The Ecology of the Muskrat, *Ondatra zibethicus*, at Luther Marsh, Ontario

GILBERT PROULX and FREDERICK F. GILBERT[1]

Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1
[1]Present address: Wildlife Biology, Washington State University, Pullman, Washington 99164-4220

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The ecology of Muskrat (*Ondatra zibethicus*) populations inhabiting areas of different floristic composition and subjected to seasonal changes in water level was studied at Luther Marsh, Ontario. House building sites consisted of open water areas and heavy emergent vegetation stands, particularly cattail (*Typha* sp.) stands, with > 15 cm water. The average home range had a ratio of vegetation:open water areas of 1:1. With a decline in water level, Muskrats extended their home range significantly ($p < 0.05$) from 484 ($\pm$ 238.4) m^2 in June-July to 1112 ($\pm$ 842.7) m^2 in August-September and increased significantly ($p < 0.05$) the average number of houses/family from 1.5 ($\pm$ 0.7) in early summer to 3.9 ($\pm$ 1.7) in late summer. Cattail was the most important foodstuff but food habits depended upon the movements of the animals and the diversity of the flora. Adult and juvenile populations usually had an even sex ratio in summer. Most females had two litters with an average of 6.3 embryos/litter. In cattail-rich areas, females produced 1 to 4 more young/litter than females of other habitat types and there were more animals/ha of home range (> 100 animals) than in any other habitat type (< 80 animals). The survival rate of juveniles was estimated at 66.4% in summer and 31.8% in winter. The maximum life span of a Luther Marsh Muskrat would be five years.

Key Words: Muskrat, *Ondatra zibethicus*, Luther Marsh, home range, populations.

Muskrats (*Ondatra zibethicus*) inhabit a wide range of community types but generally prefer lentic water containing vegetation (Perry 1982). The effect of water depth on habitat selection by Muskrat has been noticed by Sather (1958) and Danell (1978) and the direct effect of fluctuating water levels on muskrat populations has been considered greater than the indirect effect through altering the composition of the vegetation habitat (Bellrose and Brown 1941). On the other hand, McDonnell and Gilbert (1981) suggested stability in habitat usage by Muskrats even when water levels declined substantially. An obvious lack of information still exists concerning the relationship between muskrat populations and their environment and the effects of environmental conditions on muskrat reproduction (Errington 1937; Bellrose and Low 1943; Arata 1959) and food habits (Errington 1941) are poorly known.

The present study concerned the ecology of Muskrat populations inhabiting different habitats of a marsh subjected to seasonal changes in water level. The primary objective was to determine and quantify the effects of vegetative composition and water level fluctuations on the selection and utilization of marsh habitat by muskrats. Muskrat population productivity and changes over the year, were also investigated.

Study Area

The Luther Marsh Management Area is located 65 km north of Guelph, Ontario. The reservoir averages about 120 cm in depth with annual water level fluctuations of 50-70 cm. The climate is humid continental with mean maximum and minimum temperatures for July of 23.6°C and 12.1°C, and for January, -5.6°C and -13.5°C, respectively. Mean annual precipitation is 89.8 cm (Heidorn 1975). Marsh areas have predominantly submerged and emergent vegetation including cattail (*Typha* sp.), smartweed (*Polygonum* sp.), pondweeds (*Potamogeton* sp.), sedges (*Carex* sp.) and bulrush (*Scirpus* sp.) (Schiefele 1973). Peat and muck are the two major soil types of the Management Area (Canada Department of Agriculture 1962, 1963).

In 1979, five study areas representative of Luther Marsh habitats were delineated: East Bay (11.2 ha), Western Shore (0.5 ha), Teal Bay (0.8 ha), Creek (0.2 ha), Pond 1 (0.4 ha) and Pond 2 (0.3 ha) (Figure 1). In 1980, a sixth study area, Upper Shore of Teal Bay (0.3 ha), was studied (Figure 1).

