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Relationship between the availability, abundance, and nutrient quality of *Typha latifolia* and *Scirpus acutus* to summer foraging and use of space by muskrats (*Ondatra zibethica*) in south-central Alberta

by

© Catherine E. Welch

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
Spring 1980

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Relationship between the availability, abundance, and nutrient content of Typha latifolia and Scirpus acutus to summer foraging and use of space by muskrats (Ondatra zibethica) in south-central Alberta submitted by Catherine E. Welch in partial fulfilment of the requirements for the degree of Master of Science.

....

Supervisor

J. O. Murie ....

....

W. A. Fuller ....

....

Date 13 December 1979

Flowing waters melt the dwindling winter scenes
and provides you with the means
to resume your noble dance.
All the marsh listens as you whirl in consonance
a chorus in the fresh night.
A deterent to ritualized fight?
And your life settles into familiar routines.

Evening shadows take form in the deepening amber glow
and silouette you as you flow
among the riches of your kingdom.
Watching your heirs sing a tune to the setting sun,
and frolic in unending
bouts of friendly teasing.
In a time that never seems to pass too slow.

The uneven cackling to winter's early glance
fades out far in the distance.
Frozen droplets bite the core
and drain the last glimmer of life from every pore.
But you, you must remain
and secure your domain
for another summer, and another dance.

to the muskrats;
who have inspired me
more than anyone else.

Abstract

Foraging and spacing patterns of muskrats (*Ondatra zibethica*) were examined at a 35 ha pond (Bowden Lake) in south-central Alberta. Muskrats from areas where only *Typha latifolia* (common cattail) or *Scirpus acutus* (hardstem bulrush) (the dominant emergent plants) and from areas where both species were present were studied to examine the effects of availability, abundance, and nutrient content of these two plants on the foraging habits and use of space in muskrats.

The nutrient content (% protein, calcium, phosphorus, potassium, magnesium, and sodium) of *S. acutus* and *T. latifolia* were similar in spring. Nutrients in *T. latifolia* declined rapidly through the growing season, and fiber content increased. Nutrients in *S. acutus* gradually declined through the year, but remained consistently higher than those in *T. latifolia*. Fiber content of *S. acutus* was always lower than that of *T. latifolia*. The relative abundance (proportion of a plant species in an animal's home range) of *T. latifolia* declined through the field season, whereas that for *S. acutus* remained relatively constant. Absolute abundance of *T. latifolia* was highest in summer, when the biomass and fiber content were higher than in the spring or fall. The absolute abundance of *S. acutus* increased from spring to summer and fall.

Emergent plants were the major food resources in spring and summer, but muskrats switched to eating submergent

plants (Potomogeton vaginatus -pondweed, and Myriophyllum exalbescens -water milfoil) in fall. S. acutus was the preferred food of animals living in Scirpus and Scirpus-Typha-habitats, and of captive animals from all three habitats in experimental tests. T. latifolia was eaten in relation only to its relative abundance, whereas the amount of S. acutus in muskrats' diet was correlated with its absolute abundance and nutrient content. When S. acutus was available, muskrats concentrated their foraging activities on it; in its absence they ate combinations of less preferred foods (T. latifolia, P. vaginatus, and M. exalbescens). When the quality of any food resource decreased below a level where the probability that it was beneficial was low, muskrats switched to another food item.

Habitats consisting of stands of S. acutus were preferred over T. latifolia as indicated by the higher densities of muskrats and the differential dispersal of animals into Scirpus-habitat compared to Typha-habitat. Growth rates (weight and body measurements) were higher for juveniles from Scirpus-habitat than for juveniles from Typha-habitat. Overwinter survival was also higher for juveniles born in and remaining in Scirpus-habitat than in Typha-habitat.

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I. Introduction

Fretwell (1972) defined the habitat of a species as, 'any portion of the surface of the earth where the species is able to colonize, and live (temporarily or permanently) at some density greater than zero'. The ability of a habitat to provide food resources and protection from predators will influence the survival and distribution patterns of animals. Any individual that can consistently detect and occupy habitats of higher quality should make a greater contribution to succeeding generations than those individuals that inhabit areas of low quality. Habitats are heterogeneous by nature, and provide a wide variety of potential resources for an animal to exploit. Given variations in food value of the resources available in a habitat, an animal should forage selectively on foods of high quality as a means of increasing its fitness (Levins 1968). Because the way in which an animal uses its habitat plays an integral part in its overall fitness, decisions involving food selection should be essential components of habitat use.

Muskrats (Ondatra zibethica) inhabit a wide spectrum of aquatic habitats throughout North America, Northern Europe and Asia (Errington 1963). These animals consume numerous food species depending in part on their availability within the habitat (see Willner et al. 1975 for a review). Although Van Horn (1975) considered the limited number of muskrats he studied in Iowa to be nocturnal, they are easily observable during daylight and twilight hours in the long days of the northern summer. Evidence of habitat use is also readily observable since muskrats build runways, huts and feeding platforms. Muskrats may have preferred food items (Westworth 1974) and habitat-types (Danell 1978a, 1978b), but the relationship between foraging habits and habitat selection has received little detailed attention. It is the relationship of food and habitat selection to foraging patterns and use of space that is of particular concern in this study of muskrats in south-central Alberta.

II. STUDY AREA

Bowden Lake is a large spring-fed pond, encompassing an area of 47 ha, situated in a shallow depression in the rolling hills of the aspen-parkland of south-central Alberta, three km west of the town of Bowden (51°46′N, 114°04′W). The northern, eastern and western shores are surrounded by cultivated farmland, and the southern shore is bordered by a gravel road. Approximately 325 m south of the north shore, a highway crosses the pond separating it into two sections. The two portions are joined by a single culvert. The present study was conducted primarily in the 35 ha of the lake lying south of the highway.

Bowden Lake (Fig. 1) is predominately open water with emergent vegetation restricted to a bordering fringe, except for a stand of <u>Scirpus</u> <u>acutus</u> (hardstem bulrush) located approximately 150 m from the south shore. The southern and western shores are wetlands dominated by <u>Typha</u> <u>latifolia</u> (common cattail). The western shore is vegetated with <u>T</u>. <u>latifolia</u> interspersed with several <u>Carex</u> <u>lasiocarpa</u> (sedge) meadows. The northwestern corner of the south portion of the pond is vegetated by an onshore community of <u>T</u>. <u>latifolia</u> and an offshore emergent population of <u>S.</u> <u>acutus</u>. Along the rocky highway bed on the northern shore, vegetation is sparse and consists of outcroppings of <u>Agrostis</u> sp) (bent grass) and <u>Rumex</u> <u>maritimus</u> (golden dock). The eastern shore is dominated by an emergent stand of <u>S</u>. <u>acutus</u> and an onshore wetland of <u>C</u>. <u>lasiocarpa</u>, <u>S</u>. <u>acutus</u> and scattered

Figure 1. Map of Bowden Lake. The numbers between two arrow-heads represent the three habitat-types from which muskrats were studied. 1=*Typha latifolia*-habitat, 2=*Scirpus acutus*-habitat, and 3=mixed *Scirpus*-*Typha*.

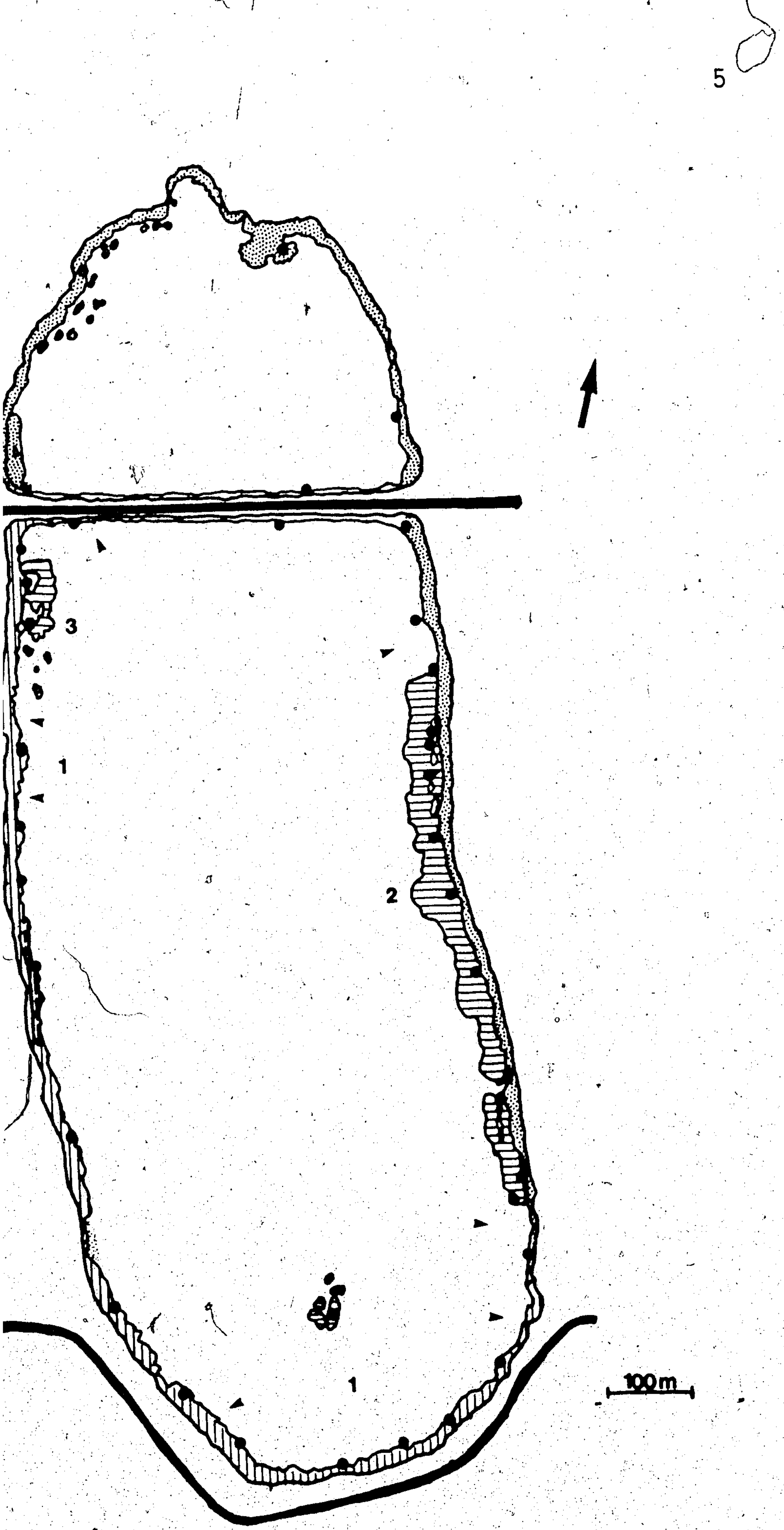
▥ -*Typha latifolia*

▤ -*Scirpus acutus*

░ -*Carex lasiocarpa*

● --muskrat huts

— --roads


5
3
1
2
1
100 m

small patches of _T. latifolia_. A submergent flora dominated by _Potamogeton vaginatus_ (pondweed) with mixings of _P. richardsonii_ and/or _P. pusillus_ and _Myriophyllum exalbescens_ (water milfoil) is present throughout the open water.

Muskrats maintained shoreline huts (except along the north-shore of the study area where bank dens were occupied) throughout most of 1976 and 1977. As water-levels declined through the summer and fall of 1976, several huts along the western shore and the bank dens were abandoned. These dwellings remained unoccupied throughout the summer of 1977. A resident adult population of about 45 muskrats in 1976 declined to about 37 in 1977.

T. latifolia areas on the south shore, _S. acutus_ habitat on the east shore, and the mixed _S. acutus-T. latifolia_ community on the northwestern shore were used as intensive study areas for an analysis of spacing-related and foraging-related behavior. These three habitats are henceforth referred to as _Typha_, _Scirpus_, and _Scirpus-Typha_.

III. GENERAL METHODS

Collection of Data

A total of 210 muskrats were live-trapped (15x15x50 cm National live traps), tagged with #1 monel metal fish tags and colored plastic ear discs in each ear, weighed (to the nearest g), measured, sexed, examined for injury and reproductive status, and released during 1976 and 1977. Measurements of tail length (to the nearest mm; after Dozier et al. 1948) and left-hind foot length (to nearest mm) were recorded for adults and juveniles, and the total length of juveniles was taken from the nose to the end of the tail. Upon recapture, all animals were identified, reweighed, and re-examined. In addition, juveniles were re-measured.

I observed muskrats from May until September (435 h) in 1976 and from April until December (1210 h) in 1977. At least 21 adults (range 21-49) were observed throughout the study, and were (as much as possible) equally distributed among the three habitat-types used as intensive study areas. I observed animals from ten different groupings of huts in the three habitat-types. Observations were rotated so that animals from each hut grouping were observed for approximately equal amounts of time. A pilot study of muskrat activity was conducted in the spring of 1976 to determine when the animals were most active during visible light. I observed muskrats at different six-hour intervals each day for eight days. The hours during which the most activity and animals were seen were the hours used for observing the animals. As the seasons changed the hours of observation were altered to correspond to the peak hours of muskrat activity in visible light. Muskrats from the intensive study areas were observed from just after sunrise (approximately 0600 h depending on the season) until approximately 1000 h (MST) and for about two hours before and after sunset (approximately 1800 h-2300 h), for an average of six hours of observation each day. Observations were made from a canoe or from selected observation posts on land. I recorded muskrat activities continuously throughout the observation periods by noting the time, and the identity, position and activity of that animal. Two methods of observation were used during the study. When fewer than three animals were in sight at any given time, continuous observations were taken on all of them. If more than three animals were present in the observation area a scan of each animals' activities was taken every five minutes.

In order to evaluate variations in time budgets, spatial relationships, foraging habits, and behavior over time, the field season was divided into three time periods that correspond to biological events in the lives of muskrats. The spring period begins with ice-breakup in early April and ends with the birth of the first litter in late May (1 April-31 May). The second period, summer, extends from the birth of the first litter to the end of the breeding season in late August (1 June-31 August). The fall period begins in September and continues through to freeze-up in mid-November (1 September-15 November).

Muskrat Home Ranges

Muskrat home ranges were determined using positional data from direct observations and trapping. Minimum area polygons, excluding the outermost five percent of an animal's locations, were drawn to represent an animal's home range (Jennrich and Turner 1969), and the area of each home range was calculated. Home range data were used in analyses of muskrat foraging and spacing.

Habitat Analysis

In order to evaluate the quality of the habitat in which muskrats reside, the abundance, nutrient quality, and density of the two major emergent plants on the study area (S. acutus and T. latifolia) were recorded during the 1977 field season. Growth and density estimates for each species were obtained once a month from May until October. Three randomly placed 0.5 m by 1 m plots for each species were staked out in each of ten muskrat home ranges. Two of the home ranges included stands of both T. latifolia and S. acutus, and the remaining eight home ranges were equally divided between stands of either T. latifolia or S. acutus. Thus, there were 18 plots for each plant species. Data on water depth (cm), density, and height of culms (cm), phenology, substrate composition, the identity of co-occurring plant species, and the percentage of culms recognizably bitten off by muskrats were recorded for each plot during each sampling period.

Estimates of productivity and nutrient content of each species were obtained each month from mid-May until mid-October. The standing crop from two 0.25 by 0.5 m plots for both S. acutus and T. latifolia was harvested each month. Samples were taken on a rotating basis from each of the ten home ranges mentioned above, and the site of the plot was chosen randomly by using a random numbers table and a grid of the study area. When a plot was harvested, data on water depth, density, height, phenology, substrate composition, co-occurring species, muskrat use, and wet weights were recorded. The harvested material was pressed and dried in a plant press placed over a 150-watt light bulb. Dried material was weighed and stored in air-tight containers until nutrient analyses were performed. Analyses for total nitrogen, total phosphorus, calcium, magnesium, sodium, potassium, moisture content, and fiber content were carried out by the Soil and Feed Testing Laboratory of the Alberta Department of Agriculture (Edmonton).

Analyses of the relationships between plant nutrient content and physical characteristics (i.e. height, density, and phenology) of those plants, water depth in plots, and the time of year were done for both species. These were done using a Spearman rank-correlation (Marascuilo and McSweeney 1977, and Siegel 1956). The resulting significant correlations ($p<0.05$), in conjunction with the data from the 0.5 by 1 m plots, were used to estimate the nutrient quality of each home range.

Activity Budget Analysis

The amount of time an animal spent performing particular behaviors was compiled from my observational data to give an estimate of activity budgets. Muskrats engaged in a wide variety of activities, which I divided into six major categories, a) traveling, either on land or swimming; b) foraging, including handling and collecting, transporting and eating of food items; c) construction of huts, bank dens, runways, platforms, etc.; d) self-grooming; e) interactions, including amicable, aggressive and sexual interactions; and f) scent marking. Each behavior category was considered with reference to variation by time period, sex, and age. A frequency index for each behavior category was calculated using the formula:

$$\frac{\text{minutes spent/category/animal subclass/time period}}{\text{Total minutes of observation/animal subclass/time period}} \times 100$$

Aggressive interactions consisted of chases and fights between two or more muskrats. Fighting behavior typically involved two animals leaping at each other and attempting to bite each other around the face and shoulders. Fights usually occurred in shallow water or on mud flats. Chases involved one or more animals swimming or running after one another. Amicable interactions involved allo-grooming and greeting behavior (i.e. nose rubbing and sniffing of the face). Sexual interactions consisted of the behavior leading up to and including copulation. Sexual behavior was characterized by one or two males swimming behind a female and vocalizing. Chases and fights between males often occurred before one male mated with the female.

Scent marking was characterized by both the use of conspicuous scent mounds and less conspicuous (visibly) marking of areas in the home range and other animals with scent from anal glands (Ewer 1968). Scent mounds, consisting of a compilation of mud, detritus, and feces, were placed around huts and on clumps of vegetation around the edges of home ranges. Muskrats used an anal drag method of marking described by Thiessen, et. al. (1971) for gerbils, in which an animal backed up to a prominent object and dragged its anus down the object. Muskrats marked vegetation, feeding platforms, huts, rocks, and other features of the environment in this manner. Marking of other animals occurred after allo-grooming bouts.

During each observational period, muskrats spent some portion of time inside a hut or bank den (Fig. 2). An animal was considered to be inside a hut or bank den, if it was seen entering the hut, whether or not it reappeared during the observation period. Only the amount of time in which animals were seen to be active was included in the estimation of the activity index.

I used a one-way analysis of variance (Neter and

Figure 2. Proportion of observation time in which muskrats were observed to be active. (See page 12 in text for a description of active and inactive times.) N=the number of hours of observation in each time period.

▨--Adult females

☐--Adult males

▩--Juveniles

Wasserman 1974; Sokal and Rohlf 1969) to evaluate differences in activity budgets among classes of animals and time periods. A probability level of 0.05 or less was considered to indicate significant differences among groups.

Juvenile Growth

Juvenile birth dates were determined from the behavior and weight changes of adult females. Immediately prior to giving birth females gathered nesting material and transported it to a hut, or bank den. The ages (±5 days) of juveniles were determined by back-dating from the time of capture to the estimated date of birth. Weights, total body length, tail length, and left-hind foot length of 49 juveniles were recorded in 1977; 32 individuals were from Scirpus-habitat and 17 were from Typha-habitat. Growth curves, using age as the independent variable and weight as the dependent variable were fitted to these data using a method outlined by Ricklefs (1967). Juveniles from each habitat were considered separately. A one-way analysis of variance (Neter and Wasserman 1974) was used to analyse the effects of sex and habitat on the growth of juveniles. All growth measures were used in this analysis.

