrows; however, bison may have had a greater influence through trampling the tunnels and open runways of bank burrows. The effect of this on the occupants is not known but it probably exposed them to greater risk of accidental death or predation. Disturbance of this type is likely less important during years of normal water levels since access to emergent forage would be limited; resulting in less contact between bison and muskrats or their dwellings.

During winter, bison came into direct competition with muskrats by feeding on their houses (Photo 13). My observations indicate that bison actively seek out houses and over the course of a winter may utilize large numbers of them as a supplementary food source. Similar use

Photograph 11. Bison on the north side of Egg Lake.

Photograph 12. Heavy grazing and trampling by bison on the west end of the study area. Note abandoned muskrat house in small willow clump near center of photo.

Photograph 13. Winter muskrat houses partially eaten by bison.



of muskrat pushups by caribou has been reported by Kelsall (1970). Trappers believe this causes muskrats to abandon houses and my limited observations suggest that this is often the case. Only the lightly compacted vegetation on the surface of most of the houses I examined had been removed, although H. Wylie (pers comm) has seen houses that were eaten down to the base. Feeding and trampling undoubtedly destroy the insulative cover over houses, thereby exposing them to heavier freezing. The effect of this may be more serious during periods of low water when muskrats experience restricted access to food and alternate dwellings. This relationship requires further study.

Other Wildlife

Two families of beaver *(Castor canadensis)* were associated with Egg Lake but their presence appeared to be of little consequence to muskrats. However, beaver are known to improve conditions for muskrats in some parts of the delta (Fuller, 1951) and may be valuable companions during periods of drought. Abandoned muskrat houses sometimes provided nest sites for black terns *(Chlidonias niger)* and coots. Moose *(Alces alces)* were occasionally seen feeding on submerged aquatic vegetation but the small number of moose precluded any competition with muskrats.

WATER LEVEL AND HABITAT RELATIONSHIPS

A Review of Delta Successional Patterns

The biotic communities that presently occur on the Peace-Athabasca delta largely reflect the historical development of delta landforms. A delta is formed as a river loses velocity upon entering a body of water and deposits its sediment load. As a delta grows, changes in stream flow and deposition patterns cause the river to branch into a number of distributaries and form levees. During high water, the heavier sediments are deposited along the sides of the distributaries where velocity is lowest with levees eventually becoming higher than average flood levels. During development, distributaries frequently change position, dividing and reuniting to enclose depressions which become deltaic lakes and marshes (Bayrock and Root, 1973). This has resulted in a typical bird's-foot pattern of development on the Peace and Athabasca deltas (Bayrock and Root, 1973).

The evolution of delta landforms is accompanied by a successional development of biotic communities. Plant species become distributed according to their particular climatic, edaphic and hydrologic requirements. Of these, the depth and fluctuations of the water regime assume overriding importance (Fuller and LaRoi, 1971; Dirschl, 1973; Van der Valk, 1970). Thus, species adapted to the aquatic conditions of early sites are replaced by less hydrophilic species as the delta ages. The long-term pattern is one of succession from aquatic to wetland to terrestrial ecosystems (Fig 2). Where hydrarch succession results from changes in the water regime it is termed "allogenic". Organisms themselves tend to promote hydrarch succession through accumulation of organic matter and trapping of sediments ("autogenic" succession). Allogenic influences tend to be most important during active development of the delta whereas autogenic influences become the dominant successional force at inactive sites (Dirschl, 1973).

Hydrarch succession from wetland to terrestrial ecosystems tends to lead to lower productivity and less species diversity. Van der Valk (1970) found that productivity of oxbow sloughs in Alberta increased from submerged through floating-leaved to emergent communities and declined in meadow communities. He attributed this to the combined effect of direct sunlight, gaseous diffusion of carbon dioxide and access to an adequate source of dissolved nutrients. Fuller and LaRoi (1971) noted that ". . . marshes may be the most productive ecosystems of the temperate and boreal zones, and are not far behind tropical rainforests in a worldwide ranking, in spite of their much shorter growing season".

The diversity of ecosystems found on the delta is directly related to its hydrologic regime. Historically the delta has been subject to periodic flooding brought about in two ways. In older parts of the delta, including the study area, flooding results primarily from the formation of ice-jams in the major rivers during break-up. Prior to construction of the Bennett Dam, the Peace River exhibited a highly variable flow with a spring peak of over 300,000 cfs (Card 1973a), followed by a lesser peak in early summer. During peak flows, the level of the Peace River exceeded that of Lake Athabasca and the direction of flow in the outlet channels was temporarily reversed. In some years this raised the water level of Lake Athabasca enough to inundate lower parts of the delta.

By offsetting water losses from evapotranspiration and seepage, periodic flooding has been responsible for maintaining much of the delta in early successional stages. Terrestrial communities are eliminated by flooding and re-establishment of the more productive wetland communities occurs. Flood water is also a vital source of dissolved nutrients. Van der Valk (1970) noted that flood water rich in bases was necessary for complete organic decomposition and efficient nutrient turnover.

It is the fluctuating nature of this water regime that has made the delta so productive of muskrats and waterfowl. Muskrats require abundant emergent vegetation for food and cover along with adequate water levels for winter survival and as such are dependent on the earlier successional stages. These conditions usually do not persist for long periods of time without periodic rejuvenation brought about by flooding. By continually setting back succession, periodic flooding has allowed aquatic and wetland ecosystems to be maintained on the delta for hundreds of years (Fuller and LaRoi, 1971).

The period between floods is similarly important in maintaining muskrat habitat. Floods were normally followed by drawdown periods of one to several years which allowed re-establishment of emergent plant communities in open water areas. Many emergent species apparently require exposed mud for successful germination (Harris and Marshall, 1963; McLeod et al., 1951). Kadlec (1962) found that germination was facilitated by an increase in soil and water fertility due to aerobic nitrification during drawdown. Artificial drawdowns have in fact been used for many years to restore muskrat and waterfowl habitat in the United States (Harris and Marshall, 1963; Kadlec, 1962). Linde (1969) discribed the effect of a drawdown on muskrats at Horicon Marsh in

Wisconsin. Drastic drawdowns in the summers of 1962 and 1963 resulted in almost complete elimination of the muskrat population. It also brought about successful revegetation of the marsh bottom, such that when water levels were restored in 1965 the muskrat population began making a comeback. In 1966 the population "literally exploded", more than offsetting the losses during the drawdown.

This technique more or less simulates dynamic processes that have been occurring naturally on the Peace-Athabasca delta for hundreds of years. The opposing forces of normal hydrarch succession on the one hand along with periodic interruption of the long term successional pattern by flooding on the other have interacted to maintain a high degree of productivity and diversity on the delta (Fuller and LaRoi, 1971).

Water Levels Since 1968

The most important class of delta water bodies with regard to muskrat production are those frequently described as "perched". Perched lakes and marshes only receive water from the main drainage system when flooding over the levees occurs. They are in contrast with other delta lakes which have some degree of connection with the main system through which water flows in or drains out depending on the level of the major delta lakes and channels. Perched lakes best satisfy the requirements for semi-stable water levels along with periodic drawdowns to re-establish emergent vegetation.

During closure of the Bennett Dam and filling of Williston Lake above the dam from 1968-71, spring flood levels of the Peace River were reduced by as much as 10 to 12 ft (3-4 m) and Lake Athabasca remained an average of 2.5 ft (0.76 m) lower than normal (Card, 1973b).

Consequently, flooding of perched basins did not occur and many of the "connected" lakes suddenly became dry.

Perched lakes on the delta are typically shallow and subject to drying since evaporation usually exceeds precipitation (Card, 1973a). Townsend (1973) determined that loss of water area and shoreline from perched basins on the delta averaged 12 percent per year between 1968 and 1971. Water lost through evapotranspiration resulted in a net water loss at Egg Lake of 36 cm in 1971 and a similar loss in 1970 (Appendix V). By October of 1971 water levels on the marsh appeared to be about 1 m below the high water level (Photo 14). At that rate, 2 more years without flooding would have almost completely dried up the lake. This was prevented in May of 1972 when an ice jam formed in the Peace River and the resulting flood restored high water levels in the lake.