Methods

In May 1979 and 1980, the vegetative composition of each study area and the degree of open water areas were determined. When possible, the vegetation of a study area was subdivided into belts, each of which consisted of a distinct cover type (Takos 1947). A transect was randomly located through each study area. Measurements of the width and length of each vegetation belt and its position relative to free water areas were made at 10 m intervals along the transect. All information was transferred onto maps at an original scale of 1:1000. Vegetation and free water areas

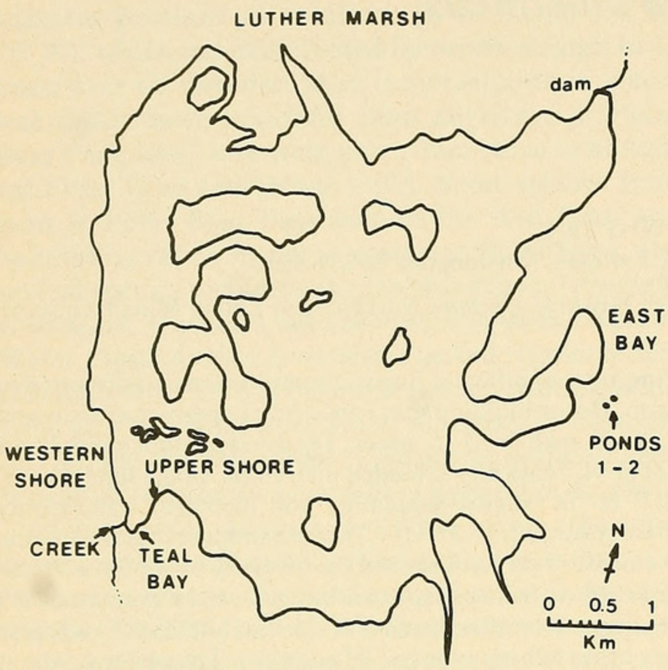

FIGURE 1. Luther Marsh showing location of the study areas.

were determined with the aid of a conventional planimeter.

The reservoir water level at the dam and the amount of precipitation were recorded by Grand River Conservation Authority staff. Daily water depths in the total area of each study area, except East Bay, were recorded at 0, 5, 10, and 15 m on each side of the transect in May and early June. In East Bay, water levels were recorded every month at Muskrat houses. In late summer, three transects were established between the shoreline and the back of East Bay and water depths were recorded every 2 m along each transect. These values, along with the reservoir water level at the dam, permitted determination of monthly water level fluctuations and delineation of regions, within the study area, with distinct water depths.

The vegetation was analysed with the aid of permanent 0.5 m × 1.0 m plots placed at random in each of the vegetation belts. In Western Shore and Teal Bay, the number of plots in a belt was proportional to the area covered by that belt. Therefore, 44 plots were inventoried in Western Shore (horsetail belt, 25; cattail belt, 12; sedge belt, 7) and 38 in Teal Bay (cattail belt, 25; spike rush belt, 13). The vegetation of the other habitats was treated as one belt and 25 plots were placed randomly in each habitat. Due to the size of East Bay, 100 quadrats were inventoried. The number of individual shoots of each taxon was counted in each plot. Two inventories were carried out in summer 1979; the first in late May-early June and the second in early July. In 1980, similar inventories were conducted with a third one in August. Considering that some plants grow slower than others and that their representation was low in the May sample, only the July results were used to compare the floristic composition of the habitats. A similarity index between 1979 and 1980 floristic compositions of each habitat was calculated according to the formula

$$S = \frac{2C}{A + B} \times 100$$

where S is the similarity index in percent, A is the number of taxa in sample A, B is the number of taxa in sample B, and C is the number of taxa common to both samples (Odum 1971). For each plot, the relative density of each plant was calculated and habitats were compared to each other by a stepwise discriminant analysis (F-to-enter = 4.0, F-to-remove = 3.9; Klecka 1975). This analysis is a multivariate statistical analysis technique that allows one to describe, differentiate and classify elements characterized by a set of "p" variables. In this analysis, according to the linear combination of "p" variables that best separated and characterized the sample plots of one study area from that of other habitats being compared, a sample plot was classified in its original study area or in another study area to which it was floristically more similar. The variables were the relative densities in a sample plot of: cattail, bulrush, spike rush (*Eleocharis* sp.), bur reed (*Sparganium* sp.), Graminae, horsetail (*Equisetum* sp.), arrowhead (*Sagittaria* sp.) and 'others'. All taxa, except those included in 'others', were used by Muskrats of all study areas in their building and feeding activities. 'Others' included taxa which were found in 1979 or 1980, but not in both years.