IV. PHYSICAL AND NUTRITIONAL CHARACTERISTICS OF <u>Typha latifolia</u> AND <u>Scirpus acutus</u>

The nutritional characteristics of plants are known to fluctuate with time, the condition of the plant, and between habitats (Boyd 1978, Dijkshoorn 1969, Goodman 1969, and Rorison 1969). I determined the relationship among the physical and nutrient components of <u>T</u>. <u>latifolia</u> and <u>S</u>. <u>acutus</u>, and then compared them with the physical characteristics of the plants in each home range (as estimated by using the data from the 0.5 by 1 m plots).

The nutrient content of both <u>T</u>. <u>latifolia</u> and <u>S</u>. <u>acutus</u> decreased through the growing season (Table 1; and Appendix 1 and 2). The fiber content of <u>T</u>. <u>latifolia</u> increased rapidly after the onset of the growing season, whereas for <u>S</u>. <u>acutus</u> there was a curvilinear relationship with a peak in July. As <u>T</u>. <u>latifolia</u> reached anthesis in late June, the inflorescence stalks became increasingly woody. The decrease in fiber content of <u>S</u>. <u>acutus</u> through August and September was probably from a secondary peak in productivity (Auclair et al. 1976) in late summer and fall, rather than an actual decrease in the fiber content of mature plants. Even though there is a tendency for older <u>S</u>. <u>acutus</u> culms to become more fibrous in the fall, muskrats were seen foraging on both old and new culms until freeze-up. In spring, I noted muskrats eating the green, underwater portions of <u>S</u>. <u>acutus</u> culms from the previous year's growth. The nutrient content of a sample of the previous year's growth was determined and very

Table 1. Mean nutrient content of *Scirpus acutus* and *Typha latifolia* (n=2 for each entry at Bowden Lake (see text for methods of sample calculations).

Table I. Mean nutrient content of Scirpus acutus and Typha latifolia (n=2 for each entry at Bowden Lake (see text for methods of sample calculations).

SPECIES	DATE	FIBER (%)	MOISTURE (%)	PROTEIN (%)	CALCIUM (%)	PHOSPHORUS (%)	MAGNESIUM (%)	SODIUM (%)	POTASSIUM (%)
T. latifolia	May 14	30.1	8.5	18.2	1.15	0.42	0.250	0.200	4.49
S. acutus		36.5	8.8	18.8	0.30	0.39	0.150	1.060	3.54
T. latifolia	May 28	30.0	8.6	17.5	1.48	0.43	0.270	0.110	5.00
S. acutus		35.7	8.7	15.0	0.91	0.28	0.280	0.100	3.42
T. latifolia	June 25	42.5	6.8	5.3	1.08	0.06	0.212	0.055	1.80
S. acutus		39.6	4.1	11.2	1.16	0.17	0.235	0.092	2.52
T. latifolia	July 25	45.4	6.4	4.3	0.87	0.05	0.143	0.049	0.86
S. acutus		43.8	3.7	11.6	0.40	0.23	0.174	0.100	2.70
T. latifolia	Aug. 17	43.4	4.5	8.2	0.18	0.19	0.100	0.089	2.10
S. acutus		----	---	----	----	----	-----	-----	----
T. latifolia	Aug. 31	----	---	----	----	----	-----	-----	----
S. acutus		38.9	2.6	8.3	0.45	0.11	0.134	0.084	1.73
T. latifolia	Sept. 18	*	*	*	*	*	*	*	*
S. acutus		38.2	5.5	10.3	0.41	0.15	0.090	0.080	1.72
T. latifolia	Oct. 18	*	*	*	*	*	*	*	*
S. acutus		35.4	5.5	4.5	0.23	0.07	0.078	0.128	1.06
S. acutus (1977 growth)	May 14, 1978	30.6	8.6	4.2	0.27	0.10	0.090	0.040	1.64

* more than 90% of culm dead.

little difference was found between plants harvested before freeze-up and those collected after ice melt the following spring (Table 1).

The nutrient contents of I. latifolia and S. acutus, were similar in spring. The decline in the nutrient value of I. latifolia throughout the growing season was greater than that of S. acutus. Nitrogen levels (% protein) and sodium levels in S. acutus were generally higher than those in I. latifolia. The consistently high biomass of I. latifolia (Table 2) may account for its lower protein and sodium levels. Boyd (1978) suggested that aquatic plant species that produce lower standing crops (i.e. biomass) generally have higher percentages of nitrogen and sodium than do species with higher standing crops. In August, there was a slight increase in the protein and sodium content of I. latifolia, associated with the growth of new shoots. However, senescence quickly followed. By late August most culms were found to be at least 90% dead. Auclair et al. (1976), Boyd (1970a, 1970b), Boyd and Hess (1970), Mason and Bryant (1975), and McNaughton (1966) have shown that secondary peaks in productivity and nutritional contents of Typha spp. and Scirpus spp. occur in late summer. In both S. acutus and T. latifolia the mean culm height decreased, whereas the mean density increased through August and September (Table 2). Towards the end of the growing season, S. acutus was consistently higher in nutrients (Table 1) than I. latifolia. The combination of a lower fiber content

Table 2. Physical characteristics of _Scirpus acutus_ and _Typha latifolia_ at Bowden Lake (n=18 for each entry except $\bar{X}$ biomass where n=4).

DATE	SPECIES	$\bar{X}$ DENSITY ($/m^2$)	$\bar{X}$ HEIGHT (cm)	$\bar{X}$ BIOMASS (g/m^2)	% VEGETATIVE CULMS	% OF CULMS GREEN
May	_Typha_	23.11	26.45	235.7	100.0	100.0
	Scirpus	100.51	32.63	130.3	80.2	100.0
June	_Typha_	40.7	61.24	924.1	100.0	100.0
	Scirpus	122.82	62.45	842.2	56.1	100.0
July	_Typha_	47.56	121.34	867.5	84.1	100.0
	Scirpus	178.44	113.36	681.7	33.4	100.0
August	_Typha_	47.88	123.07	896.3	80.7	50.0
	Scirpus	185.90	111.94	695.3	32.9	90.0
September	_Typha_	49.12	100.65	1801.74	65.1	9.0
	Scirpus	199.40	100.81	847.2	34.3	70.0

and a higher nutrient content in S. acutus may make it a more desirable food than T. latifolia.

The physical and temporal parameters of the plants which best account for the variation in nutrients are time of year, culm height, and phenology for S. acutus (Table 3) and the time of year, height of culms, and density for T. latifolia (Table 4).

Table 3. Spearman rank-correlations between the nutrient content of _Scirpus acutus_ and its physical and temporal characteristics (based on data from Tables 1 and 2).*

Nutrient	Physical/temporal characteristic	r_s	T-value	p
Fiber	Density (culms/m^2)	0.70	3.25	0.004
Protein	Time of year (days)	-0.69	-3.12	0.005
	Height of culm (cm)	-0.58	-2.34	0.02
Phosphorus	Time of year (days)	-0.76	-3.87	0.001
	Height of culm (cm)	-0.56	-2.34	0.02
Magnesium	Time of year (days)	-0.86	-5.64	0.00008
	phenology	-0.66	-2.89	0.007
Potassium	Time of year (days)	-0.90	-6.76	0.00002
	Height of culms (cm)	-0.53	-2.06	0.03

* Scatter plots of these correlations are given in appendix 1.

Table 4. Spearman rank-correlations between the nutrient content of _Typha latifolia_ and its physical and temporal characteristics (based on data from Tables 1 and 2).*

Nutrient	Physical/temporal character	r_s	T-value	p
Moisture	Density (culms/m^2)	0.67	2.03	0.05
Fiber	Time of year (days)	0.75	2.5	0.03
	Density (culms/m^2)	-0.82	-3.18	0.01
Protein	Density (culms/m^2)	0.6	1.68	0.07
Calcium	Time of year (days)	-0.95	-7.13	0.0004
	Density (culms/m^2)	0.84	3.52	0.008
Magnesium	Time of year (days)	-0.75	-2.55	0.03
	Density (culms/m^2)	0.86	3.81	0.006
Potassium	Density (culms/m^2)	0.70	1.97	0.05

* Scatter plots of these correlations are given in appendix 2.

V. MUSKRAT ACTIVITY BUDGETS

Activity budgets (Fig. 3a, b, and c; Appendix 3 and 4) represent the way in which an animal allocates its time to various activities. The proportion of time spent by an animal on any one activity, may vary as a function of season, energy requirements, position in the dominance hierarchy, age, sex, physiological state, etc. Knowledge of the activity budget can be useful in understanding foraging habits, spatial relationships among individuals, and the use of space.

Traveling. Adult males spent more time traveling than did females in the spring ($F(1,6)=7.87$ $p<0.05$). Greater movement by males at that time may be related to spring dispersal which was primarily done by males, as noted by Sather (1958). There was a general decline in the amount of time males spent traveling, from the spring to the fall ($F(1,6)=16.38$ $p<0.025$). Adult females, on the other hand spent similar amounts of time traveling through the field season. Adults tended to spend more time traveling than juveniles ($F(2,9)=4.3$ $p<0.05$) in the fall (Fig. 3c). All animals spent similar amounts of time traveling in the summer (Fig. 3b).

Foraging. Muskrats spent more time foraging than in any other activity throughout the field season ($F(1,6)=9.53$ $p<0.025$), except for adult males in the spring when they spent similar amounts of time foraging and traveling ($F(1,6)=1.24$ $p>0.10$, Fig. 3a). Within each time period, all

Figure 3a, b, and c. Activity budgets of muskrats at Bowden Lake in 1976 and 1977 (see p 9 in text for methods of calculat[illegible]umber of animals in each sample.

A = Travelling time

B = Foraging time

C = Time spent constructing huts, platforms, runways, etc.

D = Grooming time

E = Interaction time

F = Time spent scent marking

FIGURE 3A. MUSKRAT ACTIVITY BUDGETS, SPRING.

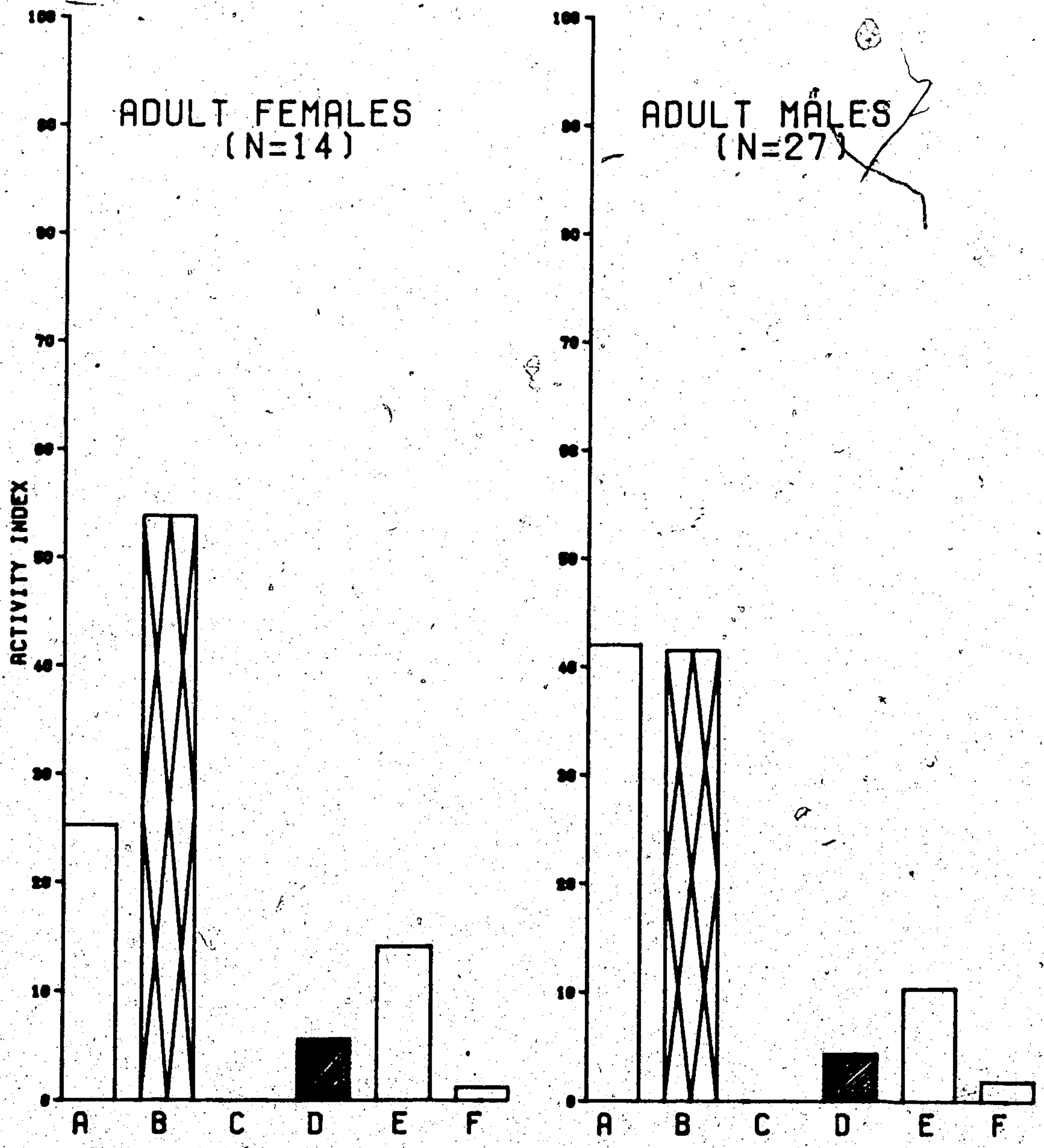


FIGURE 3B. MUSKRAT ACTIVITY BUDGETS- SUMMER.

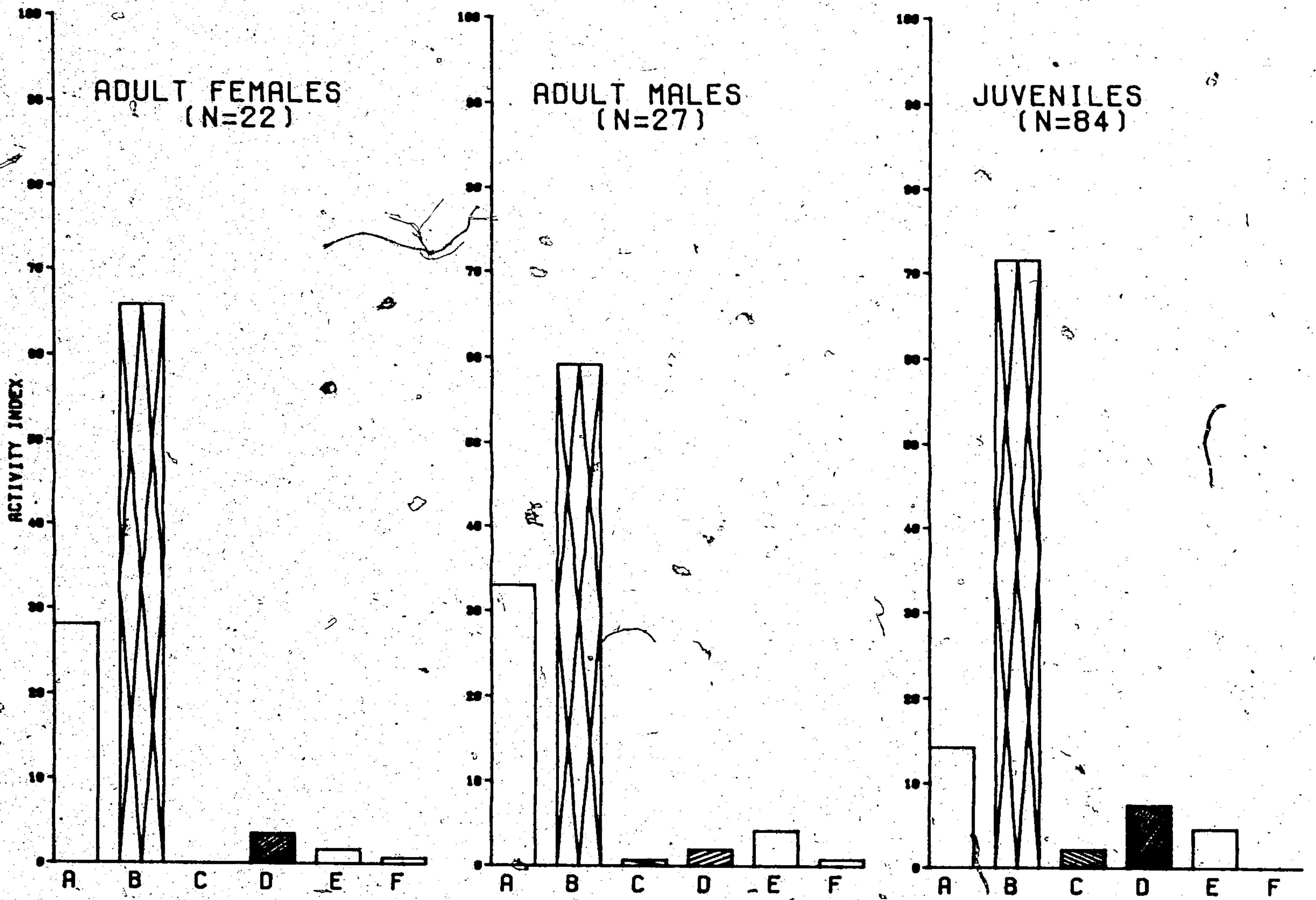
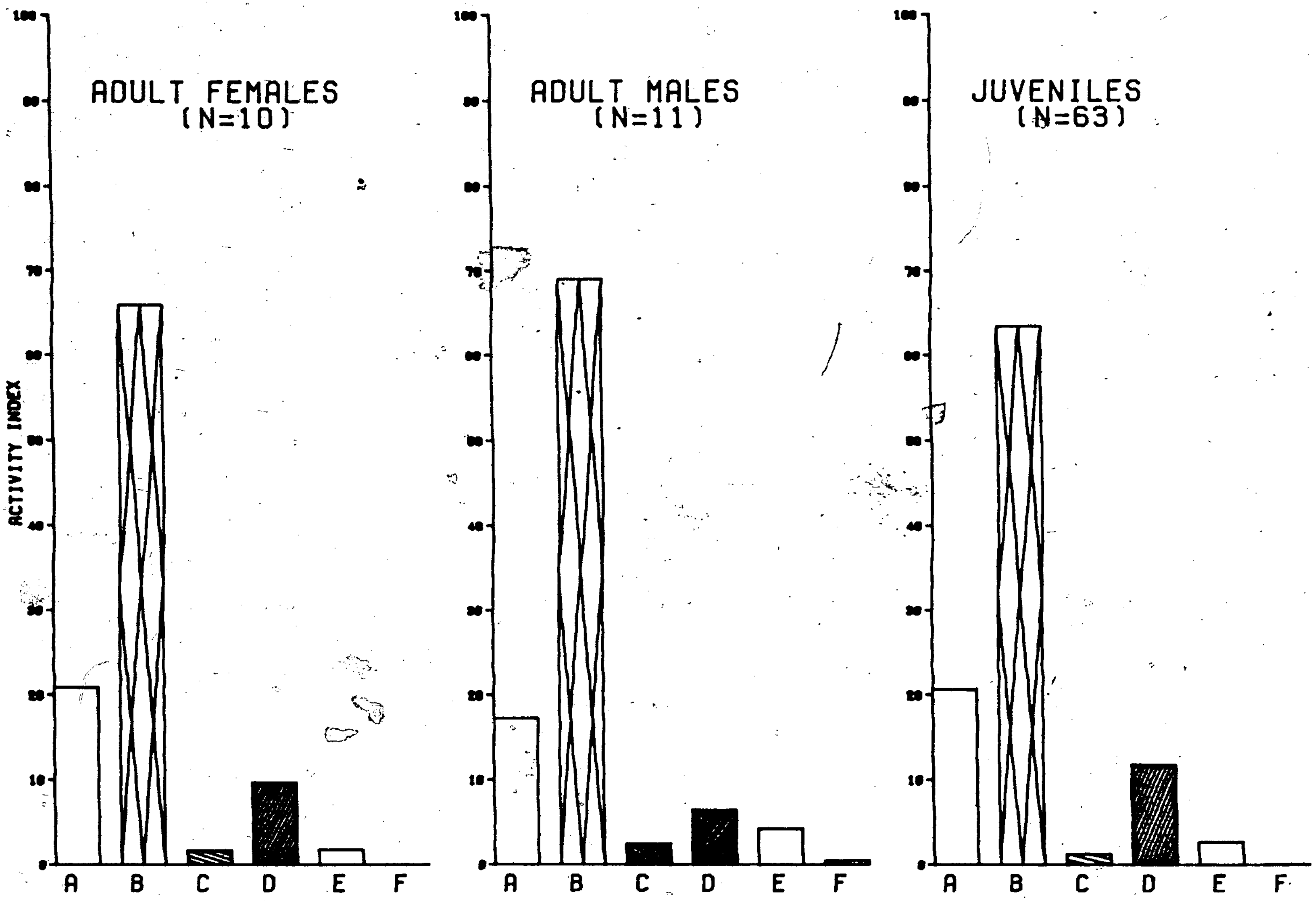


FIGURE 3C. MUSKRAT ACTIVITY BUDGETS- FALL.



three classes of animals spent roughly the same amount of time foraging. The foraging time for adult females and for juveniles did not change significantly through the field season (F(2,6)=2.6>0.1). Adult males increased their foraging time from spring to summer (F(1,6)=20.83 p<0.005), but did not change from summer to fall. Adult males transported food from the collection site to the site where it was eaten (Fig. 4) more often in summer than in spring (F(1,6)=6.10 p<0.05), due in part to greater use of feeding platforms by males during summer. Both adult males and females, collected food and transported it to a nearby hut in summer where newly emerged juveniles ate it. This may also account for the increase in transit time for males. Juveniles spent more time collecting and handling food material than did adults in the summer (F(1,6)=6.4 p<0.05), but less time transporting food material (F(1,6)=6.4 p<0.05). One reason for this may be that juveniles, when foraging, tended to travel to a feeding area and remain there while eating. Adults spent more time handling food in the fall than in summer (F(1,9)=12.1 p<0.01), partly because they were feeding more on submerged aquatics, especially Potamogeton vaginatus, and remained in one general spot to forage rather than transporting the food to platforms or huts.