Changes in Vegetation on the Study Area

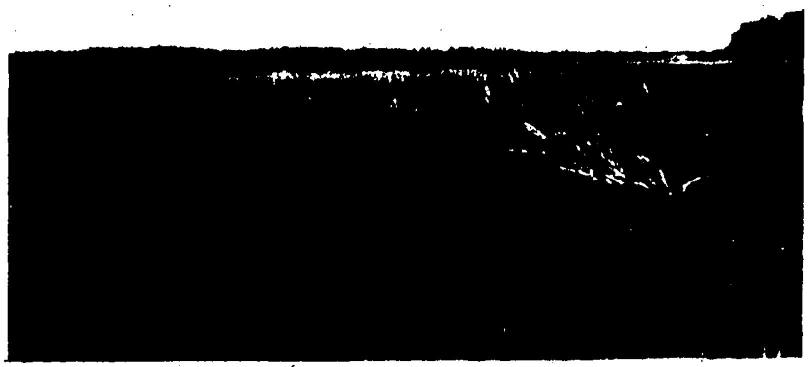
Plant succession on the delta was intensively studied since 1968 by Dirschl (1973) and since 1970 by M. Doherty (Dept of Botany, University of Alberta; pers comm). In this section I will only make a few general comments on changes noticed in the study area. Although the plant species present on the study area differ in kind and abundance from other parts of the delta, the successional processes described by Dirschl likely apply to this area as well.

The most noticeable changes during 1970 and 1971 were the encroachment of willows into the *Calamagrostis-Carex* meadow and the establishment of fen communities on exposed mud flats. Due to the uneven nature of the bottom, exposure of lake bottom was not entirely restricted to shoreline areas. Areas that were exposed in June or July were rapidly

Photograph 14. Pre-Cambrian granite outcropping near the center of Egg Lake showing previous high water line, October 1971.

Photograph 15. Recently exposed mud flats along the north side of the study area, July 27, 1971. In June, 1970 this area contained muskrat houses in approximately 30 cm of water. The dead willows became established during previous low water years from 1945-47.

Photograph 16. Looking toward the north side of the study area from a point well out on the marsh, July 27, 1971. Emergents including *Typha* (on right) and forbs such as marsh ragwort (*Senecio congestus* - in seed stage - on left of picture) rapidly colonized exposed lake bottom.



colonized by such emergents as sweetflag, cattail, burreed, bulrush and sedge as well as several mud-flat weeds including marsh ragwort *(Senecio congestus)*, dock *(Rumex maritimus)* and beggartick *(Bidens cernua)*. The rapidly growing marsh ragwort was the most prominant of these weeds and its yellow flowers became indicative of virtually all recently exposed mud-flats (Photo 16).

The most surprising change was the extensive germination and growth of cattail during 1971. Although mature stands were rare on the study area during 1970, it became the most abundant type of emergent on many of the bare mud-flats, due perhaps to its wind born method of seed dispersal.

During the study, vegetative expansion of offshore stands of emergents appeared to exceed the capacity of muskrats to consume them. Burreed, which unlike cattail and bulrush can germinate under water (Kadlec, 1962), appeared in 'solid' stands in several of the shallow bays during 1971. There was then a general increase in abundance of emergent vegetation associated with the declining water level.

Effect of Low Water on Summer Activity and Survival of Muskrats

As the water level on the study area declined, muskrats in shallow areas attemped to relocate themselves in deeper water. These movements were described earlier and appear to be a normal adjustment by drought exposed muskrats everywhere (Errington, 1963).

Due perhaps to the relatively low population density, most of these families appeared to have successfully established in more suitable areas. However, the eviction of family 26A from its home range was evidence that territorial conflicts did arise.

For those that attempted to remain in drought exposed areas, the hazards may have outweighed the intolerance of other muskrats. Although no direct sign of predation was observed, there is little doubt that exposure to predation in these areas was greater than in deeper parts of the marsh. Long bank-runs containing only a few centimeters of water would offer little protection to occupants. Sign was frequently seen of extensive foraging in dry shoreline areas, sometimes accompanied by fox or coyote tracks. On one occasion, as I approached a house built in an old willow clump and no longer connected with water to the lake itself, 3-week old young began scurrying from the house, seeking shelter in cavities among the roots.

The hazards to bank dwellers must have been further increased through trampling by bison. The low ratio of young to adults among bank dwellers was evidence that survival in exposed areas was low. By winter of 1971, use of bank burrows was almost nonexistent at Egg Lake.

This illustrates the importance of off-shore emergents in terms of muskrat habitat. The muskrat is essentially an "edge" type of animal, requiring a juxtaposition of aquatic and marsh communities. While shoreline emergents were well developed, particularly along the north and west shores, they became unavailable for food and cover as the water level declined. The home range map (Fig 8) indicates that most of the available habitat was occupied by the fall of 1971. The amount of offshore emergent vegetation may well have been a limiting factor, particularly if water levels were to continue to decline.

Effect of Low Water on Winter Activity and Survival of Muskrats

Most authors have agreed that winter poses the greatest problems in terms of muskrat survival in northern regions. The winter ice cover restricts movement, induces crowding and decreases the availability of food. Fuller (1951) reported that "winter frosts seal the lakes and sloughs containing the choicest foods and may turn the shallow ones to solid blocks of ice, forcing eviction of the muskrats living in them". He also recognized the importance of an insulating snow cover in reducing freezing of shallow lakes. Stevens (1955) agreed with Fuller, concluding that "the prime factor governing muskrat survival was the depth or thickness of winter ice". McLeod et al. (1951) similarly concluded that ". . . the winter carrying capacity is determined by the extent of unfrozen water and the quantity therein of . . . submerged species".

In cases where muskrats are unable to obtain enough food under the ice they may be forced to seek food elsewhere. During low water in Illinois in 1939, Bellrose and Low (1943) found that "when the frost line penetrated the lake bottom . . . the muskrats were forced to gnaw through the lodges and to wander about on the ice searching for food". These wanderers suffered heavy mink predation. Errington (1939) noted varying responses by muskrats during the Iowa drought of 1936-37, due in part to the availability of food. At Little Wall Lake, muskrats left their houses daily to forage above the ice with the marsh becoming depopulated by February. At Round Lake, which also froze to the bottom, "muskrats stayed under the ice and survival was comparatively high". He found that winter drought was frequently accompanied by an increase in intraspecific strife and predation.

Friend et al. (1964) reported large weight losses and increased parasitic infection during a population decline on areas of reduced winter water levels in New York. Seabloom and Beer (1963) reported on heavy mortality and winter movement of muskrats during a "freeze-out" in North Dakota. Mathiak and Linde (1954) considered "winter-running" of muskrats during a freeze-out in Wisconsin. Dilworth (1966) observed that heavy mortality during a freeze-out in New Brunswick was evident from "decaying carcasses of many muskrats" found after spring break-up.

I included the preceding review to demonstrate that winter mortality due to heavy freezing or insufficient food and water is a common and widespread occurrence in northerly parts of the muskrat's range, and to indicate some of the manifestations of "freeze-outs". Many more cases, particularly in northern Canada have undoubtedly gone undocumented. Elton and Nicholson (1942) noted that winter freezing, sometimes associated with other factors such as disease, was the most frequently mentioned cause of muskrat mortality in Hudson's Bay Company annual reports. The effects were sometimes cyclic in frequency as shown by the observation that "there seems to be a widespread belief among fur traders and naturalists that the periodic crash in numbers is brought about chiefly by the muskrats freezing to death when low water, with or without an unusually severe winter, occurs in the winter" (Elton and Nicholson, 1942).

Little information is available regarding mortality due to freezing of shallow water in Wood Buffalo Park. Fuller (1951) noted that very low muskrat populations coincided with a period of low water levels from about 1945-47. H. Wylie (pers comm) remembers that during that period, Egg Lake contained less water than in 1971 and that the tall dead willows seen throughout much of the marsh grew in at that time (Photo 15). Novakowski (1958) mentioned reports of winter "die-offs" and "freeze-outs" in shallow water areas in 1957.

The winters of 1970 and 1971 were quite similar with regard to temperature and snowfall. Snow on the ground at the Fort Chipewyan weather station measured 81 cm at the end of March, 1971 and 86 cm at the same point in 1972 (Appendix I). I measured snow and ice thicknesses on the study area twice each winter. On November 26, 1970 ice thickness around several muskrat houses averaged 12 cm. On January 6, 1971 ice thicknesses of 56 cm were measured at two places on the study area (H. Wylie, pers comm). On February 25, 1971 holes cut near the same houses measured in November averaged 51 cm of ice with over 13 cm of frozen mud on the bottom. By late or possibly mid-winter most of the lake had evidently frozen to the bottom. In the winter of 1971-72 the lake again froze solid, presumably somewhat sooner due to the lower water level. The effect of winter freezing on the activity and survival of muskrats is difficult to determine since muskrats are largely unobservable under the ice and evidence of mortality may not appear until the ice leaves the lake, if it is apparent at all.

Some indication of winter activity within a home range can be obtained by examining houses for signs of occupancy. The plunge holes of a muskrat house are kept from freezing by continuous use, consequently, frozen plunge holes are indicative of an abandoned or inactive house. In April 1971, houses on the study area were classified as "active" or "abandoned" according to condition of the plunge hole, as determined by probing with a long steel rod ("rat spear").