A forage ratio was used to relate the quantities of the various taxa found at the feeding platforms to the proportions available in the study area (Takos 1947). A ratio of 1.0 implied that the plant was found on the feeding platforms in frequencies proportional to its occurrence in the habitat. When the ratio was < 1.0, the plant was used less than would be predicted if selection was random. A ratio > 1.0 implied preferential selection of the taxon by Muskrats. Only platforms of recent origin (characterized by fresh remnants) were tabulated. Surveys of feeding platforms lasted approximately one month and were related to the period during which a vegetation analysis was done.

Study areas were surveyed for Muskrat houses during the last week of May 1979 and the second week of May 1980. Thereafter, weekly checks for houses were made during the live-trapping period. Inhabited houses were recognized by fresh signs of Muskrat activities. In 1979, the vegetation surrounding the houses was recorded in late May-early June, as the vegetation inventory was being conducted. In early June 1980, the vegetation surrounding all Muskrat houses was recorded. Each house was located by triangulation and plotted on the habitat map.

Muskrat were trapped with National live traps (17.8 × 17.8 × 50.8 cm; Tomahawk Livetrap Co.) from 25 May to 23 September 1979 and from 16 May to 25 September 1980. Two traps were set in close proximity to each active house, usually at feeding stations, defecation sites or along runways. Those sites permitted optimum sampling (Aldous 1946; Erickson 1963; Vincent 1972). Traps were maintained at each site throughout the trapping season and baited with carrots (Erickson 1963; MacArthur 1978).

Adult muskrats were immobilized with an intramuscular injection of 10 mg Ketamine (Ketaset™-BTI Products Inc.). Animals were sexed by manipulation of the urinary sheath (Sather 1958) and exposure of the penis (Baumgartner and Bellrose 1943). A numbered No. 1 monel tag was put in one ear and a numbered rabbit tag in the other (National Band and Tag Co.). Adults and juveniles were released after their tag number and capture location were recorded.

Because grid trapping is inadequate for the study of Muskrat movements (Proulx 1981), related methods for the determination of the home range size (Sanderson 1966) were rejected. The home range size of a family corresponded to the immediate site of the dwellings of a family plus the surrounding area delineated by the lines interconnecting the outermost capture sites, defecation points, feeding platforms and trails (connected to the water pool of a dwelling). However, since areas used by Muskrats wandering far from their dwelling might have been missed, either because some feeding platforms were not found or Muskrat signs were absent, the home range sizes determined in this study corresponded to minimum areas, intensively used by muskrats.

In order to determine natural mortality, all study areas were free of any trapping pressure during fall 1979 — spring 1980. However, carcasses of muskrats harvested in adjacent areas by a resident trapper were obtained in fall 1978 and 1979. Mean litter size and number of litters per breeding female were estimated from placental scars and used to provide an estimate of summer juvenile mortality. The summer mortality rate, along with live-trapping information, permitted an estimate of fall Muskrat populations, and that, together with knowledge of the breeding stock the following year, permitted an estimate of the winter mortality rate. A life table, based on summer and winter mortality rates, was developed according to Caughley (1977).

Results

Habitat Characteristics

The reservoir water level was approximately 30 cm higher in 1980 than in 1979. The amount of precipitation from 1 May to 30 September was 33.9 cm in 1979 and 53.4 cm in 1980.

Comparison of the floristic composition of the habitats by discriminant analysis indicated significant differences ($p < 0.05$) among marsh habitats. East Bay plots were characterized by high relative densities of cattail (> 46%) and Graminae (> 46%) shoots, Western Shore plots, by their relative density of horsetail shoots (> 28%) and Teal Bay plots, by their relative density of spike rush (> 41%) and arrowhead (> 11%) shoots. None of these plants was characteristic of Creek plots which consisted predominantly of sedge shoots (> 69%). Upper Shore of Teal Bay was similar to Teal Bay in its floristic composition. According to the linear combination of all these variables, > 70% of the plots of each study area remained in their original study area in which they were inventoried. This analysis indicates that each study area had a distinct floristic composition. On a scale of ascending importance of cattails, Western Shore was the lowest, followed by Creek, Teal Bay, Upper Shore of Teal Bay and East Bay. Indices of similarity > 70% indicated that the taxa composition of each habitat did not change markedly from 1979 to 1980 (Table 1), although species which grow better on dry or wet land than in flooded areas were more frequent in 1979.

The difference in vegetation between ponds and marsh habitats is attributed to a lack of emergent aquatic vegetation in the former (Table 1). A Graminae belt surrounded both Ponds 1 and 2 and indices of similarity > 80% indicated that their respective taxa composition did not change from 1979 to 1980.