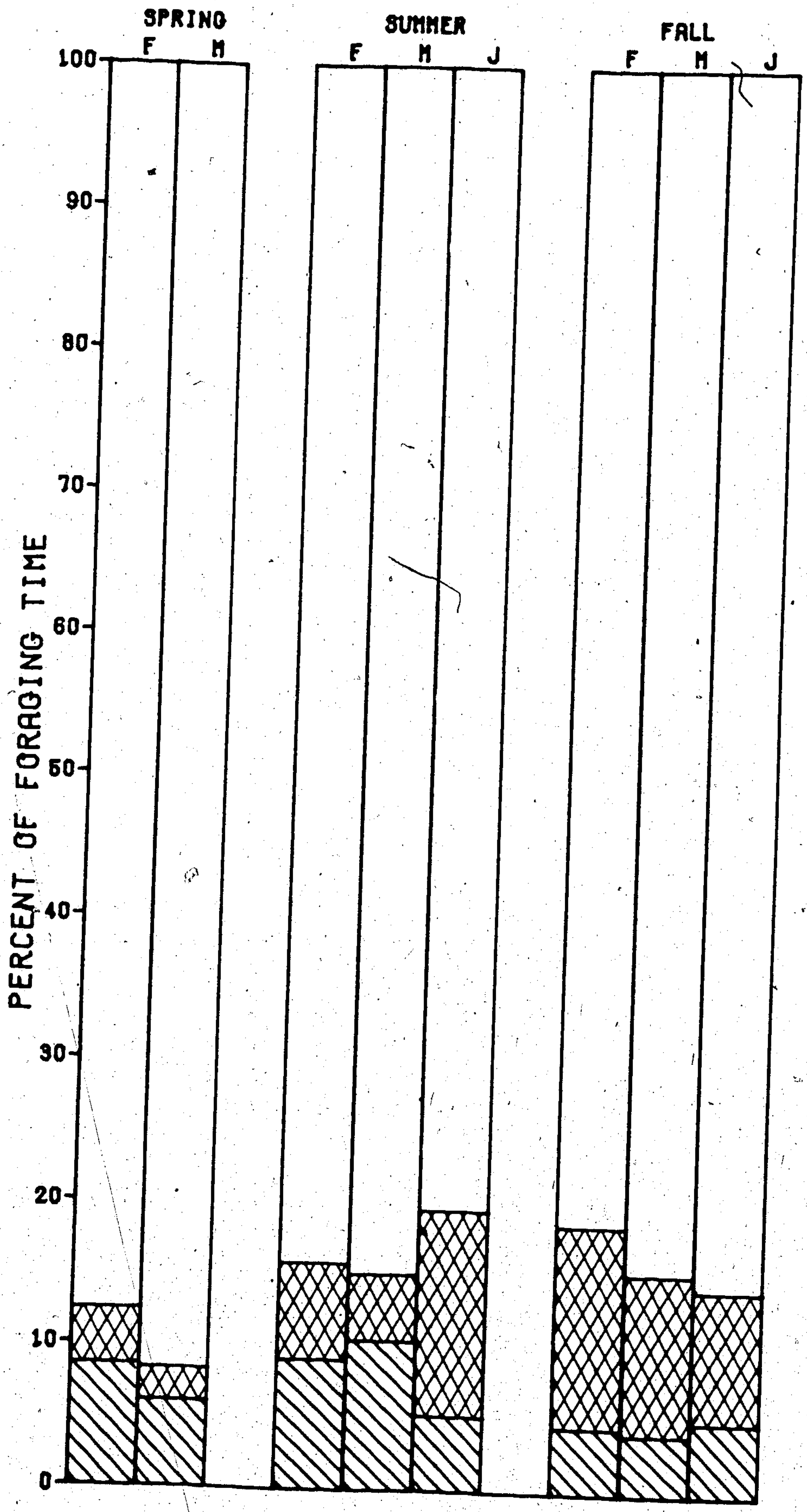
Construction of huts, platforms and runways. Most construction was done at night when I was unable to observe the animals, so my data may not reflect this activity

Figure 4. Percent of foraging time spent eating, handling, and transporting food items. F=adult females, M=adult males, J=juveniles.

☐--Eating time

▩--Handling time

▧--Transit time


SPRING
F
M
SUMMER
F
M
J
FALL
F
M
J
PERCENT OF FORAGING TIME
100
90
80
70
60
50
40
30
20
10
0

accurately. Muskrats were not seen to make any repairs to or to build new huts until late in summer as Errington (1963) also noted. In summer, most construction was done by juveniles (F(1,2)=39.8 $p<0.05$, Fig. 3a). Females were not seen to do any construction until fall, although they may have done some at night. All animals spent approximately the same amount of time building huts in the fall.

Grooming. Adult males and females spent similar proportions of time grooming in spring (Fig. 3a). Juveniles groomed more often in the summer than did adult males (F(1,6)=8.80 $p<0.05$), but not more than adult females (Fig. 3b). No differences among animal classes were evident in the fall (Fig. 3c). No significant differences were found from season to season within any of the animal classes, but there was a tendency for muskrats to spend more time grooming during the colder portions of the field season. This was particularly true in the fall and may have been due to a decrease in the ambient air and water temperatures, increasing the need for care of the pelage for insulation (McArthur 1977).

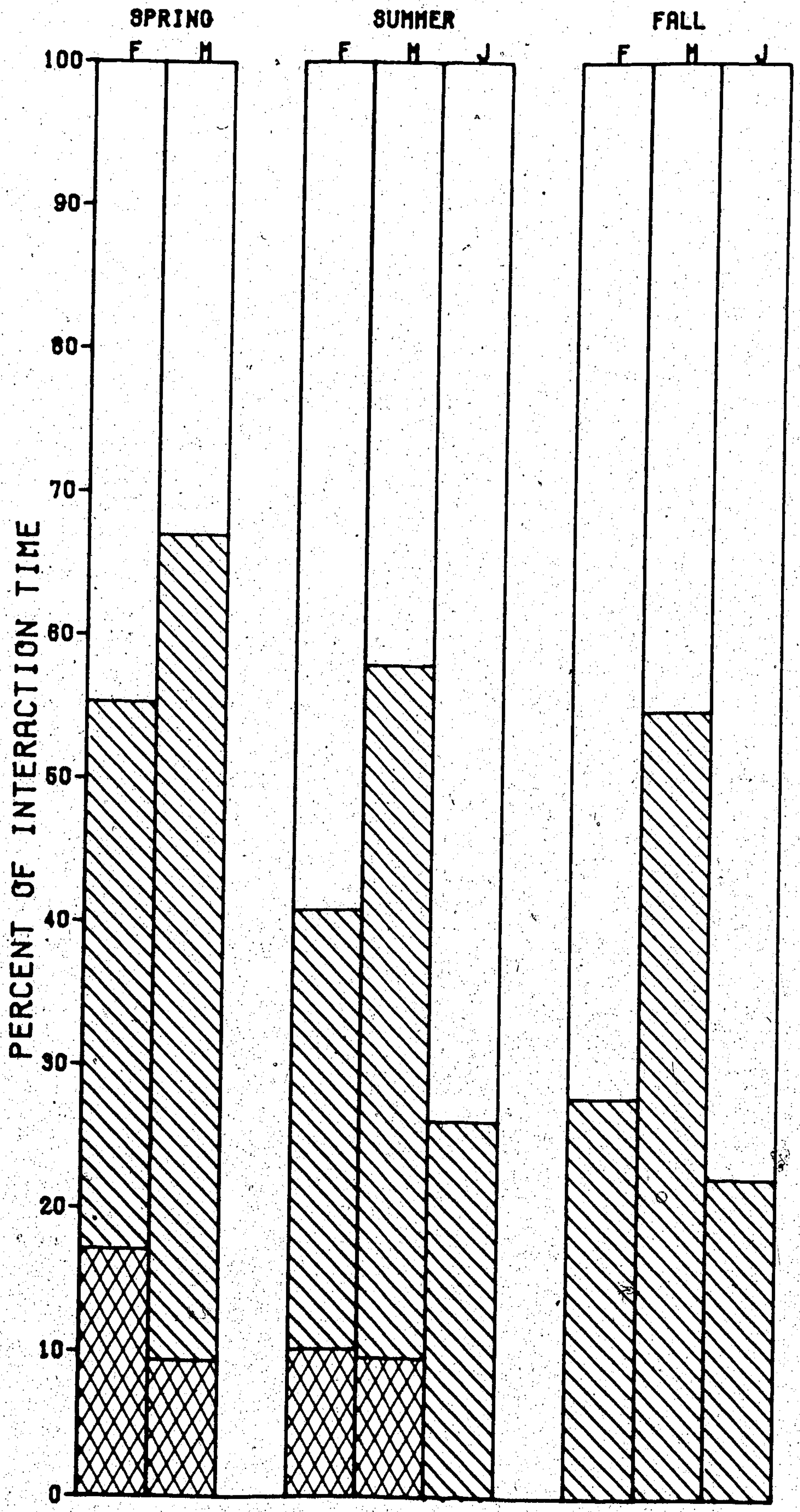
Interactions. In the spring when the majority of interactions occurred, adult males and females spent similar amounts of time interacting (Fig. 3a). Adults spent more time in aggressive interactions in the spring (F(1,6)=36.32 $p<0.001$; Fig. 5) than in amicable or sexual interactions. Females did not interact aggressively towards other females at this time. Aggressive interactions involved at least one

Figure 5. Percent of interaction time spent in amicable, aggressive, and sexual interactions. F=adult females, M=adult males, J=juveniles.

☐--Amicable interactions

▨--Aggressive interactions

▩--Sexual interactions


SPRING
SUMMER
FALL
F
M
F
M
J
F
M
J
100
90
80
70
60
50
40
30
20
10
0
PERCENT OF INTERACTION TIME

male (Table 5). The majority of amicable interactions were between females and males (Table 6), although both interacted amicably with other individuals of the same sex. The only amicable interactions I saw involving two or more males occurred between known siblings or between yearlings and the adult male who resided in the hut in which the yearlings were born. Amicable interactions between adult females occurred between yearling females and their mother, and also between two adult females (each at least two years of age) of unknown relatedness.

Levels of interactions declined from spring to summer for males (F(1,6)=15.47 p<0.01) and females (F(1,6)=9.87 p<0.025). Adult females were involved in fewer aggressive interactions in summer than in spring (F(1,6)=38.20 p<0.001). The majority of interactions involving adult males in summer were aggressive (F(1,6)=53.34 p<0.001). Adult males interacted aggressively with other males more often than with females (F(1,6)=66.87 p<0.001) or juveniles (F(1,6)=507.16 p<0.001). As in spring, all aggressive interactions involving females were with males (Table 5). No aggressive interactions were seen between juveniles in summer. Adult females spent more time in amicable interactions with adult males and juveniles than in aggressive interactions in the summer (F(1,6)=129.98 p<0.001). Most amicable interactions occurred between adults and juveniles (Table 6). No amicable interactions involving two adults of the same sex were seen in summer or fall.

Table 5. The proportion of all aggressive interactions that occurred between different animal classes for the spring, summer, and fall time periods in 1977 at Bowden Lake. N = number of aggressive interactions.

Spring (n=264)	Adult female	Adult male	
Adult female	0.0		
Adult male	40.2	59.8	
Summer (n=91)	Adult female	Adult male	Juveniles
Adult female	0.0		
Adult male	18.2	72.2	
Juveniles	0.0	9.1	0.0
Fall (n=84)	Adult female	Adult male	Juveniles
Adult female	3.0		
Adult male	6.0	53.7	
Juveniles	0.0	6.0	31.3

Table 6. The proportion of all amicable interactions that occurred between different animal classes in the spring, summer, and fall periods in 1977 at Bowden Lake. N = number of amicable interactions.

Spring (n=113)	Adult female	Adult male	
Adult female	18.4		
Adult male	65.8	15.8	
Summer (n=119)	Adult female	Adult male	Juveniles
Adult female	0.0		
Adult male	17.6	0.0	
Juveniles	36.8	29.4	16.2
Fall (n=153)	Adult female	Adult male	Juveniles
Adult female	0.0		
Adult male	0.0	0.0	
Juveniles	32.4	19.7	47.9

Males spent more time interacting than did juveniles in fall (F(1,6)=8.10 p<0.05), but spent approximately the same amount of time as did adult females (Fig. 3c). Time spent on aggressive interactions showed no appreciable difference from summer to fall for any animal class. The majority of aggressive interactions in fall occurred between two adult males. Juveniles interacted aggressively with each other, but to a lesser extent than did adult males (F(1,6)=6.2 p<0.05). Aggressive interactions between two adult females were relatively rare but did occur. Overall, adult males interacted aggressively more often than they did amicably (F(1,6)=21.68 p<0.005). Adult females (F(1,6)=565.65 p<0.001) and juveniles (F(1,6)=1095.75 p<0.001) spent more time in amicable interactions than in aggressive interactions. The amount of time that adult females spent in amicable interactions increased throughout the field season (F(1,6)=64.11 p<0.001). Juveniles also increased the amount of time spent on amicable interactions from summer to fall (F(1,6)=11.05 p<0.025). There was no significant change in time spent at amicable interactions by adult males between summer and fall. All amicable interactions taking place in the fall involved at least one juvenile. Adult females and juveniles participated in friendly interactions more often than did adult males. No significant differences in the frequency of sexual interactions were noted between spring and summer (F(1,6)=1.45 p>0.1), and none were seen in fall (Fig. 5). Sexual interactions were observed less often than aggressiv[illegible])=143.7 $p<0.001$) and amicable interactions (F([illegible])=36[illegible]<0.001) for males and females in spring and summer.

Even though the relative occurrence of interactions was low in [illegible]rat activity budgets, there are some visible trends. Adult males were generally more aggressive than either adult females or juveniles. This was especially obvious when there were dispersing or excursioning animals in the study area. Adult females were most aggressive in spring and chased any intruders from their home ranges. In spring, most amicable interactions were between adult males and females.

Scent marking. The occurrence of scent marking was difficult to recognize, hence these data may not reflect actual levels of scent marking. The frequency of scent marking was relatively low throughout the field season, and did not change appreciably over time ($F(1,6)=1.27$ $p>0.1$), or differ among any of the animal classes ($F(2,6)=2.1$ $p>0.1$). Juveniles were not observed scent marking in summer or fall.

VI. JUVENILE GROWTH

The growth rates of juvenile muskrats were examined for variations related to habitat-type and sex. An analysis of co-variance, grouping the juveniles according to sex, showed no significant differences between the growth of females and that of males. However, differences ($p<0.001$) between the growth of juveniles from different habitats were found for all growth measures (Table 7). Juveniles born in Scirpus-habitats were consistently heavier than those from Typha-habitat (Fig. 6). Weights of adult females just prior to giving birth were similar in both habitat types (mean weight for Typha females = 1100(±200)g, n=6; mean weight for Scirpus females = 1034(±150)g, n=6), indicating that differences arose after birth. The average litter size for females from each habitat was five kits. Until the animals reached an age of approximately 80 days, the rate of growth was similar for animals from both habitats (Fig. 6). Weights of animals from Scirpus-habitat then increased faster than those of animals from Typha-habitat. The consistently higher nutrient content of S. acutus (Table 2) may account for both initial higher weights, and faster growth rates of juveniles eating predominately S. acutus. Juveniles from Scirpus-habitats mainly foraged on S. acutus through the summer and on a combination of Potamogeton vaginatus and S. acutus in fall; those from Typha-hatitat ate T. latifolia and P. vaginatus in summer, and P. vaginatus and Myriophyllum exalbescens in fall. Juveniles

Table 7. Analysis of variance of the growth measures for juvenile muskrats (between the ages of 20 and 180 days) from <u>Typha latifolia</u> and <u>Scirpus acutus</u>.[1]

Independent variable: Age

a) Dependent variable: Weight (g)

Habitat	Adjusted Group Mean	Standard Error
<u>Scirpus</u>	517.71	7.82
<u>Typha</u>	375.12	10.48

	d.f.	F-value	p
Equality of Adjusted Cells	1,165	99.62	0.00001
Equality of Slopes	1,164	15.12	0.0001

b) Dependent variable: Total body length (cm)

Habitat	Adjusted Group Means	Standard Error
<u>Scirpus</u>	44.13	0.38
<u>Typha</u>	38.52	0.51

	d.f.	F-value	p
Equality of Adjusted Cells	1,165	64.91	0.0000
Equality of Slopes	1,164	65.86	0.0000

c) Dependent variable: Tail length (cm)

Habitat	Adjusted Group Mean	Standard Error
<u>Scirpus</u>	18.69	0.19
<u>Typha</u>	15.88	0.25

	d.f.	F-value	p
Equality of Adjusted Cells	1,165	66.18	0.00001
Equality of Slopes	1,164	61.13	0.0001

d) Dependent variable: Left-hind foot length (cm)

Habitat	Adjusted Group Means	Standard Error
<u>Scirpus</u>	6.91	0.04
<u>Typha</u>	6.40	0.06

	d.f.	F-value	p
Equality of Adjusted Cells	1,165	40.81	0.0000
Equality of Slopes	1,164	45.57	0.0000