Using this technique it was determined that only 45.5% of 135 active muskrat houses that were marked on the intensive study area before freeze-up in 1971 were still active the following April. This suggests that the area of activity in family home ranges declined by at least half over the winter. This compares with 37% active houses on the delta as a whole in 1971 and 55% in 1972 (Ambrock and Allison, 1973).

The relationship between house condition and muskrat survival is not clear. Ambrock and Allison (1973) considered the percentage of muskrats surviving until spring to be directly proportional to the percentage of active houses. This assumes that if a house is no longer active its occupants did not survive. At Egg Lake, this was clearly not the case since only 45.5% of the houses remained active while minimum known overwinter survival was 65%.

Evidently, as some muskrat houses froze-up and were abandoned, the average number of muskrats per remaining house increased. At Egg Lake there was an average of 6.0 houses per family home range and no apparent territorial restrictions on movement within the home range. In fact only one third of the muskrats killed in spring trapping were taken in the same house in which they were last livetrapped in the fall. Of those that moved, exactly half moved from inactive (frozen) houses while the other half moved from houses that were still active. This indicates that movement between houses was occurring during winter, regardless of whether or not a house froze.

While muskrat survival was not directly reflected by the proportion of active houses, house "activity" may well be important in winter survival. Each house constitutes a significant food supply, particularly when access to rooted vegetation is restricted by freezing of shallow water. When muskrats are unable to maintain access to all of the houses in their home range, food shortage problems are magnified. Also, avenues of escape from predators are reduced when some of the houses freeze-up. Errington (1963) has noted that intraspecific strife may increase under conditions of crowding.

Factors Affecting Winter Use of Muskrat Houses

Water Depth. Surrendi and Jorgensen (1971) found that the number of muskrat houses in active use on the delta increased with total depth of ice and water. Similar results were obtained during this study in the winter of 1971-72 (Fig 17). There was a definite trend toward greater activity as the average depth of water around the house at freeze-up increased. At depths greater than 30 cm, over 50% of the houses were still in use. Although the range of water depth that was available was small, the mean depth at active houses (33.5 ± 1.2 cm) and inactive houses (29.8 ± 1.4 cm) was significantly different ($P < 0.05$).

As houses in shallow water became frozen, muskrats evidently made more use of houses in deeper parts of their home range. This is reflected in the previously discussed movement of muskrats between fall and spring trapping locations. Of the 68 tagged muskrats that were not caught in the same house, 41 (60%) had moved to houses in deeper water. This trend is not unexpected since houses in deeper water must have provided access to under ice food supplies for a longer period of time.

Snow Depth. A relationship was also found between house condition and snow depth measured beside houses in April, 1972. Snow depths

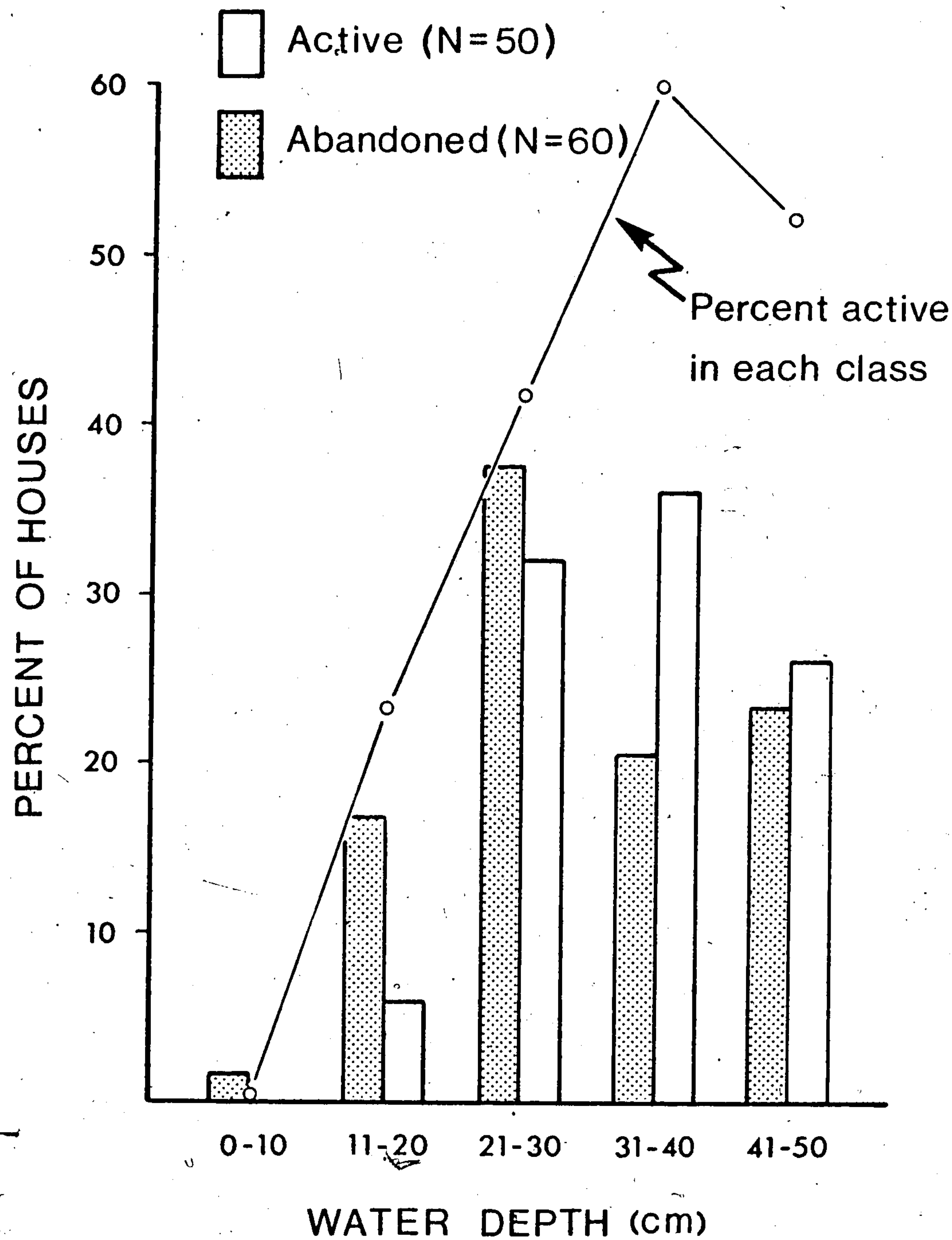


Figure 17. Condition of muskrat houses in April 1972 in relation to fall water depth.

at active houses (63.1 ± 3.0 cm) were significantly greater ($P < 0.05$) than depths at inactive houses (53.9 ± 2.9 cm). Of 71 houses at depths less than 60 cm, 36.6% (26) were active as compared with 62.2% (23) of 37 houses with more than 60 cm of snow. A heavy snow cover reduces the rate of freezing and thickness of ice cover yielding obvious benefits for muskrats.

While the insulative value of snow is important in the "survival" of muskrat houses it may have indirect negative effects through the creation of the condition called "over-flow" or "nalyodi". This is most prevalent in early winter when heavy snow falls on a thin ice layer, forcing water to seep above the surface. It may encase muskrat houses in thick layers of ice and "seal" pushups (Lavrov, 1960; Stevens, 1955) and in some cases apparently causes houses to break apart (Ambrock and Allison, 1973).

Over-flow did occur on the study area both winters and was particularly prevalent in November of 1971 when I visited the study area and found layers over 20 cm thick in places, but the effect on muskrats or their houses was not determined. It did not appear to be causing outright destruction of houses but obviously must have reduced the insulative value of snow around affected houses. Trappers feel it does cause houses to become abandoned and my limited observations tend to bear this out.

Cover Type. House condition also seemed to vary between cover types, although these differences are not statistically significant (Table 15). The proportion of active houses was uniformly higher in burreed and bulrush, and uniformly lower in the remaining categories.

Table 15. Cover types of winter muskrat houses in relation to condition of use, water depth and snow cover.

Cover Type	No. Houses Active	No. Houses Inactive	% Active In Each Cover Type	Water Depth (cm)	Snow Depth (cm)
Sweetflag	10	16	38.5	22.4 ± 1.6	51.3 ± 2.6
Burreed	11	7	61.1	27.4 ± 1.9	54.1 ± 3.6
Sedge	35	47	42.7	28.7 ± 1.2	48.8 ± 1.9
Bulrush	18	12	60.0	27.9 ± 1.0	80.5 ± 2.8
Open Water	15	21	41.7	36.3 ± 1.8	48.5 ± 3.2

The reasons for this are not clear but appear to be partially tied in with water depth tolerances for each species and the depth of the accumulated snow cover.

Sweetflag, which was highest in nutritive value, was associated with significantly shallower water compared to burreed ($P < 0.01$), sedge ($P < 0.01$) and bulrush ($P < 0.01$). The other species did not differ significantly with regard to water depth. Houses built adjacent to open water were in depths significantly greater ($P < 0.01$) than houses that were not.