In East Bay, open water accounted for 18% of total habitat area in June-July 1979, and during the entire summer 1980. In August and September 1979, 15% of the habitat was covered by free water areas. Four water regions were delineated in East Bay (Figure 2a). In 1979, only region IV was covered by more than 15 cm of water from May to September. In 1980, regions II, III, and IV were covered by more than 15 cm of water during most of the summer months. In Western Shore, five water regions were delineated in relation to the vegetation belts (Figure 4a). In 1979, only regions IV and V had > 15 cm of water from May to September. In 1980, all regions had > 15 cm of water during all summer months. In 1979, 56% of Teal Bay was covered by > 15 cm of water from June to September. In 1980, the entire habitat was covered by that much water from June to September. The water conditions of Creek varied with the amount of precipitation but there was > 15 cm of water throughout summers 1979 and 1980. Some shores of the ponds were more affected than others by a drop in water level during summer 1979. In 1980, however, all shores

TABLE 1. Floristic composition of seven Muskrat habitats at Luther Marsh, Ontario, in July 1979 and 1980.

Taxon	Percent of Plots in Each Habitat with Taxa Present																		
	East Bay		Western Shore Horsetail Belt		Western Shore Cattail Belt		Western Shore Sedge Belt		Teal Bay Cattail Belt		Teal Bay Spike Rush Belt		Creek		Upper Shore	Pond 1		Pond 2	
	1979	80	79	80	79	80	79	80	79	80	79	80	79	80	80	79	80	79	80
Epilobium sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12	—
Taraxacum sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	20	40
Sium suave	3	1	20	12	83	58	43	29	92	60	38	18	24	—	52	—	—	32	—
Eleocharis sp.	42	30	44	40	25	67	43	29	68	76	92	92	8	8	13	—	—	20	—
Sagittaria sp.	15	16	52	28	58	50	14	14	84	72	85	81	16	8	13	—	—	—	—
Scirpus validus	2	6	40	40	50	67	29	14	44	44	8	8	40	24	39	4	—	12	12
Polygonum sp.	8	—	36	8	50	8	71	43	12	4	23	—	28	—	—	—	—	—	—
Ranunculus sp.	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sparganium sp.	13	24	16	4	—	—	—	—	—	8	54	27	—	—	—	—	—	—	—
Mentha sp.	2	1	4	4	8	—	14	29	12	40	—	—	48	60	22	—	8	—	—
Equisetum fluviatile	7	5	92	96	83	92	—	—	72	76	4	73	24	40	40	—	—	—	—
Galium sp.	6	2	—	—	17	—	57	—	4	12	—	—	—	—	—	—	—	—	—
Solanum sp.	1	2	8	—	8	—	—	—	4	16	8	—	24	40	65	—	—	—	—
Graminae	87	87	32	48	67	83	29	57	24	56	38	82	44	68	17	96	100	92	100
Typha sp.	80	86	8	8	92	92	14	1	92	96	—	18	52	52	100	—	—	—	—
Carex sp.	—	1	—	—	17	17	57	57	60	40	38	8	80	72	35	4	4	40	—
Solidago sp.	—	1	—	—	8	17	71	14	—	—	—	—	8	—	—	40	20	20	40
Fragaria sp.	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4
Lycopus sp.	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lysimachia sp.	—	—	—	—	8	—	—	—	36	—	—	—	—	—	—	—	—	—	—
Plantago sp.	—	—	—	—	8	—	14	—	—	—	—	—	—	—	—	72	40	—	4
Impatiens sp.	—	—	—	—	17	—	57	—	—	—	—	—	76	32	22	—	—	—	—
Scutellaria sp.	—	—	—	—	33	—	43	57	52	—	15	—	—	—	—	—	—	—	—
Asclepias sp.	—	—	—	—	—	—	29	—	—	—	—	—	—	—	—	—	—	—	—
Equisetum arvense	—	—	—	—	—	—	71	100	—	—	—	—	—	—	—	16	32	17	76
Veronica sp.	—	—	—	—	—	—	—	—	4	—	—	—	4	—	—	—	—	—	—
Trifolium sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	76	36	11	32
Chrysanthemum sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	68	16	12	4
Vicia cracca	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	12	32	40
Cirsium sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	24	12	28
Daucus carota	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	36	28	28

were well supplied with water. No information was recorded relative to water levels in Upper Shore of Teal Bay.