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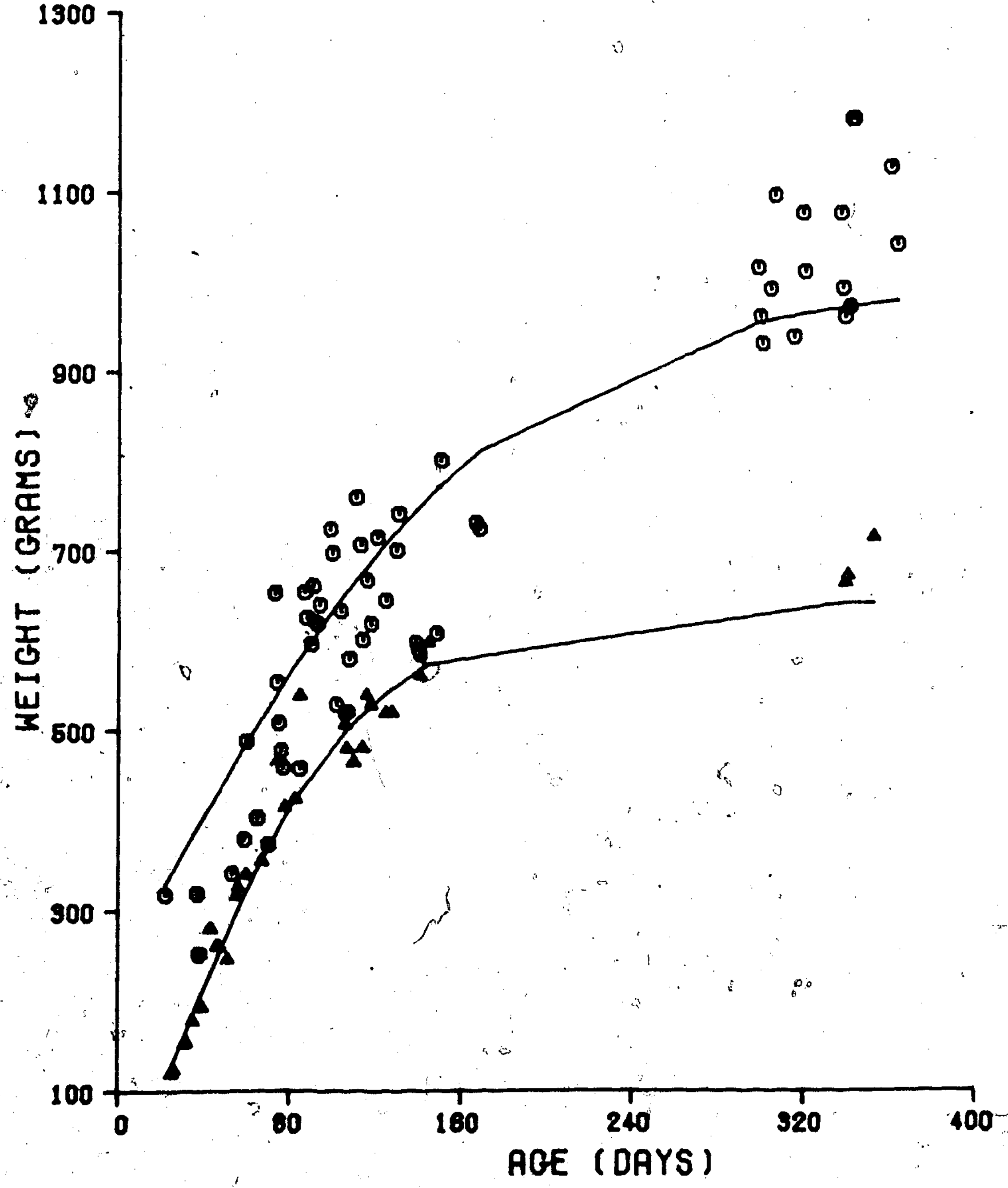
[1] Complete statistics given in Appendix 5.

Figure 6. Growth curves of juvenile muskrats born in either *Scirpus*-habitat (circles) or *Typha*-habitat (triangles). These curves are fitted to growth curves (see Ricklefs 1967) and were fitted to the data for animals less than 180 days of age. The points on the right side of the curves are weights of some of the same individuals represented on the left side of the curves and were used only for the purpose of estimating asymptotes for the curves.



-habitat spent more time foraging in summer than did juveniles from Scirpus-habitat ($F(1,2)=19.59$ $p<0.05$). The net gain in energy and nutrients from consuming S. acutus seemed to have been greater over a shorter foraging period for juveniles from Scirpus-habitat, allowing them to grow at a faster rate than juveniles from Typha-habitat.

Young muskrats consuming primarily S. acutus put on more weight before freeze-up than juveniles consuming T. latifolia. This may have affected winter survival. A significantly higher proportion of juveniles from Scirpus-habitat were recaptured the following May (16 of 32) than those from Typha-habitat (4 of 27; $X^2=5.6$ $p<0.025$). Although I do not have recapture data for the period just after ice-break up in 1978, these data do indicate a higher survival rate for animals from Scirpus-habitat.

VII. SUMMER FOOD HABITS OF MUSKRATS IN SOUTH-CENTRAL ALBERTA

Introduction

Muskrat food habits have been studied by numerous authors (Artimo 1960, Butler 1940, Danell 1978c, Dorney and Rusch 1953, Errington 1941, Fuller 1951, Mcleod 1948, Sather 1958, Sprugel 1951, and Willner et al. 1975), but only a few studies have considered the relation of muskrats' diet to the availability and nutrition of forage species (Bellrose 1950, Takos 1947, and Westworth 1974). Muskrats are known to consume a wide variety of foods (Bellrose 1951; Errington 1963; and Willner et al. 1975). The majority of these studies have used "indirect" methods such as estimating the relative proportions of food species that make up the debris left on feeding platforms by muskrats (Bellrose 1950; Schmitke 1966; Takos 1947; and Westworth 1974). Of all the numerous food species reportedly eaten by muskrats, Typha latifola was considered the most important (Bellrose 1950, Errington 1941, 1963, and Takos 1947). Errington (1941) considered muskrats to forage randomly with little or no food preferences, although preferences for certain foods have been indicated by Bellrose (1950), Schmitke (1966), and Westworth (1974).

Animal foraging habits have received much attention in recent years (Charnov 1976; Emlen 1966, 1968; Estabrook and Dunham 1976; Krebs 1978; Pulliam 1974, 1975; and Schoener 1971). The relative abundance, absolute abundance, and relative value of prey items have been considered as three important parameters in animal diet choices (Emlen 1966). Estabrook and Dunham (1976) contended that absolute abundance and, secondarily, relative value are the most important factors involved in optimal diet choices. Pulliam (1974) and Sih (1979) consider the abundances (relative or absolute) of only the preferred prey items to be important. Westworth (1974) considered the relative abundance of food items to be important in muskrat food choice. What role, if any, the absolute abundance of food species plays in diet selection of muskrats has not been investigated.

In this paper, I describe the food habits and preferences of muskrats from three different habitats and at three times of the year. Variations in the diets of animals from different habitats are considered in relation to relative and absolute abundance, as well as to the nutrient content of two major emergent food items (_Scirpus_ _acutus_ and _Typha_ _latifolia_), in an attempt to understand the rationale behind muskrat foraging behavior.

Methods

I observed muskrats during the spring and summer of 1976 and the spring, summer and fall of 1977 (see General Methods pp 7-8). During each observation time I noted the species of plant that muskrats were eating, collecting, and transporting from the collection site. The amount of time spent at these activities was calculated for all animals from a given habitat and for each season of the year (see General Methods p 11). Transit time (T) was the amount of time spent transporting food from the collection site to feeding platforms or huts where it was consumed (Schoener 1971). The amount of time muskrats spent collecting and manipulating food prior to ingestion was considered the handling time (H). The amount of time during which muskrats were observed eating was the eating time (E). The total foraging time (FT) for animal j on food item i is equal to the sum of the handling (Hij), transit (Tij), and eating (Eij) time;

$$FTij = Hij + Tij + Eij. \tag{1}$$

Data from 1976 and 1977 were combined. Foraging times for the six most commonly eaten food items and a seventh miscellaneous category were determined for animals from each of the three habitats studied at Bowden Lake (*Scirpus*, *Typha*, and *Scirpus*-*Typha*), and for each time period (spring, summer, and fall).

S. *acutus* and *T*. *latifolia* were present in varying amounts in each home range at Bowden Lake. In order to study the relationships between the abundance of either species and the foraging habits of muskrats, I estimated the area of each of these two food species in each home range by using a combination of aerial photographs taken in 1977 from a small plane at an altitude of 200-300 m, and ground surveys of the plants (see General Methods p 9). These data were used to construct maps of the plant distributions at Bowden Lake. I used a planimeter to calculate the area of each plant species in the animal's home ranges. This was done separately for each time period.

The relative abundance (RA) of species i in animal j's home range was estimated by taking the ratio between the area (A) of the plant in the total area (TA) of the home range;

$$RAij = \frac{Aij}{TAij}. \qquad (2)$$

I use relative abundance as an estimate of the area a particular food species covers within an animals' home range. It is similar to the percent cover of a plant within a given area (see Mueller-Dombois and Ellenberg 1974), but applies only to major food resources. The area covered by *I. latifolia*, for example, is not overlapped by any other food resource, and therefore gives an estimate of the relative abundance of that food in an animal's home range in relation to the other foods available. Thus, the usage of relative abundance in this context is analogous to the concept of relative abundance used in foraging theory (see Emlen 1966, Pulliam 1974).

The absolute abundance (AA) has been considered as a function of the area (A) of food item i in animal j's home range, the mean biomass (B; wet weight) of species i in animal j's home range, and the proportion of food i that is green (senescence index, S) in animal j's home range,

$$AA = (Aij)(Bij)(Sij). \qquad (3)$$

Biomass estimates (g/m^2) were taken when the plants were harvested for nutritional analyses in 1977. I included the senescence index because it indicated the decline in plant nutrients with age (Greulach 1973) and the subsequent reduction in potential food value to the consumer. A senescence index of 1.0 denotes that 100 percent of the plants in the home range were green; an index of 0.1 indicates that only 10 percent of the plants were green (Table 2).

The nutrient content of S. acutus and T. latifolia was determined in 1977 (see p 16). In order to test the hypothesis that muskrats select food on the basis of its nutrient content, I examined the relationship between the proportion of a food item in the diet and the nutrient content of the food, as indicated by certain physical characteristics of the plants that correlated with the plants' nutrient content (see p 20).

Food Preference Study

Experimental animals. Nine adult muskrats (4 females, 5 males) were live trapped from the three habitats at Bowden Lake in May 1978. Four animals (2 females, 2 males) were from Typha-habitat, three (2 males, 1 female) from Scirpus-habitat and two (1 male, 1 female) from the mixed Scirpus-Typha habitat. These animals were held individually in 1x1x0.5 m 'L-shaped' wire mesh (2.54 cm) cages with access to a 100x75x45 cm pail of feshwater. Between experiments animals were fed a mixture of rolled oats, Purina rat chow, and vegetables (carrots, lettuce, and cabbage). Twelve hours prior to the onset of each experimental period, I removed all food from the cages. Animals were kept on a 16L:8D photoperiod and all experiments were done during the evening.

Experimental plants. I collected fresh specimens of *I. latifolia*, *S. acutus*, *P. vaginatus* and *M. exalbescens* approximately six hours before each experimental period. Plants were randomly collected from all three habitats throughout the study and stored in opaque plastic bags submerged in cool water until used.

Five different experiments with ten trials per animal per experiment and four control experiments were conducted from 12-31 May, 1978. Each experiment consisted of placing a plexiglass food trough (15x6x2 cm) in each corner of one end of a fiberglass fish tank (226x119x115 cm) equipped with a central partition of 6 mm plywood with a 15 cm^2 door. Approximately 2 cm of water covered the bottom of the arena. Prior to the start of each trial animals were held in a holding chamber on one side of the partition, and a different type of food was placed in each trough. The door in the partition was opened and the animal was allowed to enter the experimental chamber. Animals were given a maximum of one minute to make a food choice. I recorded the elapsed time between entering the experimental chamber and making a food choice, and noted the food chosen. Once the animal had chosen a food (the first plant taken in its mouth or forepaws) it was gently coaxed from the experimental chamber and allowed to eat the chosen food. The food supply was replenished between each trial.

The Control experiments were of two types. The first set of experiments tested whether or not animals could distinguish between green and brown portions of plants under experimental conditions. Old plant material from previous growing seasons (brown portions) were placed in one food trough and fresh, green material was placed in the other trough. The placement of each plant type was random. Only old and new plants of the same species were tested against each other. The second set of experiments tested whether animals could find food in the experimental chamber at all. One trough contained fresh food and the other was empty. This test was used to determine whether the animal would respond under experimental conditions. In these tests the placement of the food was random between the two troughs.

The five preference experiments tested i) _S_. _acutus_ vs _T_. _latifolia_ - whole culm; ii) _S_. _acutus_ vs _T_. _latifolia_ - chopped into 3 cm pieces; iii) _P_. _vaginatus_ vs _M_. _exalbescens_; iv) _S_. _acutus_ vs _P_. _vaginatus_; and v) _S_. _acutus_, _T_. _latifolia_, _P_. _vaginatus_ and _M_. _exalbescens_ all presented at once.

Statistical Analysis

A Kruskal-Wallis (Siegel 1956; Sokal and Rohlf 1969) test was used to determine differences in the amount of time muskrats foraged on various food species. A one-way analysis of variance was used to examine changes in muskrat foraging throughout the year. Least-squares regression analyses, univariate linear and polynomial, and multivariate tests were used to study the relationships between the abundance and nutritional quality of the food and the animals' diet. The Kolmogorov-Smirnov test was used to test for normality of data and residuals in the regressions (Neter and Wasserman 1974; Cooley and Lohnes 1971). Chi-square tests were used to determine differences in muskrat food choices. Levels of $p<0.05$ were considered statistically significant.

Data from 1976 and 1977 were used to determine muskrat food habits, but only the data from 1977 were used in the remainder of the tests because estimates of food abundance and nutrition were only made in 1977.

Results and Discussion

My observations of muskrat foraging suggest that determining food habits from debris left on feeding platforms, as done by Bellrose 1950, Schmitke 1966, Takos 1947, and Westworth 1974, may be misleading. Emergent plants, such as _Typha_, _Scirpus_, and _Sparganium_, are often transported to feeding platforms where they are eaten, whereas submergent plants (e.g. _Potamogeton_, _Myriophyllum_, and _Sagittaria_) tend to be eaten at the collection site. The amount of time that muskrats spent transporting food from the collection site to huts or feeding platforms is small in comparison to the eating time (not more than 10% of total foraging time - see p 28). Another problem with this method of determining muskrat food habits is that muskrats eat different proportions of each food species. Some food species are eaten almost entirely, whereas only certain portions of other plants were eaten. Since muskrats are readily observable and because they spend the vast majority of their observable time foraging (see p 23), I believe that a direct method of observing what muskrats were eating gave a more reliable indication of their food habits.

Muskrat Foraging Habits

The food items for muskrats at Bowden Lake were S. acutus, Potamogeton spp., Myriophyllum exalbescens, T. latifolia, and several other species that were eaten in small amounts (Table 8). All have been mentioned as muskrat foods in previous studies on muskrat food habits (Willner et al. 1975). They were eaten in different proportions by animals from different habitats throughout the field season (Table 9 and 10).

Food habits of animals from Scirpus and Scirpus-Typha habitats were similar except for the inclusion of small amounts of T. latifolia in the diets of animals from Scirpus-Typha. S. acutus was the most frequently eaten food in spring ($H=28.1$ $df=3$ $p<0.005$, $H=15.1$ $df=2$ $p<0.005$) and summer ($H=44.4$ $df=5$ $p<0.005$, $H=15.0$ $df=4$ $p<0.005$; Table 9). Potamogeton spp. were eaten in increasing amounts from spring to fall when they became the main food in muskrats' diets ($H=17.56$ $df=2$ $p<0.005$; Table 10). M. exalbescens was

Table 8. Muskrat food items at Bowden Lake in 1976 and 1977 determined from observations of feeding muskrats.[1]

Scirpus acutus Muhl. - hardstem bulrush
Typha latifolia L. - common cattail
Potamogeton pusillus L. - pondweed
P. richardsonii (Benn.)Tydb. - pondweed
P. vaginatus Turcz. - pondweed
Myriophyllum exalbescens Fern. - water milfoil
Eleocharis acicularis (L.)R. & S. - spikerush
E. palustris (L.)R. & S. - spikerush
Sagittaria cuneata Sheld. - arrowhead
*Carex lasiocarpa Ehrh. - sedge
*Sparganium eurycarpum Engelm. - burreed
*Trifolium repens L. - clover
*Utricularia minor L. - bladderwort
*Lemna minor L. - duckweed
*L. trisulca L. - duckweed

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[1] Classification according to Moss (1959).
*These species constitute the miscellaneous category of food items i[illegible] 9.

Table 9. Proportion of muskrat foraging time spent on various food resources during 1976 and 1977. Sample sizes are the number of muskrats observed and the number of minutes which animals were observed feeding in each habitat during each time period. Super-scripts refer to significant differences in feeding patterns of animals from a particular habitat (*Kruskal-Wallis test; Siegel 1956*).

	HABITAT								
	Spring			Summer			Fall		
FOOD SPECIES	Scirpus (n-13)	Typha (n-9)	Scirpus-Typha (n-8)	Scirpus (n-18)	Typha (n-17)	Scirpus-Typha (n-8)	Scirpus (n-65)	Typha (n-6)	Scirpus-Typha (n-10)
Scirpus acutus (S)	53.60[1]	0.59	49.08[6]	72.42[9]	12.96	74.12[12]	28.32[14]	3.54	27.15[18]
Typha latifolia (T)	0.0	41.98[3]	5.50	0.0	33.37[10]	5.78	0.0	2.17	0.0
Potamogeton spp. (P)	11.57	44.96[4]	18.13[7]	12.75	41.52[11]	11.64[13]	69.10[15]	77.17[16]	48.69[19]
Myriophyllum exalbescens (M)	34.06[2]	12.05[5]	23.26[8]	5.98	4.13	0.73	2.20	16.54[17]	24.17[20]
Eleocharis spp. (E)	0.0	0.0	1.28	5.75	1.85	3.91	0.35	0.0	0.0
Sagittaria cuneata (SG)	0.0	0.0	0.0	0.55	2.78	0.0	0.0	0.39	0.0
Miscellaneous spp. (MI)	0.77	0.45	2.75	3.05	3.39	3.82	0.03	0.20	0.0

[1] S>T,P,E,M,SG,MI
[2] M>P,T,E,SG,MI
[3] T>S,M,E,SG,MI
[4] P>S,M,E,SG,MI
[5] M>E,SG
[6] S>T,E,SG,M,MI,P
[7] P>T,E,SG,MI
[8] M>T,E,SG,MI

[9] S>T,P,M,E,SG,MI
[10] T>E,SG,MI
[11] P>M,SG,E,MI
[12] S>T,P,M,E,SG,MI
[13] P>T,M,E,SG,MI

[14] S>T,M,E,SG,MI
[15] P>S,T,M,E,SG,MI
[16] P>S,T,M,E,SG,MI
[17] M>S,T,E,SG,MI
[18] S>T,E,SG,MI
[19] P>T,M,E,SG,MI
[20] M>T,E,SG,MI

Table 10. Changes in muskrat foraging habits throughout the field season. Only the significant differences are shown ($p<0.05$, Kruskal-Wallis test). Sp = Spring, Su = Summer, and F = Fall.

FOOD SPECIES	HABITAT TYPE		
	Scirpus	*Typha*	*Scirpus-Typha*
Scirpus acutus	Sp<Su>F	Sp<Su>F	Sp<Su>F
Typha latifolia	------	Sp>Su>F	Su>F
Potamogeton spp.	Su<F	Sp>Su<F	Sp>Su<F
Myriophyllum exalbescens	Sp>Su>F	Su<F	Sp<Su<F
Eleocharis spp.	Sp<Su>F	------	Sp<Su>F
Sagittaria cuneata	------	------	------
Miscellaneous spp.	Sp<Su>F	Sp<Su>F	Sp<Su>F

eaten most often in the spring for animals from *Scirpus*-habitat (H=18.2 df=2 p<0.005; Table 10). Animals from *Scirpus*-*Typha*-habitat ate *M*. *exalbescens* in similar proportions in the spring and fall but spent very little time eating it in the summer (H=19.4 df=2 p<0.005, Table 10). *T*. *latifolia* was a minor food item for these animals in the spring and summer and was not eaten at all in the fall (H=7.61 df=2 p<0.005). The switch in diet from predominantly *S*. *acutus* to *P*. *vaginatus* in the fall correlates with a decline in the nutritional quality of *S*. *acutus*. Unfortunately, I do not have data on the nutrients of *P*. *vaginatus* for comparison.