Cover types did not differ with regard to accumulated snow depths except for bulrush which had a significantly deeper snow cover ($P \leq 0.001$). This probably accounts for the relatively high rate of active houses in this cover type. The insulative importance of this species was evident in a qualitative condition peculiar to houses in bulrush with over 80 cm of snow. The walls of these houses were usually unfrozen with loosely packed snow melting back to form an air cavity over the house. Houses and pushups in such areas sometimes had chambers extending from the house into the snow cover itself. Active houses in bulrush usually had water in the plunge holes but due to the small size of most of the bulrush clones, the area of reduced freezing probably did not extend very far from the houses.

The relatively shallow snow cover might explain the low rate of active use among houses built adjacent to open water. While allowing greater access to submerged aquatic vegetation, these sites were subject to heavier ice formation.

House Size. A definite relationship was found between house height and the number of houses remaining active (Fig 18). There was

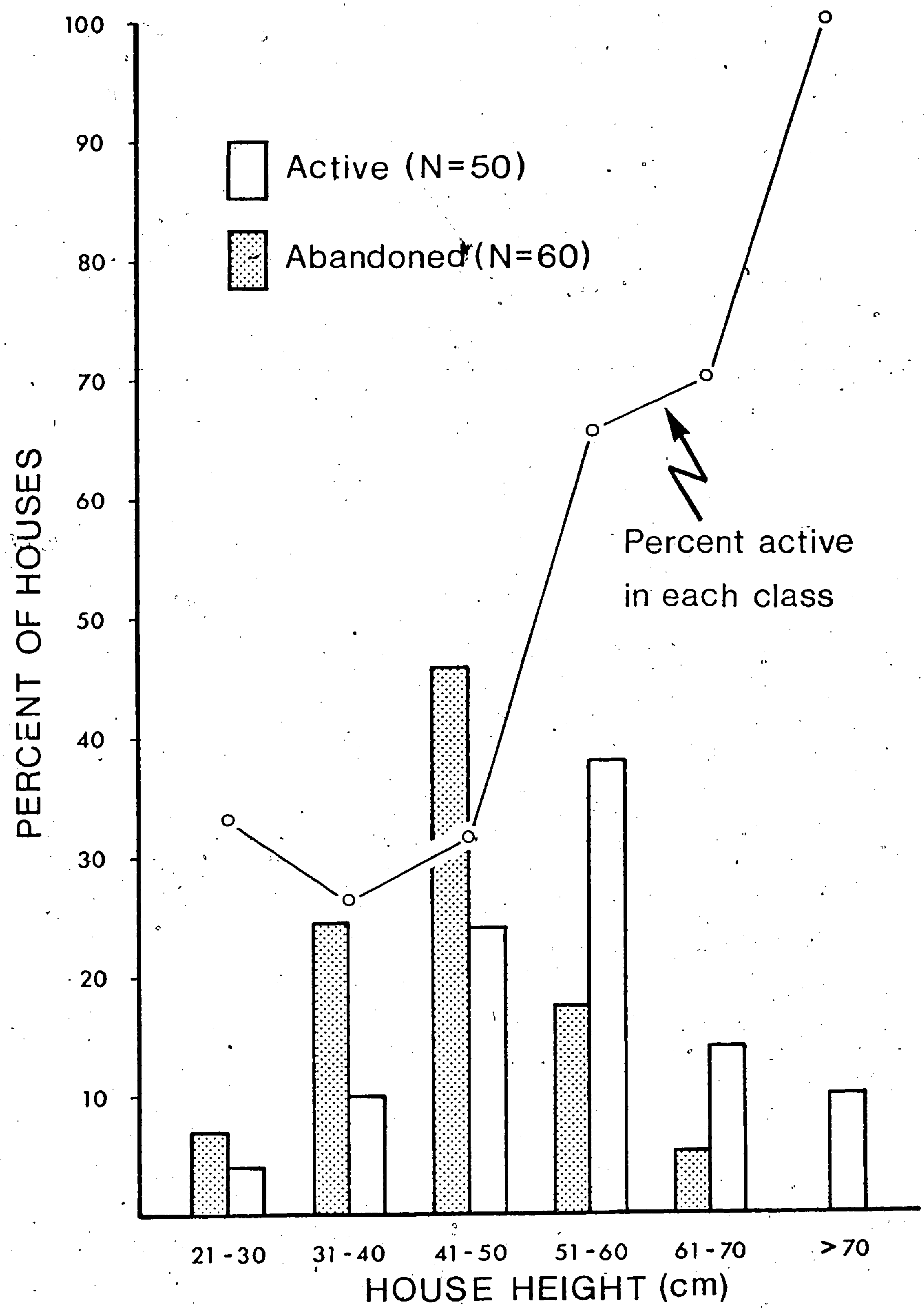


Figure 18. Condition of muskrat houses in April 1972 in relation to house height.

a stepwise increase in the proportion of active houses as heights increased from 30 to 70 cm. Differences in mean height between active houses (56.7 ± 2.3 cm) and inactive houses (46.6 ± 1.3 cm) are highly significant ($P < 0.01$). This is not surprising since larger houses constitute a larger food supply and the thicker walls provide increased insulation and possibly greater protection from predators.

Disturbance. The effect of grazing by bison on muskrat houses was previously discussed. Disturbance by predators may also cause some abandonment but this does not appear to be an important factor. Push-ups were occasionally destroyed and houses damaged by foxes and coyotes, but damaged houses were, in some cases at least, repaired and active. The incidence of predation at houses on the study area appeared to be low. Muskrat trapping may also affect house activity and this is given as a reason by some of the delta trappers against fall trapping. Fall trapping did not take place on the study area so this was not evaluated.

While freezing reduced the number of active houses and accessibility to the food supplies therein, it also made forage at active houses difficult to obtain. Muskrats were forced to burrow through the relatively firm lake bottom to obtain whatever root stocks were available. When the ice left the lake this was evident from the undermined vegetation around the houses and the deep trenches often seen leading away from them. By late winter most of the houses had been reduced to thin shells. Freezing of the shallow water also must have increased stress due to cold, particularly where the snow cover was not deep. This may have been partially offset by an apparent tendency for muskrats to dig downward when the lake becomes frozen to the bottom. This allowed muskrats to maintain some unfrozen water under the house and may have served to moderate their micro-climates.

On the basis of the reported effect of freezing of shallow water on muskrats in other areas, some concern was felt that a "freeze-out" or "die-off" was in the offing. However, in addition to the reasonably high survival rate, there are several other indications that muskrats at Egg Lake, during the winters studied, did not face stress of a limiting nature:

(1) Abnormal numbers of dead animals were not found in houses during spring trapping nor were they seen following break-up. The only carcass found during spring trapping in either year was an untagged adult found on April 14, 1972. It was in obviously poor condition, being devoid of subcutaneous and visceral fat deposits and lacking its left foreleg.

(2) The population largely remained in their houses and under the ice. Although my visits to the study area were infrequent, H. Wylie (pers comm) has assured me that during his more frequent visits he saw no sign of extensive "winter-running". During my winter visits I noticed the snow trails of only two individuals. The serpentine trail of one was followed for almost 2 km before it entered a deep and well-used bison trail. I do not consider those movements to be more than normally occur in most muskrat populations.

(3) No torn pelts were taken prior to the onset of mating activity in either 1971 or 1972. This indicates that increased crowding or competition for restricted food supplies did not result in increased fighting.

(4) Most of the muskrats taken during spring trapping were judged to be in good condition on the basis of abundant, subcutaneous and visceral, white fat deposits. Of nearly 100 carcasses that I examined during both harvests, less than 20% were recorded as having sparce or no visible fat.

(5) All of the marked juveniles weighed during the spring harvest were heavier than their fall weights. Thirty juveniles taken in April 1972, which had been last weighed in October, gained an average of 242.5 ± 26.8 g. This represents an average over-winter weight gain of approximately 40 g per month. Of four adults weighed after the same period, two gained an average of 165 g and two lost an average of 205 g. In contrast, Olsen (1959) found no weight gain in juveniles over winter and at Big Island Lake, Alberta, Schmitke (1971) reported a substantial over-winter weight loss in both juveniles and adults, which he attributed to reduced food supply.

Adjustments for Survival during Low Water

The preceding data have shown that the obviously reduced survival capacity of the habitat during winter did not result in widespread starvation, emigration, disease, or intraspecific competition. This is probably due in part to the fact that population density was not high and forage around houses was apparently of high nutritive quality (although its availability was reduced). There is also good reason to believe that certain behavioral responses by the muskrats themselves were important in assuring survival during the period of reduced water levels:

(1) *Selection of House Building Sites*. Muskrats selected winter house building sites on the basis of water depth (Fig 6) and

cover type (Fig 7). This was important since the proportion of active houses increased with water depth and snow cover thickness. An increase in the selection of bulrush and burreed sites from summer to fall was associated with greater snow accumulation and higher rates of activity than in other cover types. Selection of winter house sites did not appear to be associated with forage preference as much as with availability since sweetflag, which was highly preferred as food, was selected less for house building. Sweetflag grew in shallower water, trapped less snow and had fewer houses that remained in use.

(2) *House Size*. H. Wylie (pers comm) has observed that winter houses constructed during periods of low water are larger than during high water. As well as providing muskrats with a larger food supply at a time when access to rooted vegetation is restricted, large houses offer greater resistance to freezing and disturbance than do small ones.

(3) *Number of Houses per Home Range*. There is also some evidence that muskrats construct proportionately more houses during periods of low water than they do during high water. The number of pushups in the study area was higher before and following the low water years of 1970 and 1971 (H. Wylie, pers comm). Muskrats may have compensated by building more houses. Houses would have greater survival value than pushups since deep and consequently unfrozen water was generally not available in late winter. Similarly, the presence of multiple dwellings within a home range would alleviate the effect of some houses becoming frozen or destroyed. The density of 2.5 muskrats per fall house observed on the study area would tend to support this idea since the most frequently reported figure in the literature is 5.0 muskrats per house (Dozier, 1948; McLeod, 1950).

(4) *Intraspecific Relationships*. Although proof is not available, adjustments in social tolerances may have been important in winter survival of this population. Complete freezing of the shallow water along with a high rate of house desertion created conditions of crowding which did not result in intraspecific fighting or eviction from home ranges. This is illustrated, for example, by home range 52 (Fig 8). In April 1972, 11 of the 12 fall occupants were trapped although only two of the original eight houses were still active. Some trappers can recall finding groups of muskrats huddled together in frozen houses. "Huddling" may be an important behavioral adaptation for conserving energy. The lack of knowledge about the behavior and physiology of muskrats during winter continues to be the largest gap in our understanding of muskrat ecology.

These adjustments apparently mitigated the effect of deteriorating environmental conditions on muskrat survival. Muskrats responded to declining water levels with adjustments aimed at maintaining adequate winter food supplies.

CONCLUDING DISCUSSION

In concluding, I propose to summarize the relative roles of mortality controlling factors regulating this population. I will do this in two parts, distinguishing between factors that appeared to operate during the period of study and those that determine long-term population levels of muskrats on the Delta.

Factors Controlling the Egg Lake Population from 1970-72.

The average reproductive rate of 18 young per adult female in the study is comparable to the optimum reproductive rates reported in the literature. This potentially represents a ten-fold annual increase in population size. However, the observed increase in the breeding population from 1970 to 1971 was only around 20%. A number of proximate factors, discussed previously, were responsible for removing the balance of the annual production either through direct mortality or by causing emigration from the study area. These factors tend to operate together, with the impact of each affected by other biological or environmental influences. These interrelationships and the relative importance of each factor can be summarized diagramatically (Fig 19).

While the declining water level did not appear to cause mortality directly, it did affect the population by reducing the amount of suitable habitat and predisposing muskrats to other mortality factors. It is therefore considered a primary controlling factor. The amount of habit.. on the study area declined by about one-third from 1968 to 1971 through direct loss of water area. This affected the number of breeding territories that could be established each year and resulted in population tensions, death and emigration as the area of secure habitat

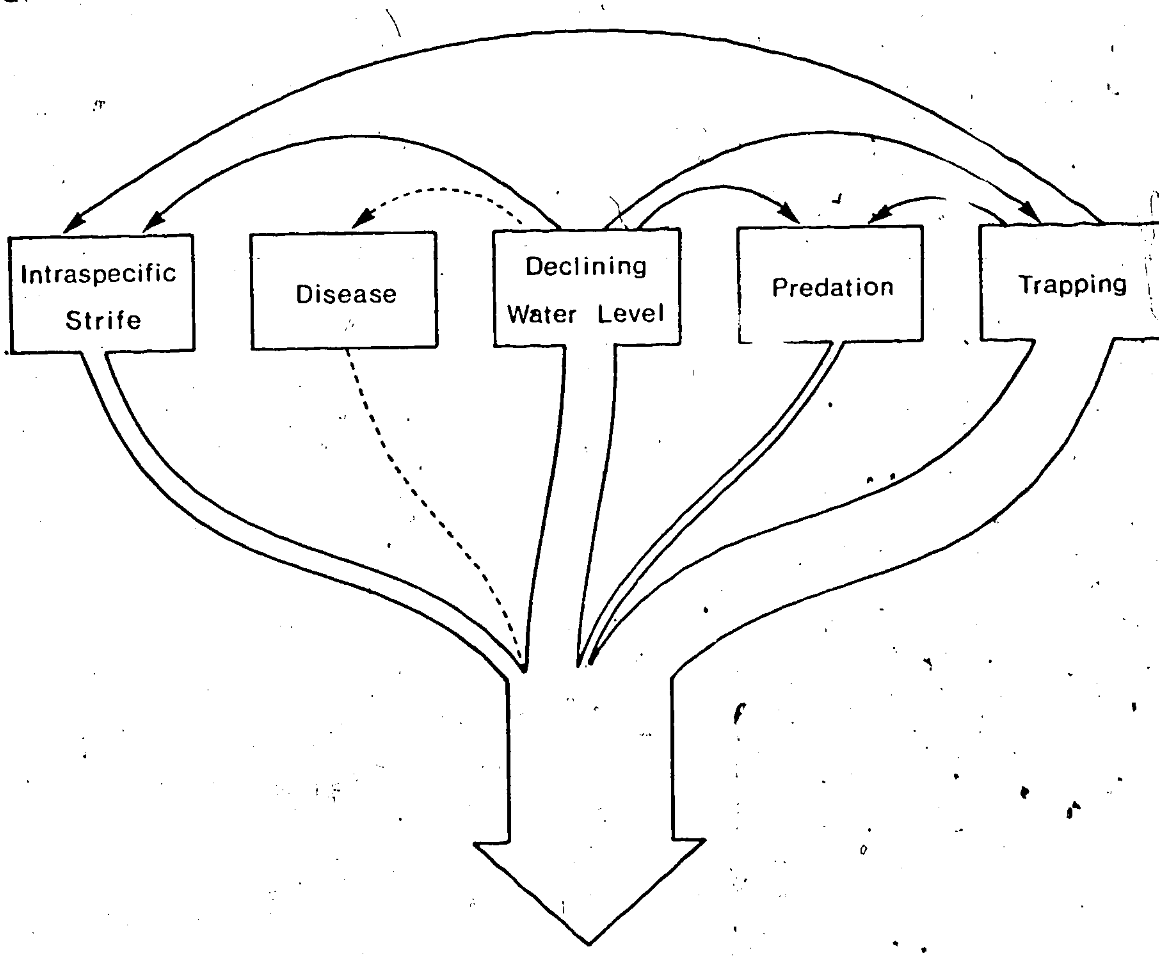


Figure 19. Diagramatic summary of the interrelationships and relative importance of muskrat mortality factors.

diminished. The magnitude of population losses due to low water is difficult to determine since losses usually resulted from interaction with other mortality factors. The relative importance attached to low water level in Figure 19, therefore, considers the overall rather than the direct consequences.

Intraspecific fighting can regulate populations by causing death or dispersal or by affecting reproduction. A low level of fighting was observed throughout the breeding season with an increase during the fall and during spring mating, however, little actual mortality from wounds was detected. Some fighting was attributed to deteriorating environmental conditions as muskrats in shallow areas tried to extend home ranges into deeper parts of the marsh. Most of the intraspecific mortality observed involved predation on nestlings. Since the population density was low during the period of study, density-dependent factors were likely of reduced importance in population regulation.

With the exception of a litter taken by a mink in 1971, there was little evidence of predation on well-situated muskrats. Exposure to predators was increased by declining water levels and the lower age ratio apparent among bank dwellers was evidence that mortality was higher in less secure areas. As I have suggested previously, low water levels may also have resulted in an increased number of "wring-offs" which could be more vulnerable to predators.

While mortality caused by humans is another form of predation, it is considered separately here for convenience. Trapping was the principal proximate mortality factor accounting for 40% of all muskrats tagged during 1971 and 50% of the annual production in areas that were trapped. Trapping success may also have been affected by the declining water level. Decreased use of bank burrows and reduction in the number of active houses during winter may have increased trapping efficiency.

An important aspect affecting the roles of these mortality factors is population density. For example, losses from dispersal, disease or fighting may be higher during periods of high numbers. Similarly, the ability of this population to adjust to low water and freezing during winter may not have been as great if population density had been high.