Muskrats from *Typha*-habitat ate *Potamogeton* *vaginatus* and *T*. *latifolia* in similar proportions in the spring and summer but spent more time consuming *P*. *vaginatus* in the fall (H=9.3 df=1 p<0.001). The continuous decline in the amount of time spent foraging on *T*. *latifolia* throughout the year may be due, in part, to the decline in nutrients and to the rapid increase in fiber content with the onset of anthesis in *T*. *latifolia* (Mason and Bryant 1975, and Boyd 1970). The fiber content of a plant is negatively correlated with the ability of an herbivore to extract nutrients from the plant (Crampton and Lloyd 1959). High fiber content, along with reduction of nutrients in *T*. *latifolia* during late summer and fall probably account for its disappearance from muskrat diets. *S*. *acutus* was eaten in small quantities throughout the year by these animals. It was eaten most often during summer ($H=17.1$ $df=2$ $p<0.005$) when the density and nutrient content of S. acutus were high. Muskrats from Typha-habitat on the south shore began feeding in S. acutus patches located 150 m north of the south-shore (Fig. 1) in summer. In August of 1977 one family of muskrats built several platforms and a hut on the eastern edge of this stand. Other muskrats from the south-shore foraged in this stand and tended to travel further from their huts to forage on S. acutus than on T. latifolia ($X^2=13.63$ $df=4$ $p<0.01$, mean distance from hut to forage on S. acutus = 155.8 m, T. latifolia = 32.6 m).

Muskrat Food Preferences

S. acutus was chosen most often by muskrats from all three habitats in the food preference studies (Table 11). When a choice among S. acutus, T. latifolia, M. exalbescens and P. vaginatus was presented to the animals, S. acutus was chosen more often than any other species. M. exalbescens, P. vaginatus and T. latifolia were chosen, in that order, after S. acutus. The preference order follows that of the food habits of muskrats from Scirpus-Typha habitat in the spring of 1976 and 1977 (Table 9). The Scirpus-Typha-habitat was the only area in which all four species were present in sufficient quantities for muskrat feeding to reflect preferences rather than simply availability. This correlation with field data supports the reliability of the results from the food preference tests. No significant differences in food choices were found between males and

Table 11. Muskrat food preferences as indicated by muskrat food choices in captivity (n = 90 trials per experiment, see p 47 in text for methods). S = Scirpus acutus, T = Typha latifolia, M = Myriophyllum exalbescens, P = Potamogeton vaginatus.

Experiment	Outcome[1]	X^2	d.f.	prob
Scirpus acutus vs. Typha latifolia (whole plants)	S(50)>T(21)	8.73	1	0.005
S. acutus vs. T. latifolia (chopped)	S(40)>T(14)	11.79	1	0.005
Potamogeton vaginatus vs. Myriophyllum exalbescens	P(37)=M(30)	0.73	1	0.1
S. acutus vs. P. vaginatus	S(63)>P(16)	27.96	1	0.005
S. acutus, T. latifolia, M. exalbescens, P. vaginatus (all presented together)	S(35)>T(8)	12.74	1	0.005
	S(35)>P(11)	11.82	1	0.005
	M(24)>T(8)	8.0	1	0.005
	M(24)>P(11)	4.83	1	0.05
	S(35)>M(24)*			

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[1] numbers in brackets are the number of times each food was chosen.

*Kruskal-Wallis trends test, Z=2.01, $p<0.05$

females and among animals from different habitats, indicating that muskrats have definite food preferences but will alter their diets in accordance with the food species available to them. These preference studies suggest that muskrats at Bowden Lake prefer S. acutus over other foods and in particular I. latifolia.

Food Availability and Nutrition

The major foods eaten by muskrats at Bowden Lake were I. latifolia, S. acutus, and the submergent species of Potamogeton, and M. exalbescens (making up a total of over 90% of the animals' diet, see Table 9). Since my measure of relative abundance estimates the area of the home range occupied by the two emergents or the submergent foods available, I contend that it serves as an index of the relative abundance used in foraging theory. Since no estimates of the quality and quantity of the submergent foods were available, only the relative abundances of the emergent foods (I. latifolia and S. acutus) were used in this analysis. Absolute abundance, on the other hand, gave more of an indication of the actual quantity (i.e. its biomass) and potential quality (as indicated by the senescense of the plants) of a food species. The relation of animal food habits to these measures of food availability, only became important to optimal foraging when changes in the availability of preferred food items occurred (Sih 1979). The relative abundance of S. acutus in the home range did not change appreciably through the field season, whereas that of I. latifolia declined from summer to fall for adults (F(1,10)=27.89 p<0.001) and juveniles (F(1,10)=10.27 p<0.01; Table 12). As the relative abundance of I. latifolia decreased through the year, there was a corresponding decrease in the proportion of I. latifolia in muskrats diets (F(1,18)=26.08 p<0.01, R^2=0.592; Fig. 7, and Appendix 6). There was no relationship between the relative abundance of S. acutus in the home range and the amount of S. acutus in the diet. Reductions in the relative abundance of I. latifolia occurred in summer when its fiber content increased (Table 2). At the same time muskrats began foraging on other food species (Table 9). I. latifolia was not the dominant food resource for muskrats in the spring and summer, as was S. acutus. I. latifolia was eaten in about the same proportions as P. vaginatus (Table 9) until it was virtually absent from muskrats' diet in the fall. I. latifolia was the least preferred food item in the food preference studies (Table 11), which were conducted in the spring when I. latifolia had its highest nutrient content (Table 2), highest relative abundance (Table 12), and was eaten most often by animals from Typha-habitat (Table 10). The rate of consumption of the less preferred food species (I. latifolia) was related to the relative abundance of that species in the home range, whereas the rate of consumption of the more-preferred food (S. acutus) was independent of its relative abundance.

Table 12. Mean relative abundance (percentage of home range in which the food occurs) of *Scirpus acutus* and *Typha latifolia* in muskrat home ranges (adults and juveniles) in the spring, summer, and fall.

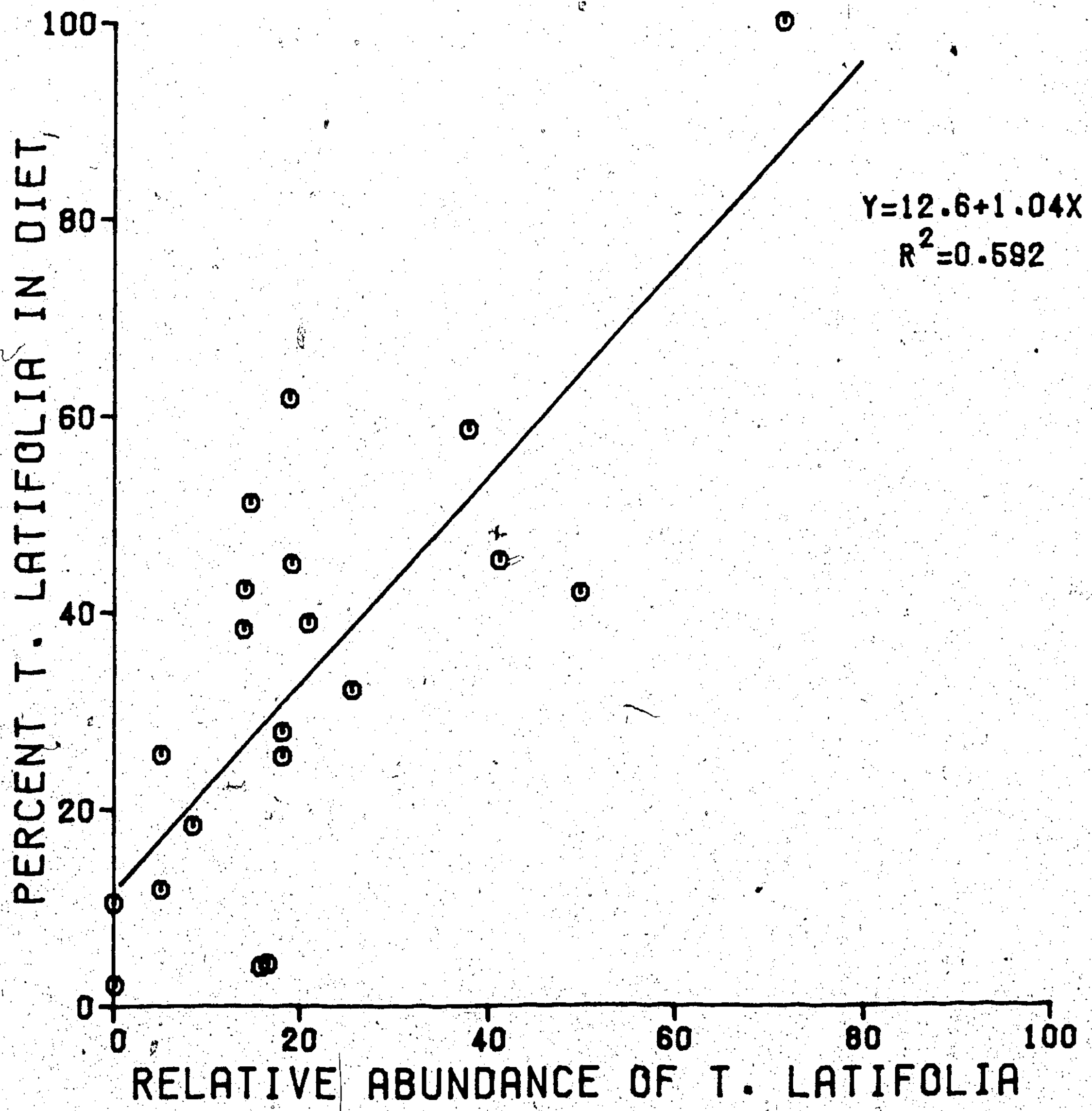
a) *S. acutus*

	HABITAT-TYPE					
	Scirpus		*Typha*		*Scirpus*-*Typha*	
	Adults	Juvs.	Adults	Juvs.	Adults	Juvs.
Spring	40		1		7	
Summer	36	16	4	20	16	20
Fall	32	31	6	27	10	29

b) *T. latifolia*

	HABITAT-TYPE					
	Scirpus		*Typha*		*Scirpus*-*Typha*	
	Adults	Juvs.	Adults	Juvs.	Adults	Juvs.
Spring	0		24		11	
Summer	0	0	16	60	10	0
Fall	0	0	1	4	2	0

Figure 7. Percent of _Typha latifolia_ in the diet as a function of the relative abundance of _T. latifolia_.



The absolute abundance (Table 13) of I. latifolia was higher in summer than in spring ($F(2,9)=5.6$ $p<0.025$) or fall ($F(3,11)=16.9$ $p<0.005$). This is to be expected since the biomass increased as the plants reach anthesis (McNaughton 1970) and therefore caused an increase in the absolute abundance. In S. acutus there was an increase in the absolute abundance from spring to summer ($F(2,16)=6.79$ $p<0.01$ - for Scirpus-habitat; $F(1,2)=19.6$ $p<0.05$ for Scirpus-Typha-habitat). There was no significant change in the absolute abundance of S. acutus from the summer to the fall. The proportion of S. acutus in muskrats' diet was correlated with the absolute abundance of S. acutus ($F(2,35)=24.65$ $p<0.001$, $R^2=0.587$; Fig. 8, and Appendix 7). No relationship between the proportion of I. latifolia in muskrats' diets and its absolute abundance existed.

The proportion of S. acutus in muskrats diets was found to correlate with a matrix of physical characteristics of S. acutus which were used to predict its nutrient content (Table 14; and Appendix 8). No relationship between the amount of I. latifolia in the diet and its nutrient content was found. Muskrats seemed to choose S. acutus, over other foods, on the basis of its nutrient content and absolute abundance, indicating that more-preferred food resources are chosen in relation to their nutritional quality, whereas less preferred foods (I. latifolia) were included in the diet as a function of its relative abundance and because of

Table 13. Mean absolute abundance (g x 10^5) of *Scirpus acutus* and *Typha latifolia* in muskrat home ranges (adults and juveniles) in the spring, summer, and fall.

a) *S. acutus*

	HABITAT-TYPE					
	Scirpus		Typha		Scirpus-Typha	
	Adults	Juvs.	Adults	Juvs.	Adults	Juvs.
Spring	88		1		34	
Summer	416	32	15	34	262	254
Fall	108	97	40	46	55	35

b) *T. latifolia*

	HABITAT-TYPE					
	Scirpus		Typha		Scirpus-Typha	
	Adults	Juvs.	Adults	Juvs.	Adults	Juvs.
Spring	0		102		95	
Summer	0	0	285	72	349	0
Fall	0	0	18	8	7	0

Figure 8. Relationship between the absolute abundance of Scirpus acutus (g x 10^6) and the proportion of S. acutus in muskrats' diet.

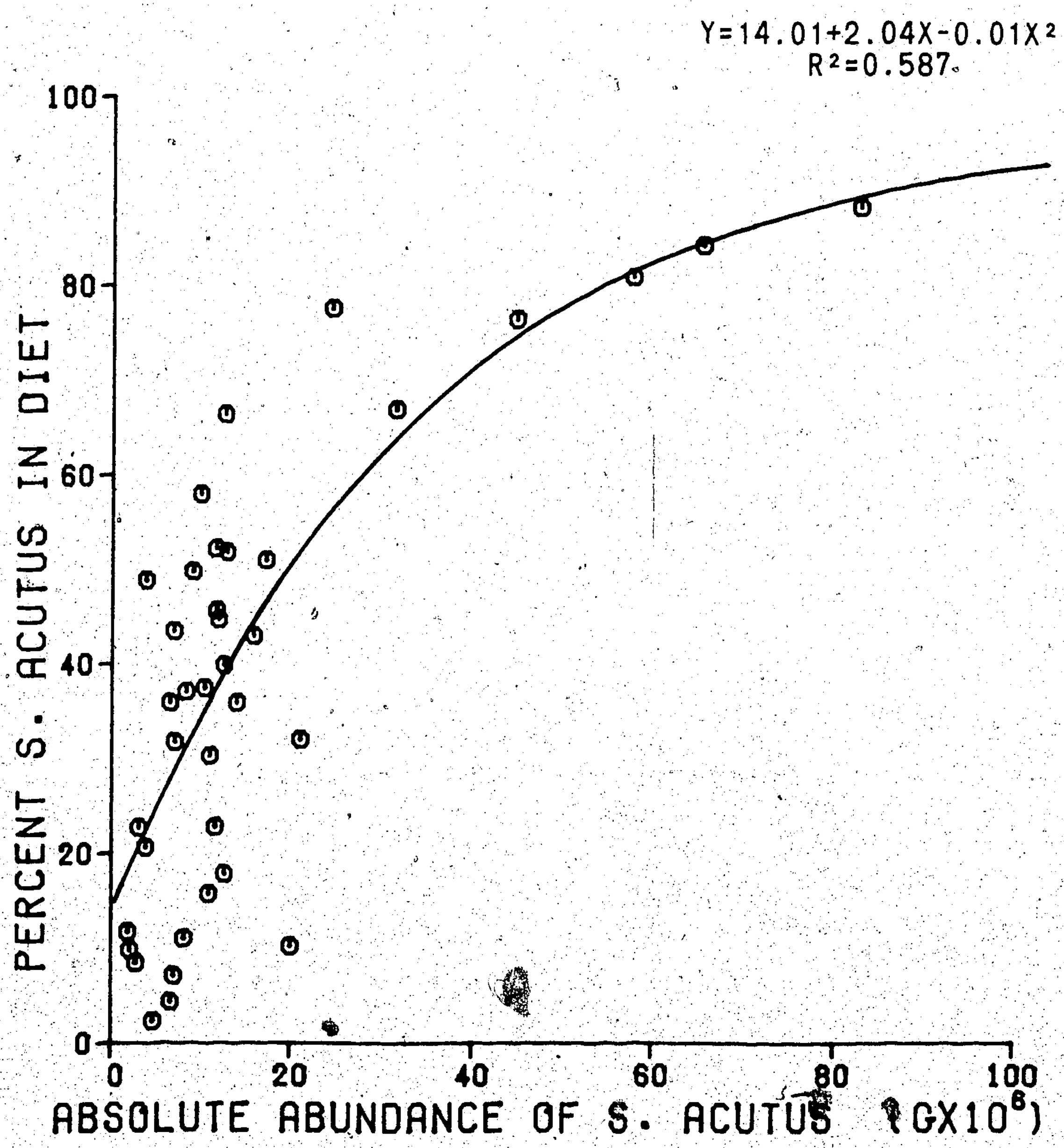


Table 14. The proportion of *Scirpus acutus* in the diet as a function of the physical characteristics of *S. acutus*.*

Independent Variable	Beta	F-value	d.f.	p
Date (X_1)	0.34	19.93	1,43	p $6.0\text{x}10^{-5}$
Phenology (X_2)	-0.7	5.29	1,43	p 0.026
Height (X_3)	0.65	9.64	1,43	p 0.0034
Full Model	37.07	14.23	3,43	p $2.0\text{x}10^{-6}$

Regression equation: $Y=37.07-0.34X_1+0.7X_2+0.65X_3$

* Regression statistics given in appendix 8.

the absence of a more-preferred food (Table 9).

Muskrats appeared to use three different approaches to foraging:

1. When a preferred food was available to the animals, they concentrated their foraging activities almost solely on it until its quality declined to a point where it no longer was the preferred item, as was the case for S. acutus in the fall.
2. In the absence of a more-preferred food, muskrats ate species that were available in their home ranges as long as a balance between energy gained from consuming them and energy expenditures was maintained.
3. When the quality of any food decreased past a point where its benefits reached a low threshold, then animals switched to another, supposedly better quality food item (Krebs 1978).

Although I do not have any data on the quality of P. vaginatus, I suspect that in the fall its nutrient content was higher than that of either S. acutus or T. latifolia. Boyd (1970b) showed that, in general, the nitrogen and sodium levels in submergent plants were higher than those of emergents. The abundance of P. vaginatus seemed to increase throughout the season, and tended to be highest in late summer and fall, which may suggest why muskrats switched to P. vaginatus as their main food in fall. M. exalbescens seemed to be more abundant in the spring in Scirpus-habitat than in summer or fall, but was more abundant in

Scirpus-Typha and Typha-habitats in the late summer and fall. These patterns of abundance may be related to water depth; in the former habitat M. exalbescens was present as an inshore population, whereas in the latter habitats it was in deeper water (about 2-3 m), where it may take longer to grow because light penetration decreases with increasing water depth (Sculthorpe 1967). The standing crop of M. exalbescens was found by Rickett (1924) to be higher in water depths of 3-4 m than in shallow water, and to reach its highest productivity in late summer and early fall.

Sih (1979) contended that the relative importance of absolute abundance and relative abundance of food items were inconsequential to optimal foraging because both were important only if they affected the absolute abundance of more-preferred prey items. If the relative abundance of a preferred food item was positively correlated with its absolute abundance then, and only then, according to Sih, will the relative abundance be an important component in the estimation of optimal diets for animals. The relative abundances of neither S. acutus or T. latifolia could predict their absolute abundances (i.e. the absolute abundance of both species was not dependent on the respective relative abundance, S. acutus $r=0.13$ $p>0.1$; T. latifolia $r=0.3$ $p>0.2$). It follows, then, that the relative abundance of food items in a muskrats' home range alone cannot predict food preferences for muskrats. Correlations between muskrat diets and the absolute abundance of the major food species were more apt to indicate muskrat food preferences and optimal foraging patterns, than were relative abundances.