Factors Determining Long-Term Population Levels on the Delta

Of the extrinsic factors affecting muskrats on the Delta, water level fluctuations have the greatest potential for long-term population control. In their extremes, water levels can exert severe depressive influences on muskrat populations. Drawdowns lasting a few years greatly reduce the amount of suitable habitat and may eliminate local populations. Similarly, floods can be very disruptive, particularly when they occur during the breeding season (Ambrock and Allison, 1973).

I have already described the importance of periodic flooding in maintaining marsh ecosystems. Evidence from this study also supports the need for occasional drawdowns to re-establish emergent vegetation. The major prerequisite for winter survival during low water appears to be the availability of sufficient food. Muskrat survival on the study area was directly associated with the presence of extensive stands of offshore emergent vegetation which provided access to food sources in the deepest water available. Delta lakes lacking offshore emergents were apparently subject to greater losses.

It is not yet clear what long-term effect the Bennett Dam will have on muskrat populations on the Peace-Athabasca Delta. It is expected that flows in the Peace River will continue to be subject to some degree of modification. Although flooding did not occur during initial filling of Williston Reservoir from 1968 to 1971, ice jams have subsequently resulted in extensive flooding two years out of three. Flooding in May 1972 restored high water levels in many of the perched basins including Egg Lake, and flooding in the spring of 1974 was the most extensive in the memory of local residents. The importance of the Delta as a whole, and the value of its fur resources should warrant some form of continuing investigation.

LITERATURE CITED

Allison, L. 1973. Status of bison on the Peace-Athabasca Delta. Append. M, Vol. 2, Ecol. Invest. Peace-Athabasca Delta Project, Edmonton, Alberta.

Ambrock, K. and L. Allison. 1973. Status of the muskrat on the Peace-Athabasca Delta. Append. L, Vol. 2, Ecol. Invest. Peace-Athabasca Delta Project, Edmonton, Alberta.

Aspisoff, D.I. 1957. Acclimatization of Muskrats in the Volga-Kama Region: Material on Muskrat Biology. Trans. Russian Game Reports, Vol. 2. Can. Wildl. Serv., Ottawa. 224 pp.

Bayrock, L.A. and J.D. Root. 1971. Geology and geological history of the Peace-Athabasca Delta area: a summary. pp. 28-31. *In* Proceedings of the Peace-Athabasca Delta Symposium. Water Resources Centre, Univ. of Alberta, Edmonton.

Bayrock, L. and J.D. Root. 1973. Geology of the Peace-Athabasca Delta. Append. N, Vol. 1, Hydrologic Investigations. Peace-Athabasca Delta Project, Edmonton, Alberta.

Beard, E. 1953. The importance of beaver in waterfowl management at the Seney National Wildlife Refuge. J. Wildl. Mgmt. 17(4):398-430.

Beckett, J.V. and V. Gallicchio. 1967. A survey of helminths of the muskrat, *Ondatra z. zibethica* Miller, 1912, in Portage County, Ohio. J. Parasit. 53(6):1167-1172.

Beer, J.R. and R.K. Meyer. 1951. Seasonal changes in the endocrine organs and behavior patterns of the muskrat. J. Mammal. 32:173-191.

Beer, J.R. and W. Truax. 1950. Sex and age ratios in Wisconsin muskrats. J. Wildl. Mgmt. 14(3):323-331.

Bellrose, F.C. 1950. The relationship of muskrat populations to various marsh and aquatic plants. J. Wildl. Mgmt. 14(3):299-315.

Bellrose, F.C., Jr., and J.B. Low. 1943. The influence of flood and low water levels on the survival of muskrats. J. Mammal. 24:173-188.

Bennett, R.M. 1971. Lake Athabasca water levels 1930-1970. pp. 32-56. *In* Proceedings of the Peace-Athabasca Delta Symposium. Water Resources Centre, Univ. of Alberta, Edmonton.

Brant, D.H. 1962. Measures of the movements and population densities of small rodents. Univ. Calif. Pub. Zool. 62(2):105-184.

Brown, L.E. 1966. Home range and movement of small mammals. Sym. Zool. Soc. Lond. 18:111-142.

Burt, W.H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. Univ. Michigan Mus. Zool. Misc. Pub. 45. 58 pp.

Card, J.R. 1973a. Factors influencing water levels. Append. B, Vol. 2, Hydrologic Investigations. Peace-Athabasca Delta Project, Edmonton, Alberta.

Card, J.R. 1973b. Peace River flows and their effect. Append. D, Vol. 1, Hydrologic Investigations. Peace-Athabasca Delta Project, Edmonton, Alberta.

Connell, R. and A.H. Corner. 1957. *Polymorphus paradoxus* sp. nov. (Acanthocephala) parasitizing beavers and muskrats in Alberta, Canada. Can J. Zool. 35(3):525-533.

Davenport, L.B. 1964. Structure of two *Peromyscus polionotus* populations in old-field ecosystems at the AEC Savannah River Plant. J. Mammal. 45(1):95-113.

Dilworth, T.G. 1966. The life history and ecology of the muskrat under severe water level fluctuations. M.S. Thesis. Univ. New Brunswick. 125 pp.

Dirschl, H.J. 1973. Trends in vegetation succession in the Peace-Athabasca Delta. Append. J, Vol. 2, Ecological Investigations. Peace-Athabasca Delta Project, Edmonton, Alberta.

Dorney, R.S. and A.J. Rusch. 1953. Muskrat growth and litter production, Wis Conserv. Dept., Tech. Wildl. Bull. 8. 32 pp.

Dozier, H.L. 1953. Muskrat production and management. U.S. Dept. Int. Circ. 18. 42 pp.

Elton, C. and M. Nicholson. 1942. Fluctuations in numbers of the muskrat *(Ondatra zibethica)* in Canada. J. Anim. Ecol. 11(1):96-126.

Erickson, H.R. 1959. Muskrat reproduction, growth, and movement in small water areas of central New York. Ph.D. Thesis, Cornell Univ. 106 pp.

Errington, P.L. 1937. The breeding season of the muskrat in northwest Iowa. J. Mammal. 18:333-337.

Errington, P.L. 1939. Reactions of muskrat populations to drought. Ecology 20(2):168-186.

Errington, P.L. 1940. Natural restocking of muskrat-vacant habitats. J. Wildl. Mgmt. 4(2):143-185.

Errington, P.L. 1941. Versatility in feeding and population maintenance of the muskrat. J. Wildl. Mgmt. 5(1):68-89.

Errington, P.L. 1963. Muskrat populations. Iowa State Univ. Press, Ames, Iowa. 665 pp.

Friend, M., G.E. Cummings and J.S. Morse. 1964. Effect of changes in winter water levels on muskrat weights and harvest at the Montezuma National Wildlife Refuge. N.Y. Fish and Game J. 11(2):125-131.

Fuller, W.A. 1951. Natural history and economic importance of the muskrat in the Athabasca-Peace Delta, Wood Buffalo Park. Wildl. Mgmt. Bull., Ser. 1, No. 2, Dept. of Resources and Development, Ottawa. 82 pp.

Fuller, W.A. and G.H. LaRoi. 1971. Historical review of biological resources of the Peace-Athabasca Delta. pp. 153-173. *In* Proc. Peace-Athabasca Delta Symp. Water Resources Centre, Univ. of Alberta, Edmonton.

Gashwiler, J.S. 1950. A study of the reproductive capacity of Maine muskrats. J. Mammal. 31(2):180-185.

Green, G. and A.H. Laycock. 1967. Mountains and plains. pp. 69-89. *In* W.G. Hardy (ed.) Alberta - A Natural History.

Gunson, J.R. 1968. Muskrat population studies in the Highbank Lake unit Cumberland Marshes. Unpubl. rep., Sask. Dept. of Nat. Resources. 38 pp.

Gunson, J.R. 1969. Helminths of muskrats from Wabamun Lake. Unpubl. rep., Dept. of Zool., Univ. of Alberta, Edmonton. 8 pp.

Harris, S.W. and W.H. Marshall. 1963. Ecology of water-level manipulations on a northern marsh. Ecology 44(2):331-343.

Holmes, J.C. and R. Zeuge. 1962. Helminths of muskrats from Big Island Lake. Unpubl. rep., Dept. of Zool., Univ. of Alberta, Edmonton. 3 pp.

Kadlec, J.A. 1962. Effects of a drawdown on a waterfowl impoundment. Ecology 43(2):267-281.

Kelsall, J.P. 1970. Interaction between barren-ground caribou and muskrats. Can. J. Zool. 48(3):605.

Kerr, G.R. 1963. Changes in the helminth population infesting muskrats one year following heavy muskrat mortality. Unpubl. rep., Dept. of Zool., Univ. of Alberta, Edmonton. 3 pp.

Knight, I.M. 1951. Diseases and parasites of the muskrat *(Ondatra zibethica)* in British Columbia. Can. J. Zool. 29:188-214.

LaRoi, G.H. 1967. The boreal forest-taiga. pp. 151-169. *In* W.G. Hardy (ed.) Alberta - A Natural History.

Lavrov, N.P. 1960. Acclimatization of muskrats in the USSR. Trans. Russian Game Reports, Vol. 7. Can. Wildl. Serv., Ottawa. 150 pp.

Linde, A.F. 1969. Techniques for wetland management. Res. Rep. 45, Dept. of Nat. Resources, Madison, Wisconsin. 156 pp.

Mathiak, H.A. 1966. Muskrat population studies at Horicon Marsh. Tech. Bull. No. 36, Wisconsin Conservation Dept., Wisconsin. 57 pp.

Mathiak, H.A. and A.F. Linde. 1954. Role of refuges in muskrat management. Tech. Wildl. Bull. No. 10, Wisconsin Conserv. Dept., Wisconsin. 15 pp.

McLeod, J.A. and G.F. Bondar. 1952. Studies on the biology of the muskrat in Manitoba. Part I. Oestrus cycle and breeding season. Can. J. Zool. 30:243-253.

McLeod, J.A., G.F. Bondar and A. Diduch. 1951. An interim report on a biological investigation of the muskrat in Manitoba, 1950-1951. Game and Fish Branch, Dept. Mines and Nat. Resources, Winnipeg. 65 pp (mimeo).

Moncrieff, Montgomery and Associates Ltd. 1973. A socio-economic study of Fort Chipewyan and the Peace-Athabasca Delta region. Append. B, Vol. 3, Supporting Studies. Peace-Athabasca Delta Project, Edmonton, Alberta.

National Academy of Sciences - National Research Council. 1966. Nutrient requirements of rabbits. Publ. 1194. Washington, D.C. 17 pp.

Neal, T.J. 1968. A comparison of two muskrat populations. Iowa State J. of Sc. 43(2):193-210.

Novakowski, N.S. 1958. Fur resources survey of Wood Buffalo National Park. Unpubl. rep., Can. Wildl. Serv. 45 pp.

Olsen, P.F. 1959. Muskrat breeding biology at Delta, Manitoba. J. Wildl. Mgmt. 23(1):40-53.

Peace-Athabasca Delta Committee. 1970. Death of a delta. Peace-Athabasca Delta Committee, Edmonton, Alberta. 19 pp.

Raup, H.M. 1935. Botanical investigations in Wood Buffalo National Park. Bull. No. 74, Biol. Ser. No 20, National Museum of Canada.

Sadleir, R.M.F.S. 1969. The ecology of reproduction of wild and domestic mammals. Methuen and Co. Ltd., London. 321 pp.

Sather, J.H. 1958. Biology of the great plains muskrat in Nebraska. Wildl. Monogr. No. 2:1-35.

Schmitke, R.G. 1971. Some aspects of muskrat ecology at Big Island Lake, Alberta. M.Sc. Thesis, Utah State Univ. 54 pp.

Seabloom, R.W. and J.R. Beer. 1963. Observations of a muskrat population decline in North Dakota. N. Dakota Acad. of Sc. Proc. 17:66-70.

Snead, I.E. 1950. A family type live trap, handling cage, and associated techniques for muskrats. J. Wildl. Mgmt. 14(1):67-79.

Soper, J.D. 1942. Mammals of Wood Buffalo Park, northern Alberta and District of Mackenzie. J. Mammal. 23(2):119-145.

Stelfox, J.G. 1971. Biotic-abiotic factors influencing forage palatability, preference, and range carrying capacity. Can Wildl. Serv. rep., Edmonton, Alberta. 37 pp.

Stevens, W.E. 1955. Adjustments of the northwestern muskrat *(Ondatra zibethicus spatulatus)* to a northern environment. Ph.D. Thesis, Univ. of British Columbia. 194 pp.

Stickel, L.F. 1954. A comparison of certain methods of measuring ranges of small m mmals. J. Mammal. 35(1):1-15.

Surrendi, D.C. and C. Jorgenson. 1971. Some aspects of muskrat winter ecology on the Peace-Athabasca Delta. Can. Wildl. Serv. Rept. 113 pp.

Takos, M. 1947. A semi-quantitative study of muskrat food habits. J. Wildl. Mgmt. 11(4):331-339.

Tomich, P.Q. 1969. Movement patterns of the mongoose in Hawaii. J. Wildl. Mgmt. 33(3):576-584.

Townsend, G.H. 1973. Vegetation mapping and topography of the Peace-Athabasca Delta. Append. I, Vol. 2, Ecological Investigations. Peace-Athabasca Delta Project, Edmonton, Alberta

Van Cleave, H.J. 1953. Acanthocephala of North American mammals. Univ. of Illinois Press, Urbana. 179 pp.

Van der Valk, A.G. 1970. Hydrarch succession and primary production of oxbow lakes in central Alberta. M.Sc. Thesis, Univ. of Alberta, Edmonton. 116 pp.

Wolfe, J.L. 1968. Average distance between successive captures as a home range index for *Peromyscus leucopus*. J. of Mammal. 49(2): 342-343.

Wuetherick, R.G. 1973. A history of Fort Chipewyan and the Peace-Athabasca Delta region. Append. A, Vol. 3, Supporting Studies. Peace-Athabasca Delta Project, Edmonton, Alberta.

APPENDIX I. Summary of climatic data for Fort Chipewyan provided by the Atmospheric Environment Service, Edmonton.

		Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Annual Precip.
1970	a	-13.0	-5.5	6.6	31.9	45.9	60.5	61.8	58.9	45.4	33.3	9.1	-9.8	
	b	0.6	0.5	1.2	1.3	2.5	0.7	2.0	2.8	1.4	1.6	0.8	0.7	15.5
	c	14	16	15	Tr	0	0	0	0	0	1	5	11	
1971	a	-19.7	-1.5	7.9	33.6	51.0	59.4	60.5	61.5	47.3	36.4	11.7	-13.0	
	b	0.9	1.1	0.5	0.4	1.1	1.8	3.7	1.7	3.2	0.7	1.4	0.6	16.9
	c	21	29	32	0	0	0	0	0	0	3	13	14	
1972	a	-20.7	-15.3	11.4	23.4	49.3	59.6	59.1	60.5	38.1	28.9	13.0	-10.4	
	b	0.8	0.7	0.9	2.3	0.6	1.8	3.4	0.8	2.3	1.0	0.5	1.2	16.3
	c	23	31	34	Tr	0	0	0	0	0	Tr	4	16	
10 yr mean (1963-1972)														
	a	-16.9	-5.0	6.9	29.8	45.9	57.2	61.6	58.8	46.4	35.1	11.8	-3.9	
	b	0.9	0.7	0.8	0.9	1.2	1.6	2.5	2.0	2.2	1.2	1.0	0.7	15.7
	c	19.7	25.1	23.0	0.5	0	0	0	0	0	1.2	7.2	12.9	

a = mean daily temperature (°F); b = total monthly precipitation (in.); c = snow on ground at end of month (in.)

APPENDIX II. Plant species found on the study area.

Scientific Name	Common Name
Shoreline	
Agrostis scabra Willd.	bunt grass
Beckmannia syzigachne (Steud.) Fern.	slough grass
Bidens cernua L.	nodding beggar-ticks
Calamagrostis canadensis (Michx.) Beauv.	bluejoint
Carex sychnocephala Carey	sedge
Cicuta douglasii (D.C.) Coult. & Rose	water hemlock
Eleocharis palustris (L.) R. & S.	creeping spike rush
Ranunculus aquatilis L. var. *capillaceus* (Thiull.) D.C.	water crowfoot
Rumex maritimus L.	golden dock
Scolochloa festucacea (Willd.) link	whitetop
Senecio congestus (R. Br.) D.C. var. *palustris* (L.) Fern.	marsh ragwort
Zizania aquatica L.	wild rice
Emergent	
Acorus calamus L.	sweetflag
Carex vesicaria L.	sedge
Equisetum fluviatile L.	horsetail
Lemna minor	duckweed
Lemna trisulca L.	duckweed
Phragmites communis (L.) Trin.	reed grass
Sagittaria cuneata Sheld.	arrowhead
Scirpus acutus Muhl. ex Bigel	hardstem bulrush

APPENDIX II continued.