VIII. SPACING AND HABITAT USE BY MUSKRATS IN SOUTH-CENTRAL ALBERTA

Introduction

Habitat selection is the choice of a particular type of environment in which an animal is to live (Partridge 1978) and to gain access to resources (Fretwell 1972). Variations in the kind and quality of resources available within a habitat should influence an animals' decision as to which areas to inhabit. Habitat selection may have profound effects on an animals' fitness (Wiens 1976), since quality of resources will directly affect its survival and that of its offspring. Habitat selection by muskrats has been investigated only indirectly by noting the occurrence of huts and burrows in particular habitat-types (Danell 1978a, 1978b), and not from the standpoint of the individuals and their use of resources in a patchy environment.

In this chapter I examine the dispersion of muskrats in relation to their food resources, and relationships between conspecifics. I also consider habitat selection in relation to muskrat dispersion, food preferences, survival and dispersal.

Methods

Muskrat home ranges were determined from direct observations of muskrat movements and from trapping data (see p 7). The area (m²) of overlap between animals from adjacent home ranges was determined for each animal during each time period in 1977. Groups of animals inhabiting the same hut or bank den and adjacent marsh have traditionally been considered family-groups (Errington 1963). The area in which an individual did not overlap with any other individuals (family or non-family) was considered its exclusive area. Areas of overlap with family members were considered the family area and were distinguished from areas of non-family overlap. The straight line distance from the major hut to the location of interactions was calculated for each interaction. The distances from the hut at which animals were chased or were chasing another animal were compared with a Kruskal-Wallis test to provide information on the relationship of aggression to spacing patterns. The relative densities of S. acutus and T. latifolia were determined for patches of these plants during 1977 from ground and aerial surveys (see p 9). Plant densities were divided into four categories, low(T. latifolia, ≤10 culms/m²; S. acutus, ≤25/m²), medium(T. latifolia, >10,≤40culms/m²; S. acutus, >25,≤100/m²), high(T. latifolia, >40,≤80culms/m²; S. acutus, >100,≤200/m²), and very high(T. latifolia, >80culms/m²; S. acutus, >200/m²). Since S. acutus tends to grow in denser patches than does T. latifolia, a different set of criterion was used to estimate patch densities. I estimated patch densities throughout the marsh using the above criterion for both S. acutus and T. latifolia and recorded these on maps of the area. The criteria for assigning these densities were subjective, but

I feel that they correspond to the actual densities of the plants within each patch.

The relative densities of patches in which muskrats were observed feeding were noted for each foraging observation. Mean plant densities in exclusive, family and non-family areas were calculated for each animal during each time period. These data were used to examine the relationship of patch density and muskrat foraging activities, and the relationship of plant densities to exclusive, family and non-family areas. Kruskal-Wallis one-way analysis of variance (Marascuilo and McSweeney 1977; Siegel 1956) and Hotelling's T^2 (Sokal and Rohlf 1969) were used to analyse these data.

The number of muskrat huts and/or bank dens known to be occupied in 1976 and 1977 were located and their position was recorded on detailed maps of the study area, during each time period. These data were used to estimate the number of occupied dwellings within a certain length (100 m) of shoreline in each habitat-type throughout the year. Comparisons between habitat-types were made with Chi-square Tests (Sokal and Rohlf 1969).

Results

Muskrats foraged in areas of higher relative plant densities than in patches where no feeding was observed, whether eating S. acutus ($H=39.2$ $p<0.001$) or I. latifolia

(H=28.16 p<0.001). Relative densities of I. latifolia (H=24.49 p<0.001) and S. acutus (H=47.76 p<0.001) in foraging patches increased throughout the growing season. Males and females foraged in areas with similar densities regardless of which species they ate. Juveniles that ate S. acutus foraged in denser stands of S. acutus than did adults (H=17.73 p<0.001). This was not true for juveniles that ate I. latifolia.

Plant densities in family-group areas were greater than those in non-family areas (T(5)=46.30 p<0.001; Hotellings T^2). Exclusive areas had higher plant densities than did family-group areas only for S. acutus (T(64)=2.22 p<0.05). There were very few animals with exclusive areas in 1977. Plant densities within family-group areas increased from spring to summer (T(66)=3.58 p<0.001), but no change occurred from summer to fall. In non-family areas, the opposite was true; densities were equal in spring and summer but increased in fall (T(66)=5.36 p<0.001). The overall density of S. acutus was greater than that of I. latifolia (Table 15). Densities of S. acutus were greater in both family and non-family areas in Scirpus-habitat than in Scirpus-Typha-habitat (family-group areas: T(19)=2.08 p<0.05; non-family areas: T(79)=2.32 p<0.02) whereas densities of I. latifolia were about the same in family-group areas in Typha-habitat and Scirpus-Typha-habitat (T(36.2)=1.93 p>0.05), but were higher in non-family area in Scirpus-Typha than in non-family areas of Typha-habitat

Table 15. Mean density (culms/m²) of Typha latifolia and Scirpus acutus in family-group areas and areas of overlap between family-groups in the three habitats at Bowden Lake in 1977.

PLANT SPECIES	FAMILY-GROUP AREAS	OVERLAP BETWEEN FAMILY-GROUPS
i) Typha latifolia		
Typha-habitat	15.8(±0.9)	19.5(±1.2)
Scirpus-Typha-habitat	35.7(±0.2)	27.2(±0.2)
ii) Scirpus acutus		
Scirpus-habitat	175.3(±0.3)	135.7(±0.3)
Scirpus-Typha-habitat	134.7(±0.9)	116.8(±0.3)

(T(34)=2.61 p<0.02). Plant densities in family-group areas frequented most often by juveniles were higher than those areas where adults were observed most often (T(100)=3.11 p<0.002). Densities in areas of overlap with non-family members were not different for the various age classes.

The number of muskrats in any particular family-group changed from 1976 to 1977 and throughout the field season (Table 16). In 1976 there were 11 family-groups distributed among the three habitat types (Figs. 9, 10, and 11). There were three adults (two females and one male) in each family-group in Scirpus and Scirpus-Typha-habitats. These densities were consistant throughout the field season. In Typha-habitat, three of the five family-groups had two males and one female residing together, whereas the other two family-groups consisted of one female and one male. One of the two males in each family dispersed early in the summer leaving an adult of each sex in each family. Family groups consisted of one female and one male in all habitats throughout 1977; except in the spring when there were at least two males per female in all areas (Table 16). As in 1976, all but one male dispersed by summer. The overall number of family-groups decreased from 1976 to 1977. Changes occurred in Typha and Scirpus-Typha-habitats. Areas in which two families had resided in 1976 were occupied by only one family-group in 1977 (Figs. 9 and 10). The number of family-groups remained constant throughout the spring and summer of 1977 in all habitats. There was an increase in

Table 16. Muskrat dispersion in different habitat-types at Bowden Lake in 1976 and 1977.

HABITAT-TYPE	NUMBER OF FAMILY-GROUPS	TOTAL NUMBER OF RESIDENT INDIVIDUALS	SEX RATIO M:F[1]
1976[2]			
Scirpus	4	12	4:8
Typha	5	13[3]	8:5
Scirpus-*Typha*	2	6	2:4
1977 Spring			
Scirpus	4	13	9:4
Typha	4	12	8:4
Scirpus-*Typha*	1	8	6:2
1977 Summer			
Scirpus	4	10 adults	5:5
		43 juveniles	28:15
Typha	4	9 adults	5:4
		35 juveniles	19:16
Scirpus-*Typha*	1	2 adults	1:1
		6 juveniles	4:2
1977 Fall			
Scirpus	6	10 adults	5:5
		55 juveniles	28:27
Typha	1	2 adults	1:1
		2 juveniles	2:0
Scirpus-*Typha*	2	4 adults	2:2
		10 juveniles	7:3

[1] M = male, F = female

[2] Adults only; full year

[3] in three of these family-groups there were 2 males/female; one male from each group dispersed in late June.

Figures 9, 10, and 11. Detailed maps of Bowden Lake.

Figure 9. The southern portion of Bowden Lake.
Figure 10. The northwestern portion of Bowden Lake.
Figure 11. The eastern portion of Bowden Lake.

▤ --*Scirpus acutus*

░ --*Typha latifolia*

▤ --*Carex lasiocarpa*

▥ --*Eleocharis parvula*

▩ --mudflat

▲ --huts occupied in fall 1976 and 1977

□ --feeding platforms used in 1977

■ --feeding platforms used in 1976 and 1977

○ --huts built in fall 1977

● --huts or bankdens occupied in 1977

- - - - --approximate home range boundaries for family groups - 1976 and 1977

-●-●- --approximate home range boundaries for family groups - 1976

-▽-▽- --approximate home range boundaries for family groups - 1977

Figure 9. The southern portion of Bowden Lake (legend on p76).

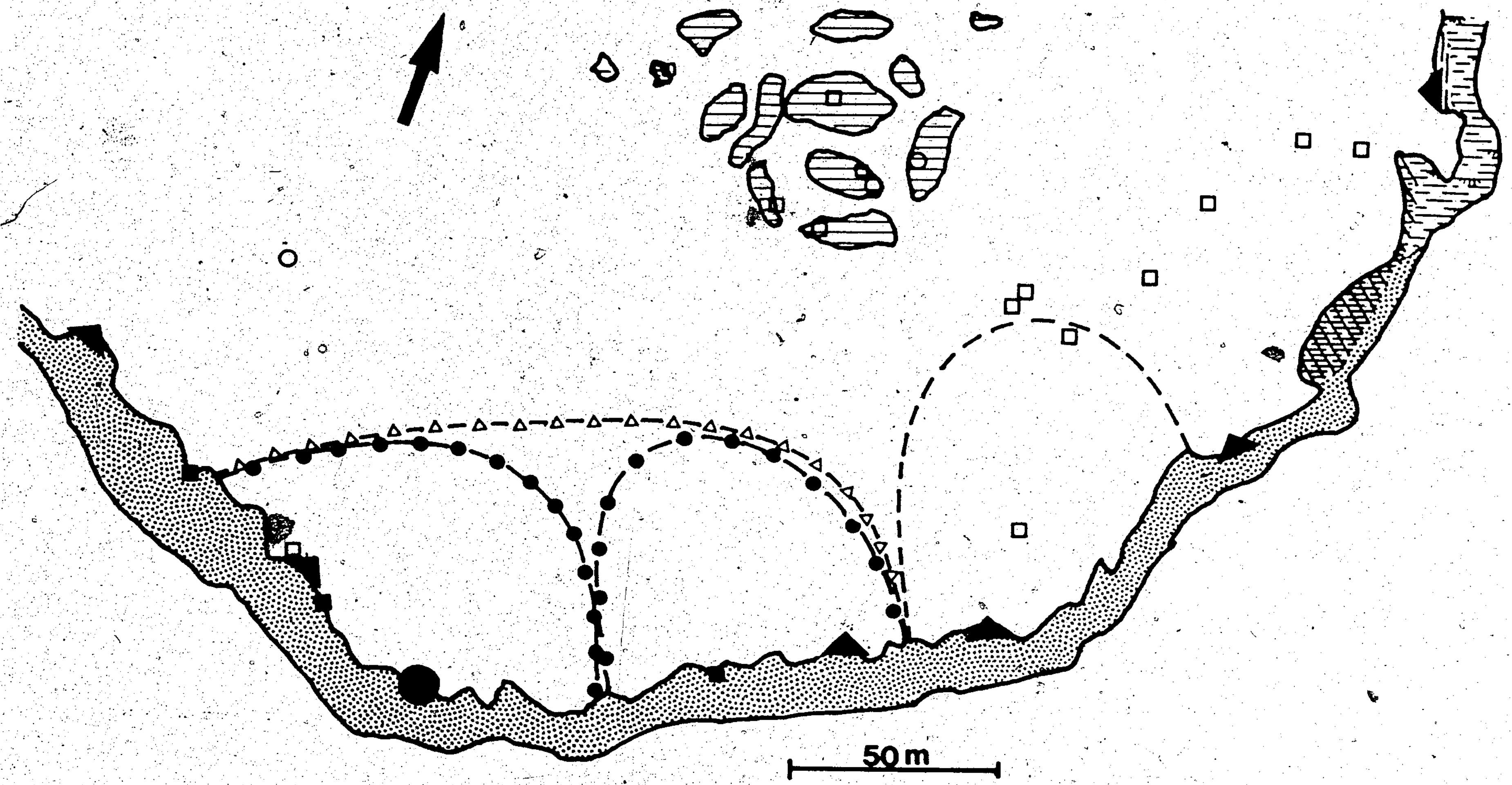


Figure 10. The northwestern portion of Bowden Lake (legend on p76).

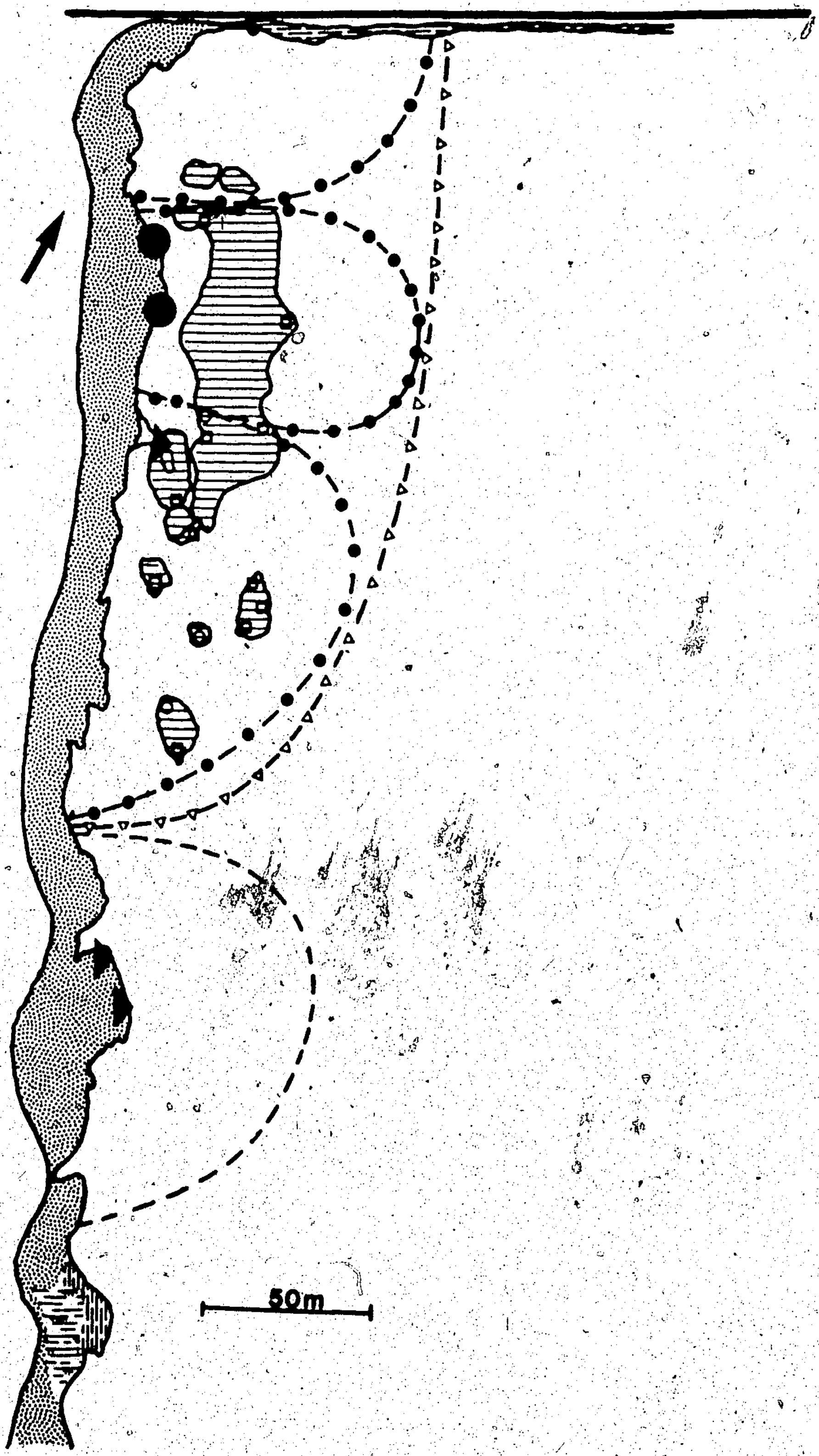
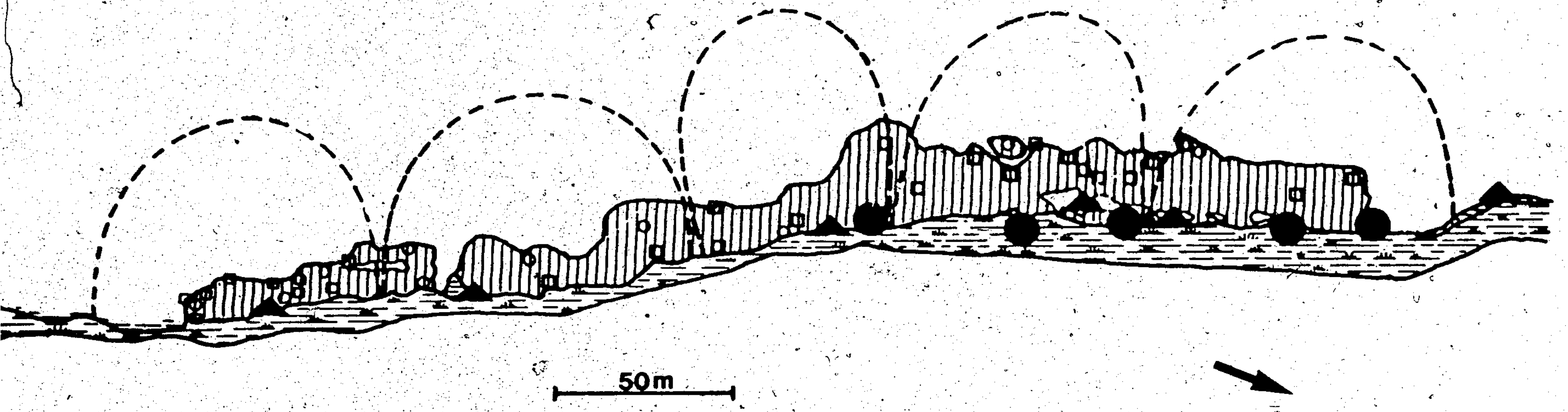


Figure 11. The eastern portion of Bowden Lake (legend on p76).



number of family-groups in Scirpus and Scirpus-Typha-habitats and a decrease in number of family-groups in Typha-habitat in the fall (Table 15). Of the three Typha areas that became vacant in the fall, two families (4 adults and their 10 juveniles) moved to Scirpus-habitat and one (2 adults) moved to Scirpus-Typha-habitat (Table 16 and Fig. 12). The size (m^2) of family-group areas did not change appreciably from 1976 to 1977 (Figs. 9, 10, and 11), except in the southern (Fig. 9) and northwestern (Fig. 10) portions of the lake. In the fall of 1977, the size of family areas in the south-end of the S. acutus stand (Fig. 11) decreased, as a result of the dispersal of a group of animals into the area. Animal densities were consistently higher in Scirpus (Chi-square test; $X^2=31.34$ $p<0.005$) and Scirpus-Typha habitats ($X^2=5.76$ $p<0.025$) than in Typha-habitat in 1976 and 1977 (Table 17). Unlike the fluctuations in animal densities, the number of occupied huts and bank dens remained essentially constant throughout the study (Table 18). More huts were found per 100 m of shoreline in habitats containing S. acutus than in Typha-habitat (Scirpus-habitat $X^2=9.19$ $p<0.005$; Scirpus-Typha habitat $X^2=4.75$ $p<0.05$).

Movements of animals from one habitat type to another were observed in the spring and fall of 1976 and 1977 and in the spring of 1978. The vast majority of all dispersals from one habitat type to another were movements from Typha-habitat to Scirpus-habitat (Fig. 12, $X^2=36.5$ $p<0.0001$).

Figure 12. Movements of muskrats between habitats at Bowden Lake. Thin arrows represent non-significant changes in numbers of animals (n) moving from one habitat to another; thick arrows are significamt movements of animals between habitat-types ($X^2=35.6$ $p<0.001$).

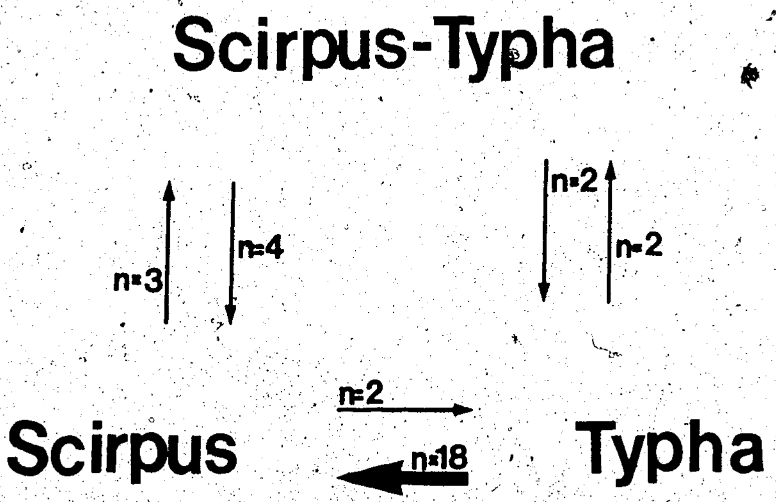


Table 17. Mean number of muskrats per 100m of shoreline at Bowden Lake in 1976 and 1977. Numbers in brackets are the total length (m) of shoreline for each habitat.

HABITAT	1976		1977		
	Spring	Fall	Spring	Summer	Fall
Typha (515.3)	3.2	4.0	2.0	6.4	2.0
Scirpus (558.6)	5.3	13.3	3.7	7.3	13.3
Scirpus-*Typha* (178.3)	5.0	10.0	8.0	6.0	6.0

Table 18. Mean number of occupied huts per 100m of shoreline at Bowden Lake in 1976 and 1977.

HABITAT	1976		1977		
	Spring	Fall	Spring	Summer	Fall
Typha	1.2	1.2	1.2	0.8	0.8
Scirpus	4.0	4.0	4.0	3.3	5.3
Scirpus-*Typha*	3.0	3.0	3.0	3.0	4.0

The proportion of overlap between animals from adjacent family-groups was generally lower in Scirpus and Scirpus-Typha-habitats than in Typha (Table 19). In the spring, overlap areas were the smallest in Scirpus-Typha-habitat (H=10.35 p<0.01; Kruskal-Wallis one-way analysis of variance). Overlap areas among animals from Scirpus-habitat were smaller than those in Typha-habitat (H=6.45 p<0.05) in the summer and of those in Scirpus-Typha and Typha-habitats in the fall (H=21.78 p<0.001). No overlap was evident for animals from Scirpus-Typha-habitat in the summer (Table 19). Overlap occurred among females, males and females, and males throughout the spring (Table 20). Females overlapped with one other female and one or two males, whereas males overlapped with up to three other males. Again, in summer, most of the overlap among individuals occurred between two adult males, and between adult males and females; female-female overlap only occurred in Scirpus-habitat. Juveniles did not overlap with any non-family members in the summer. Adults, generally, overlapped with only one other adult in the fall. Females from Scirpus-habitat did not overlap with non-family members in the fall. Most of the overlap involved juveniles and adult males. Only in Scirpus-habitat did juveniles overlap with each other, probably because of the large numbers of juveniles residing in Scirpus-habitat in the fall (Table 16).

Mean home range sizes (Table 21) for adults did not differ significantly between habitat types throughout the

Table 19. Percent of muskrat's home range which overlaps with the home range of residents in different family groups. N = number of animals in each habitat.[1]

HABITAT TYPE	% OF HOME RANGE IN OVERLAP WITH NON-FAMILY MEMBERS[2]	NUMBER OF ANIMALS IN OVERLAP[2]
Spring		
Scirpus (n=13)	16.7(11.9-24.1)	3.3(3-4)
Typha (n=12)	18.7(8.7-48.63)	3.3(2-4)
Scirpus-*Typha* (n=8)	2.84(0.2-12.8)	1.7(1-3)
Summer		
Scirpus (n=52)	2.09(0-7.7)	1.6(0-2)
Typha (n=44)	5.1(0-33.0)	1.5(0-2)
Scirpus-*Typha* (n=8)	0.0	0.0
Fall		
Scirpus (n=65)	6.9(0-20.4)	4.7(0-6)
Typha (n=4)	19.6(1.5-53.9)	1.5(1-4)
Scirpus-*Typha* (n=10)	11.4(0.6-39.3)	2.8(1-6)

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[1] excludes dispersing animals.
[2] mean values

Table 20. Mean number of animals from adjacent family groups with whom an individual overlaps.

	OVERLAP BETWEEN INDIVIDUALS					
HABITAT	Female-Female	Female-Male	Male-Male	Female-Juvenile	Male-Juvenile	Juvenile-Juvenile
Spring						
<u>Scirpus</u>	1.0	2.0	2.0			
<u>Typha</u>	1.0	1.7	2.6			
<u>Scirpus-Typha</u>	1.0	1.0	1.0			
Summer						
<u>Scirpus</u>	1.0	1.0	1.2	---	---	---
<u>Typha</u>	---	0.7	1.5	---	---	---
<u>Scirpus-Typha</u>	---	---	---	---	---	---
Fall						
<u>Scirpus</u>	---	---	0.3	0	2.3	0.7
<u>Typha</u>	1.5	1.0	---	1.0	---	---
<u>Scirpus-Typha</u>	1.0	1.0	1.0	2.0	2.0	---

Table 21. Mean home range size (ha) for adults and juveniles from different habitats in 1977 at Bowden Lake.

Time Period/Habitat	Adult females	Adult males	Juveniles
Spring			
<u>Scirpus</u>	.47	.48	-
<u>Typha</u>	.49	.51	-
<u>Scirpus</u>-<u>Typha</u>	.48	.50	-
Summer			
<u>Scirpus</u>	.42	.47	.046
<u>Typha</u>	.44	.46	.024
<u>Scirpus</u>-<u>Typha</u>	.68	.73	.045
Fall			
<u>Scirpus</u>	.42	.42	.35
<u>Typha</u>	.47	.52	.14
<u>Scirpus</u>-<u>Typha</u>	.40	.42	.15

year ($H=1.61$ $p>0.1$), except for animals from Scirpus-Typha in summer. Home range sizes were about the same for adult females and males throughout the year. Juveniles had smaller areas than adults in summer and fall. Juveniles from Scirpus-habitat had larger areas than did juveniles from the other habitats in fall ($H=7.22$ $p<0.01$).

An animal was more likely to chase another animal when it was closer to its own hut, and was chased more often when closer to the other animal's hut ($X^2=9.8$ $p<0.01$) throughout the study (Table 22).

Discussion

The pattern in which animals are distributed in an environment is indicative of the dispersion patterns of resources, and the degree of sociality among the animals (Brown 1975). Muskrats live in small groupings of two to four adults and numerous young. These family-groups (Errington 1963) are distinguished by the high amount of home range overlap among individuals (at least 75% of an animal's home range). The amount of overlap among non-family members may reflect the distribution and quality of available resources (Weins 1976).

In spring, when the nutrient content of *I. latifolia* and *S. acutus* were both high and comparable to each other (Table 1), the amount of overlap among non-family members was similar in the two habitats (Table 19). The low overlap in Scirpus-Typha-habitat may have been due to the high

Table 22. Summary of the proximity to an animal's own hut where it was chased by or was chasing another animal. Comparisons were made with Student's t-test and Chi-Square tests (Sokal and Rohlf 1969).

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a) Mean distance from own hut where an animal was chased or was chasing another animal.

	Chases	Chased
Mean distance from own hut (m)	19.14	98.36

$t = 4.14$ d.f. $= 15$ $p<0.001$

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b) Number of chases occurring in the proximity of an animal's own hut.

	Chases	Chased
Closest hut is own hut	20	9
Closest hut is another's hut	7	19

$X^2 = 9.8$ d.f. $= 1$ $p<0.01$

---

quality of the habitat because of the presence of both T. latifolia and S. acutus, and to the relative isolation of the area (Fig. 10) in the northwest corner with only one adjacent family-group. These animals had home ranges about twice the size of animals from the other habitats in 1977 (Table 21) and used areas that two family-groups had inhabited in 1976. In the spring there were more dispersing and excursioning animals (see p 23) and there were more individuals per hut than in summer of fall (Table 16). This was especially true of males. On average males overlapped with two males from adjacent family-groups (Table 20). Males seemed to be competing for females at that time, as indicated by the frequency of aggressive interactions between males preceding sexual activity (see p 11), which may account for the high overlap of individuals in the spring. As the predictability and quality of a given set of resources increased, the overlap among non-family members decreased, since the probability that the area contains sufficient resources for the family-group was high.

Lower percentages of overlap of animals in Scirpus and Scirpus-Typha may result from the high quality and predictability of S. acutus over that of T. latifolia. Even though animals from Scirpus-habitat overlapped with about the same number of individuals as did animals from Typha-habitat, the amount of overlap was significantly lower, suggesting that the exclusion of non-family members from an animal's home range was more likely to occur in

Scirpus-habitat than in Typha-habitat. Overlap increased in fall for animals in all habitats but overlap among animals in Scirpus-habitat was lower than in either Typha or Scirpus-Typha-habitats, while at the same time the number of animals in the overlap increased. Overlap in Typha-habitat was comparable to that in spring, even though few animals overlapped, possibly due to the decline in habitat quality. Overlap in Scirpus-Typha increased from summer to fall, mainly because of the dispersal of two adults into the area.

Home range sizes did not change significantly through the field season, but they tended to be larger in spring before the animals were settled into family-groups, and tended to decrease in summer (except for those in Scirpus-Typha). In Scirpus-habitat home range sizes for males decreased in fall when there was more overlap between non-family members than in spring or summer. As the density of animals in Scirpus-habitat and Scirpus-Typha-habitat increased (due to dispersal of animals into these areas), home range sizes decreased. In Typha-habitat home range sizes of adults increased while the number of individuals in the habitat declined.

Aggressive behavior in muskrats was observed by Beer and Meyer (1951) mainly in spring and fall. My own observations indicate that muskrats at Bowden Lake were most aggressive in April and early May (Fig. 3a). Beer and Meyer (1951) also noted that males were more aggressive than females, whereas Errington (1963) considered females to be more aggressive. In the spring, males and females were equally aggressive towards other individuals, but during summer and fall females became less aggressive than males (Fig. 5 and Table 5). Aggressive behavior was characterized by chases and fights by animals, with others from neighboring family-groups or with dispersing animals, and invariably involved at least one adult male (Table 5). That an animal was more likely to be chased by a neighboring animal the further it traveled from its home hut, and that areas existed in which only family members were observed, suggests that muskrats use aggressive behavior to exclude non-family members from family areas.

Several rodent species have been shown to defend food resources (e.g. Smith 1968). Higher plant densities within exclusive group areas as compared to areas of overlap indicate that muskrats were using areas with a potentially greater food supply, and more cover than other unused areas of the habitat. Since muskrat food habits were based on the abundance of preferred foods, it seems logical that the animals would defend an area which would ensure at least a minimum amount of food of high quality. In using areas of higher densities of preferred foods, the animals inhabited areas that provided the needed food resources for them and their offspring.

Habitat preferences exhibited by animals are responses to differences in the 'quality' of the habitat (Wiens 1976). Habitat quality involves numerous attributes of which suitable foraging sites, nesting sites, refugia from predators and overwintering areas are important considerations (Fretwell 1972). At low population densities, the first habitats to be colonized by animals are the ones with the highest quality (i.e. the habitat in which an animal's fitness is highest (Levins 1968). As densities increased the quality of the 'good' habitat decreased, and a point is reached where its quality is equal to that of the next lowest habitat. At that time individuals entered the 'second best' habitat at no loss in fitness (Fretwell and Lucas 1969).

Higher densities of muskrats and greater numbers of occupied dwellings were found in Scirpus and Scirpus-Typha habitats than in Typha during 1976 and 1977 (Tables 16 and 17). Higher densities of animals in Scirpus-habitats may be indicative of a preference for residing in areas of S. acutus. These data correspond with muskrats' preference for S. acutus over T. latifolia. If muskrats selected habitats dominated by S. acutus, then one would expect a differential dispersal of animals from Typha-habitat to Scirpus-habitat, as was demonstrated (Table 16 and Fig. 12).

Population density declined throughout the study from 31 adults in the three habitats in 1976 to 16 adults by the fall of 1977. As population density decreased, a decrease in the habitat-types used by the animals also occurred. Pitelka (1973) demonstrated that in years of low population density, brown lemmings (Lemmus trimucronatus) were found predominantly in areas of high quality habitat and that in peak years they were found in a wide variety of habitats. In 1976 muskrats were evenly distributed among the three habitats, but by the fall of 1977 the majority of animals had moved into areas dominated by S. acutus, indicating that Typha was the least preferred habitat at Bowden Lake.

Muskrats lived in exclusive family areas in which the relative densities of food resources were higher than in areas of overlap between groups. I contend that Scirpus-habitats were of higher quality than were Typha-habitats as indicated by higher densities of animals in Scirpus-habitats, the tendency for animals to disperse from Typha into Scirpus-habitat, higher nutrient content of S. acutus compared to T. latifolia, preference of S. acutus over T. latifolia, and higher survival of juveniles from Scirpus-habitat.

IX. CONCLUDING DISCUSSION

Errington (1963) suggested that Typha latifolia was the most important resource available to muskrats in North America. Assessment of the dependence of an animal on any particular resource may be approached in many different ways. It may be considered in relation to its importance in foraging strategies (Krebs 1978), or its role in the selection of a habitat that enhances survival, reproductive success, and survival of young (Wiens 1976). In the foregoing discussion, I have presented evidence on muskrat foraging habits, food preferences, habitat preferences, and the growth and survival of offspring, to suggest that Scirpus acutus was a more valuable resource than was I. latifolia in south-central Alberta.

Optimal foraging theory predicts that animals will specialize their foraging activities on quality foods when the foods are abundant (Ellis et al. 1976). Food quality is based on its nutrient content and digestibility, as influenced by its fiber content (Crampton and Lloyd 1959). The high fiber content of I. latifolia, in combination with a declining nutrient content, makes this species increasingly undesirable as a forage item to muskrats from spring to fall. That I. latifolia was not the dominant food in the animals' diet at any time, and that it was not chosen in relation to any measures of its nutrient content, suggests that the species was not a preferred food item, but rather was eaten in the absence of a more valuable food resource. S. acutus seemed to be a preferred food based on data showing that it was the dominant food during the spring and summer, was chosen in relation to its quality as opposed to its relative abundance, and was chosen most often when other foods were equally available (both in the wild and under experimental conditions).

Habitat selection involves the choice by an individual of an area that contains the best set of needed resources, whether these be food resources, nesting sites, mates, and/or shelter from predators (Fretwell 1972). Muskrat densities were highest in Scirpus-habitats. Dispersal into Scirpus-habitat was differentially higher than movements from Scirpus-habitat into other habitats, suggesting that muskrats actively selected the Scirpus-habitat.

Differences in the growth of juveniles existed between animals living in habitats with S. acutus and those in Typha-habitat. Consistently higher weights and faster growth rates of juveniles from Scirpus-habitat may be related to the quality of S. acutus as a forage species. The overall quality of this habitat (in terms of availability of food, nesting or overwintering sites, and possibly protection from predators) may account for the higher survival rates of these juveniles.