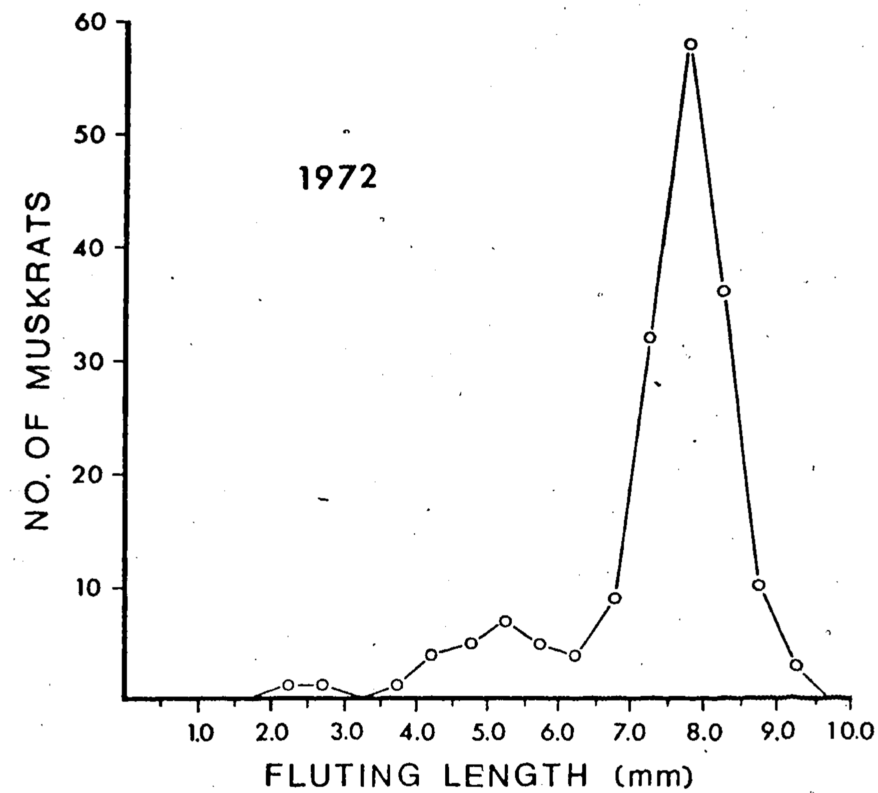
Scientific Name	Common Name
Scirpus fluviatilis (Torr.) Gray	river bulrush
Sparganium eurycarpum Engelm.	giant burreed
Typha latifolia	common cattail
Submerged Aquatic	
Myriophyllum exalbescens Fern.	water milfoil
Myriophyllum spicatum L. var. *exalbescens*	water milfoil
Nuphar variegatum Engelm. ex. Clint	yellow pond-lily
Polygonum amphibium L. var. *natans* Michx.	water smartweed
Potamogeton filiformis Pers.	pondweed
Potamogeton richardsonii (Benn.) Ryd.	clasping leaf pondweed
Po[illegible]*aginatus* Turcz.	large-sheath pondweed
Pot[illegible]*osteriformis* Fern.	flat-stemmed pondweed
[illegible]*andica* (Oeder) Borbas var. [illegible]*rnaldiana* Butters & Abbe	yellow cress

APPENDIX III. Evaluation of the fluting length technique for determining the age of muskrats.

In October, adults and juveniles were still separable on the basis of weight and length, however, by March or April these criteria were no longer reliable. The age of kill-trapped muskrats was determined using the fluting length technique described by Olsen (1959). This technique involves measuring the length of the anteriormost buccal fluting on the first upper molar. The basis is that adults have undergone a longer period of tooth wear which results in longer root development and shorter crown height. Sather (1958) found this technique reliable for 58 known age muskrats. Olsen (1959) reported agreement with 12 known age muskrats, however, these were all juveniles. Gunson (1968) found a close correlation between fluting length of muskrats in spring harvests and estimated fall ages.

Following cleaning with dermestid beetles, the upper right molar was removed from each skull. Using a binocular dissecting microscope with an ocular micrometer, the distance from the occlusal surface to the end of the fluting was measured to the nearest tenth of a millimeter. Measurements were then grouped in half millimeter intervals and the frequencies plotted to determine the major separation point (Fig 20). A major break in the curve around 6.5 mm appears to separate adult and juvenile age classes.

The accuracy of the technique was checked using data from 127 known age (tagged) muskrats taken in spring 1972. None of the 111 juveniles had fluting lengths under 6.5 mm. However, 5 of 16 adults had fluting lengths greater than 6.5 mm. While this error only involved 4 percent of the entire tagged sample, 31 percent of the adults were



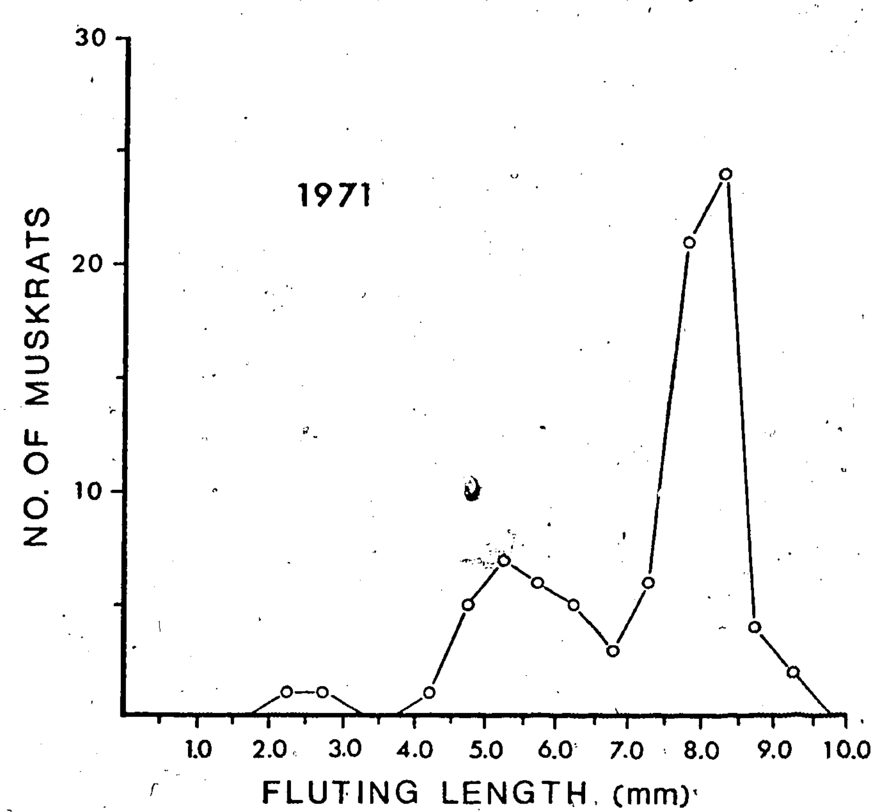


Figure 20. Frequency distribution of fluting lengths for muskrats taken during the 1971 and 1972 spring harvests.

incorrectly aged. This seriously limits the usefulness of this technique, particularly with regard to determining age ratios.

Similar results were obtained by Elder and Shanks (1965). They found that 9 of 50 known age muskrats were aged incorrectly and concluded that "the bias is the more serious because all errors were in the same direction -- skulls of adults that had clearly juvenile molar types".

APPENDIX IV. Bird species associated with Egg Lake.

Family	Scientific Name	Common Name
Anatidae	*Anas platyrhynchos*	mallard
	Anas strepera	gadwall
	Anas acuta	pintail
	Anas carolinensis	green-winged teal
	Anas discors	blue-winged teal
	Aythya valisneria	canvasback
	Aythya affinis	lesser scaup
	Aythya americana	redhead
	Branta canadensis	Canada goose
	Bucephala clangula	common goldeneye
	Bucephala albeola	bufflehead
	Oxyura jamaicensis	ruddy duck
	Mareca americana	American widgeon
	Spatula clypeata	shoveler
Accipitridae	*Haliaeetus leucocephalus*	bald eagle
	Circus cyaneus	marsh hawk
	Buteo jamaicensis	red-tailed hawk
Ardeidae	*Botaurus lentiginosus*	american bittern
Charadriidae	*Charadrius melodus*	piping plover
Colymbidae	*Podiceps auritus*	horned greb
	Aechmophorus occidentalis	western greb

APPENDIX IV continued.

Family	Scientific Name	Common Name
Gruidae	*Grus canadensis*	sandhill crane
Icteridae	*Agelaius phoeniceus*	red-winged blackbird
	Euphagus carolinus	rusty blackbird
	Quiscalus quiscula	common grackle
	Xanthocephalus xanthocephalus	yellow-headed blackbird
Laridae	*Chlidonias niger*	black tern
	Sterna hirunda	common tern
	Larus pipixcan	Franklin's gull
Phalaropidae	*Steganopus tricolor*	Wilson's phalarope
Rallidae	*Fulica americana*	coot
	Porzana carolina	sora rail
Scolopacidae	*Erolia melanatos*	pectoral sandpiper
	Erolia minutilla	least sandpiper
	Totanus melanoleucus	greater yellowlegs
	Tringa solitaria	solitary sandpiper
Strigidae	*Bubo virginianus*	great horned owl
	Nyctea scandiaca	snowy owl
Troglodytidae	*Telmatodytes palustris*	long-billed marsh wren

APPENDIX V. Absolute change in water level of Egg Lake during 1971 as indicated on a staff-type water gauge.