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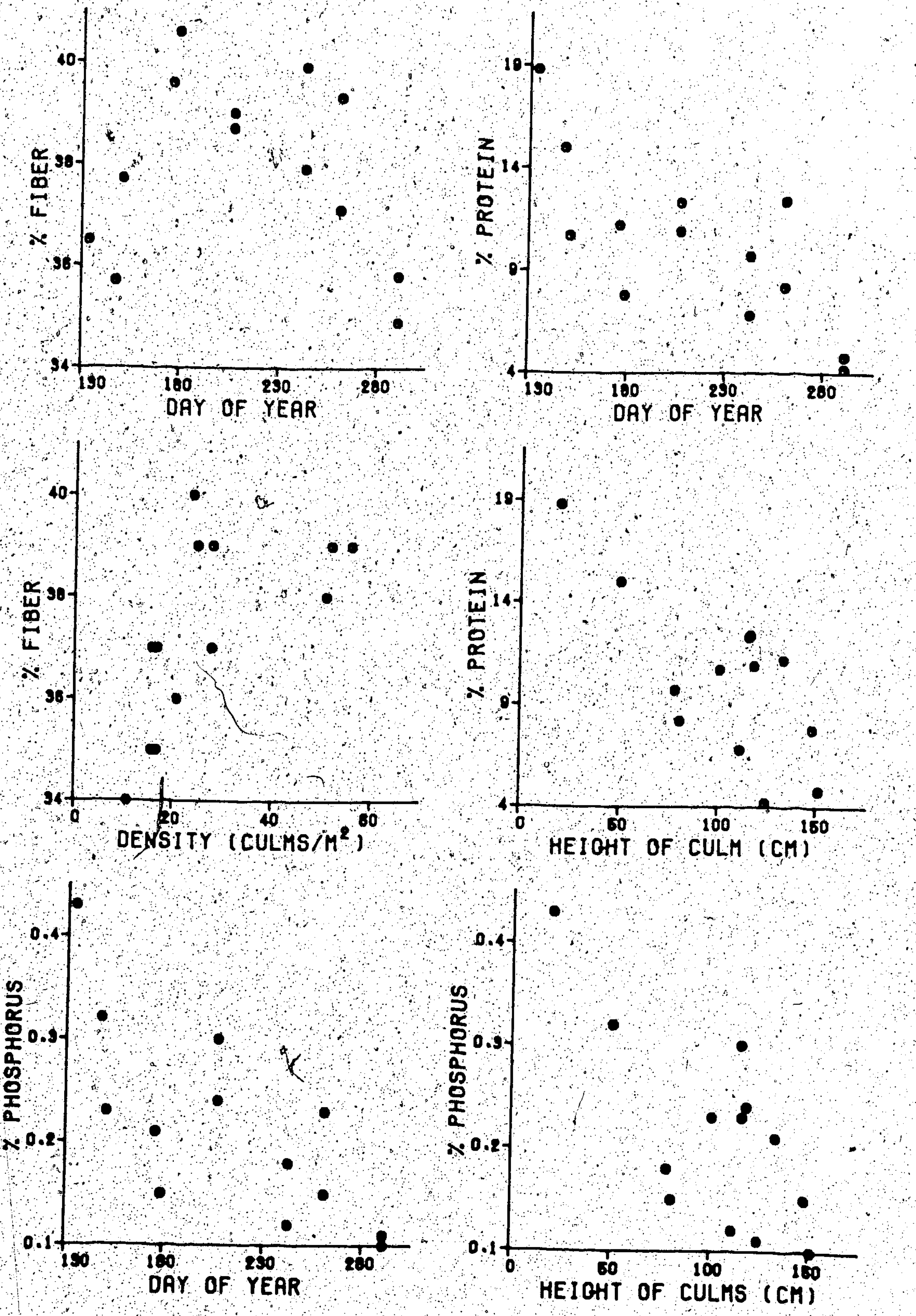
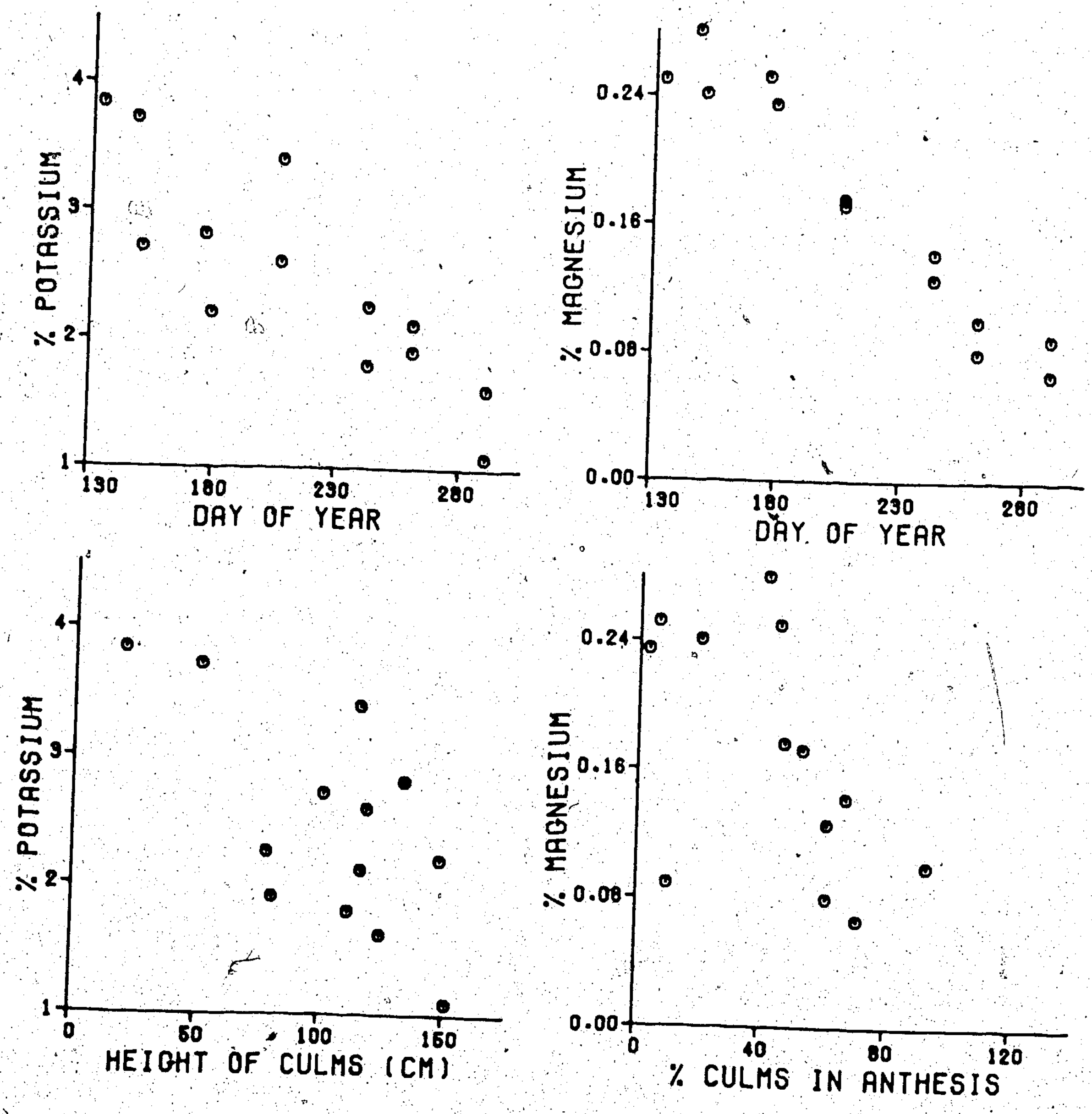
Appendix 1

Scattergrams of the correlations between the physical and temporal characteristics of <u>Scirpus</u> <u>acutus</u> and its nutrient content (Table 3).

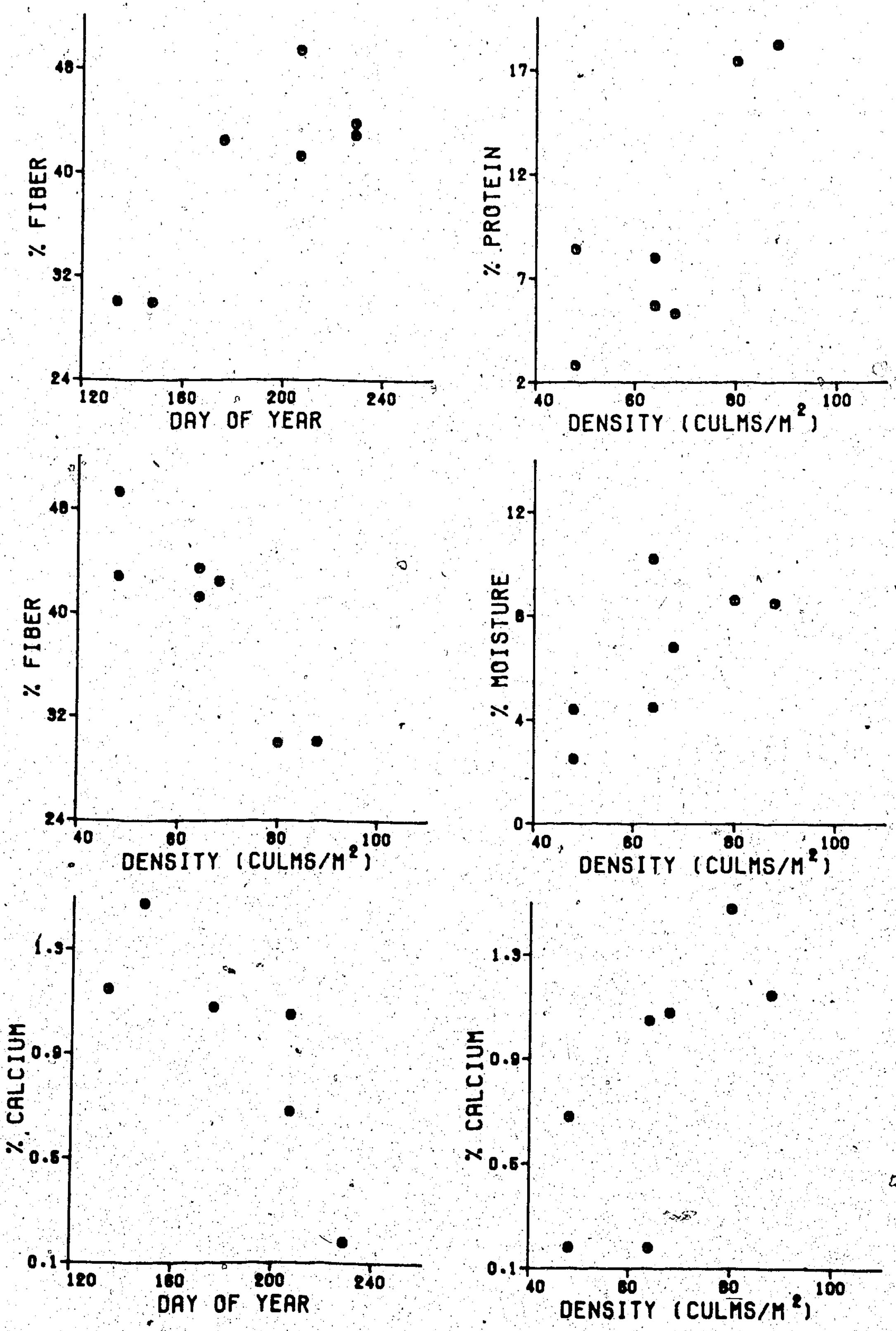


Appendix 1 -continued

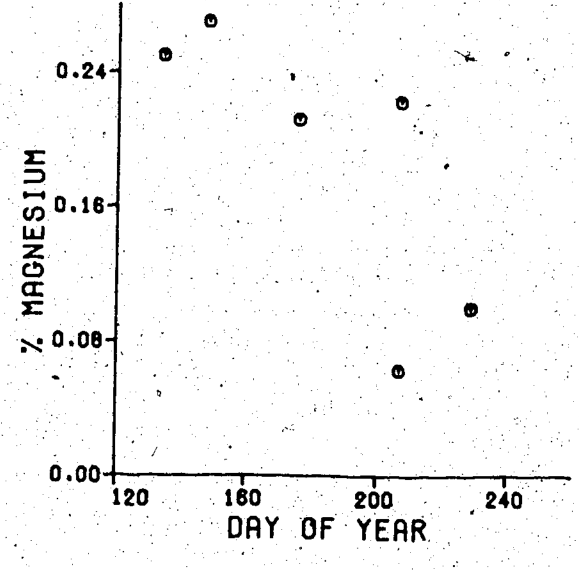


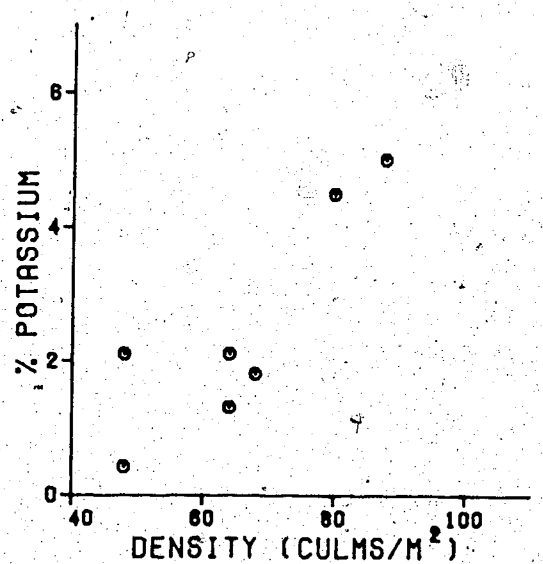
Appendix 2

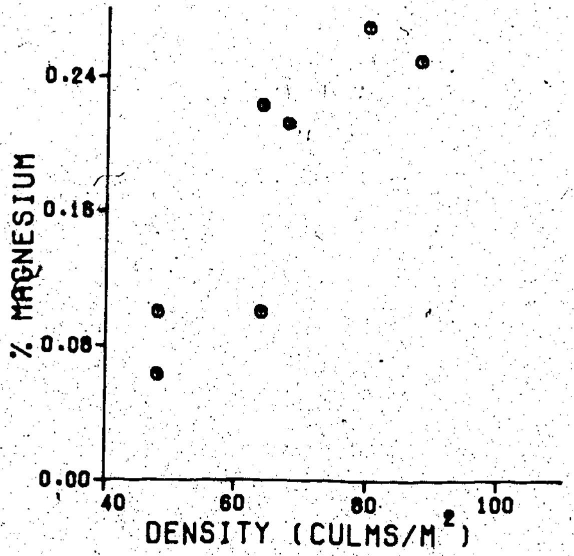
Scattergrams of the correlations between the physical and temporal characteristics of Typha latifolia and its nutrient content (Table 4).



Appendix 2 -continued







Appendix 3. Summary of the cross-comparisons (ANOVA's) of muskrat activity budgets by behaviour category. T1 = Spring, T2 = Summer, T3 = Fall. F = Adult females, M = Adult males, J = Juveniles. * P < 0.05, ** P < 0.005, *** P < 0.001.

	SPRING		SUMMER			FALL		
	Adult ♀	Adult ♂	Adult ♀	Adult ♂	Juvenile	Adult ♀	Adult ♂	Juvenile
a) Travelling								
Spring								
Adult ♀	--	F < M*						
Adult ♂		--						
Summer								
Adult ♀	T1 = T2		--	F = M	F > J*			
Adult ♂		T1 = T2		--	M > J*			
Juvenile					--			
Fall								
Adult ♀	T1 = T3		T2 = T3			--	F = M	F > J*
Adult ♂		T1 > T3*		T2 = T3			--	M > J**
Juvenile					T2 = T3			--

Appendix 3 - continued

	SPRING		SUMMER			FALL		
	Adult ♀	Adult ♂	Adult ♀	Adult ♂	Juvenile	Adult ♀	Adult ♂	Juvenile
b) Foraging								
Spring								
Adult ♀	--	F = M						
Adult ♂		--						
Summer								
Adult ♀			--	F = M	F = J			
Adult ♂		T2 > T1		--	M = J			
Juvenile					--			
Fall								
Adult ♀			T2 = T3			--	F = M	F = J
Adult ♂	T3 > T1**		T2 = T3				--	M = J
Juvenile					T2 = T3			--

Appendix 3 - continued

	SPRING		SUMMER			FALL		
	Adult ♀	Adult ♂	Adult ♀	Adult ♂	Juvenile	Adult ♀	Adult ♂	Juvenile
c) Hut Construction								
Spring								
Adult ♀	--							
Adult ♂		--						
Summer								
Adult ♀			--					
Adult ♂				--	M < J*			
Juvenile					--			
Fall								
Adult ♀						--	F = M	F = J
Adult ♂				T2 = T3			--	M = J
Juvenile					T2 = T3			--

Appendix 3 - continued

	SPRING		SUMMER			FALL		
	Adult ♀	Adult ♂	Adult ♀	Adult ♂	Juvenile	Adult ♀	Adult ♂	Juvenile
d) Grooming								
Spring								
Adult ♀	--	F = M						
Adult ♂		--						
Summer								
Adult ♀	T1 = T2		--	F = M	F = J			
Adult ♂		T1 = T2		--	M < J*			
Juvenile					--			
Fall								
Adult ♀	T1 = T3		T2 = T3			--	F = M	F = J
Adult ♂				T2 = T3			--	M = J
Juvenile								--

Appendix 3 - continued

	SPRING		SUMMER			FALL		
	Adult ♀	Adult ♂	Adult ♀	Adult ♂	Juvenile	Adult ♀	Adult ♂	Juvenile
e) Interacting								
Spring								
Adult ♀	--	F = M						
Adult ♂		--						
Summer								
Adult ♀	T1 > T2*		--	F = M	F = J			
Adult ♂		T1 > T2*		--	M = J			
Juvenile					--			
Fall								
Adult ♀			T2 = T3			--	F = M	F = J
Adult ♂				T2 = T3			--	M > J*
Juvenile					T2 = T3			--

Appendix 3 - continued

	SPRING		SUMMER			FALL		
	Adult ♀	Adult ♂	Adult ♀	Adult ♂	Juvenile	Adult ♀	Adult ♂	Juvenile
f) Scent Marking								
Spring								
Adult ♀	--	F = M						
Adult ♂		--						
Summer								
Adult ♀	T1 = T2		--	F = M				
Adult ♂				--				
Juvenile					--			
Fall								
Adult ♀						--		
Adult ♂		T1 = T3					--	M = J
Juvenile								--

Appendix 4. Summary of ANOVA comparisons of muskrat activity budgets in the three time periods. T = Traveling, F = Foraging, G = Grooming, I = Interactions, SM = Scent Marking, HC = Hut Construction, AF = Adult Females, AM = Adult Males, J = Juveniles. * P < 0.05, ** P < 0.005, *** P < 0.001.

	T		F		G		I		SM	
	AF	AM	AF	AM	AF	AM	AF	AM	AF	AM
a) Spring										
AF	-		*							
T										
AM		-				***		***		***
AF			-		***		***		***	
F										
AM				-		***		***		***
AF					-					
G										
AM						-		**		
AF							-			
I										
AM								-		*
AF									-	
SM										
AM										-

Appendix 4 - continued

		T			F			HC			G			I			SM		
		AF	AM	J	AF	AM	J	AF	AM	J	AF	AM	J	AF	AM	J	AF	AM	J
b) Summer																			
	AF	-			**			-			**			**			**		
T	AM		-			**			***			***			***			***	
	J			-			***			**						*			-
	AF				-			-			***			***			***		
F	AM					-			***			***			***			***	
	J						-			***			***			***			-
	AF							-			-			-			-		
HC	AM								-						*				
	J									-									-
	AF							-			-								
G	AM											-							
	J												-						-
	AF													-			*		
I	AM														-			*	
	J											-				-			-
	AF																-		
SM	AM																	-	
	J																		-

Appendix 4 - continued

		T			F			HC			G			I			SM	
		AF	AM	J	AF	AM	J	AF	AM	J	AF	AM	J	AF	AM	J	AF	AM	J
c) Fall																			
	AF	-			***			**						*			-		
T	AM		-			**												*	
	J			-			***			*			*			*			**
	AF				-			***			***			***			-		
F	AM					-			***			**			***			***	
	J						-			***			***			***			***
	AF							-									-		
HC	AM								-										
	J									-			*						
	AF										-			***			-		
G	AM											-							
	J												-			*			*
	AF													-			-		
I	AM														-				
	J															-			
	AF																-		
SM	AM																	-	
	J																		-

Appendix 5. Summary of ANOVA statistics of juvenile growth comparisons between *Scirpus*- and *Typha*-habitat (Table 7).

SOURCE OF VARIATION	d.f.	S.S.	M.S.	F-VALUE
Independent Variable: Age				
a) Dependent Variable: Weight (g)				
Equality of Adjusted Cell Means	1	528764.0	5287640.0	99.62
Zero Slope	1	1656701.0	16556701.0	312.13
Error	165	875781.0	5307.76	
Equality of Slopes	1	73911.94	73911.94	15.12
Error	164	801869.06	4889.45	
b) Dependent Variable: Total Body Length (cm)				
Equality of Adjusted Cell Means	1	820.29	820.29	64.91
Zero Slope	1	3040.22	3040.22	240.59
Error	165	2085.03	12.64	
Equality of Slopes	1	597.39	597.39	65.86
Error	164	1487.64	9.07	

Appendix 5 - continued

SOURCE OF VARIATION	d.f.	S.S.	M.S.	F-VALUE
c) Dependent Variable: Tail Length (cm)				
Equality of Adjusted Cell Means	1	204.85	204.85	66.13
Zero Slope	1	618.05	618.05	199.51
Error	165	511.14	3.09	
Equality of Slopes	1	138.79	138.79	61.13
Error	164	372.35	2.27	
d) Dependent Variable: Left-hind Foot Length (cm)				
Equality of Adjusted Cell Means	1	6.77	6.77	40.81
Zero Slope	1	16.49	16.49	99.46
Error	165	27.35	0.17	
Equality of Slopes	1	5.95	5.95	45.57
Error	164	21.41	0.13	

Appendix 6

Regression statistics for the relationship between the relative abundance of _Typha latifolia_ and the percent of _T. latifolia_ in muskrats' diet ($p<0.01$; Fig. 7).

Source of Variation	S.S.	d.f.	M.S.	F-ratio	R^2
Regression	6337.06	1	6337.06	26.08	0.592
Error	4373.04	18	242.95		
Total	10710.10				

Appendix 7

Regression statistics for the relationship between the absolute abundance of *Scirpus acutus* and the percent of *S. acutus* in muskrats' diet ($p<0.001$); Fig. 8).

Source of Variation	S.S.	d.f.	M.S.	F-ratio	R^2
Regression	12614.61	2	6307.31	24.65	0.587
Error	8955.96	35	255.88		
Total	21570.57				

Appendix 8

ANOVA statistics for the regression of the physical characteristics of _Scirpus acutus_ and the percent of _S. acutus_ in muskrats' diet (Table 14).

Independent Variable	Source of Variation	S.S.	d.f.	M.S.
Time of year	Regression	7291.69	1	7291.69
	Error	15692.72	43	364.95
	Total	22984.41		
Phenology	Regression	1929.04	1	1929.04
	Error	15692.72	43	364.95
	Total	17621.76		
Height of culms (cm)	Regression	3517.42	1	3517.42
	Error	15692.72	43	364.95
	Total	19210.14		
Full model	Regression	15580.41	3	5193.47
	Error	15692.72	43	364.95
	Total	31273.13		