Muskrat Installations and Home Ranges

East Bay — In 1979, the vegetation stands surrounding 11 of 24 houses built in spring were carefully recorded. The majority (82%) of houses were surrounded by mixed Reed Canary Grass (*Phalaris arundinacea*)-cattail stands. In 1980, there were only 14 houses active in May and 67% of them were surrounded by the same mixed stands. The frequency of those stands was not significantly different from that observed in the habitat in 1979 ($\chi^2 = 0.297$, $p > 0.05$) and 1980 ($\chi^2 = 0.601$, $p > 0.05$). In 1979, 10 of the 24 installations were used intensively and maintained by Muskrats during June and July. These were the main dwellings where the young-of-the-year were born and weaned. The other 14 houses were used in early summer by bachelors and in July by first litter juveniles investigating the surroundings of their main dwelling. In 1980, 10 of the 14 houses were main dwellings and the four others were used as shelters by adults of some families or first litter juveniles moving around the main dwelling. In July, another main dwelling, a burrow, was found. The average distance between two main dwellings in 1979 was 87.6 (± 51.4) m and was not significantly different from that in 1980 (87.2 ± 39.3 m; $t = 0.023$, $p > 0.05$). In 1979, two of the main dwellings were built in region II, two in region III and six in region IV. Region I was a dry-out in May and no main dwellings were built there. The reachable free water areas covered 19 280 m^2 and 19% of the covered area was in region II, 31% in region III and 50% in region IV (Table 2). The hypothesis that muskrats utilize open water areas in exact proportion to their relative importance in each region of the study area was tested by the chi-square test. No significant difference existed between the observed occurrence of main dwellings in each region and the one expected according to the proportion of free water areas in each region of the study area ($\chi^2 = 0.406$, $p > 0.05$). In 1980, the proportion of main dwellings / region was also similar to the proportion of open water areas in each region ($\chi^2 = 0.119$, $p > 0.05$; Table 2). In early summer of both years, Muskrats were concentrating their activities by their main dwellings (Figure 2a, 3a). The average area of 1979 June-July home ranges (484 ± 238.4 m^2) was not different from that of 1980 (302 ± 202.3 m^2; $t = 1.664$, $p > 0.05$). No home range in early summer 1979 or 1980 had < 25% of either open water or vegetation and the average home range had a ratio of vegetation:open water areas of 1:1 (Table 3). The average number of houses used by a family in June-July was 1.5(± 0.7) in 1979 and 1.2(± 0.6) in 1980 ($t = 1.867$, $p > 0.05$).

Building activity occurred in late summer 1979 and there were 44 active houses in August-September. The observed occurrence of main dwellings per region was significantly different from the one expected according to the proportion of open water areas in each region of the study area ($\chi^2 = 11.097$, $p < 0.05$; Table 2). Then, animals concentrated their building activity towards the edge of the lake. They were "over-using" region IV, the region where free water areas were surrounded by vegetation stands with > 15 cm of water. Only eight new houses were built in August-September 1980 and a total of 23 installations were used by Muskrats in late summer. The proportion of dwellings in each region was not significantly different from the proportion of open water areas found in each region ($\chi^2 = 0.790$, $p > 0.05$; Table 2). The average distance between the main dwellings and the new houses was 39.6 (± 33.1) m in 1979 and 33.4 (± 19.7) in 1980 ($t = 1.460$, $p > 0.05$). In 1979, the late summer home ranges (Figure 2b) were significantly larger than early summer ones ($t' = 2.268$, $p < 0.05$) and averaged 1112 (± 842.7) m^2. In 1980, the average late summer home range was 470 (± 182.7) m^2 (Figure 3b) and was not significantly larger than that of June-July ($t = 1.664$, $p > 0.05$). It was, however, significantly smaller than August-September 1979 ($t' = 2.361$, $p < 0.05$). There was no summer home range in 1979 or 1980

TABLE 2. Distribution of Muskrat dwellings and relative importance of open water areas (%) in East Bay in summers 1979 and 1980.

	June-July				August-September			
	1979		1980		1979		1980	
Water Regions	Dwellings	Open Water Areas %	Dwellings	Open Water Areas %	Dwellings	Open Water Areas %	Dwellings	Open Water Areas %
I	0	0	1	5	0	0	1	5
II	2	19	2	18	2	8	4	18
III	2	31	3	29	6	35	5	29
IV	6	50	5	48	36	57	13	48

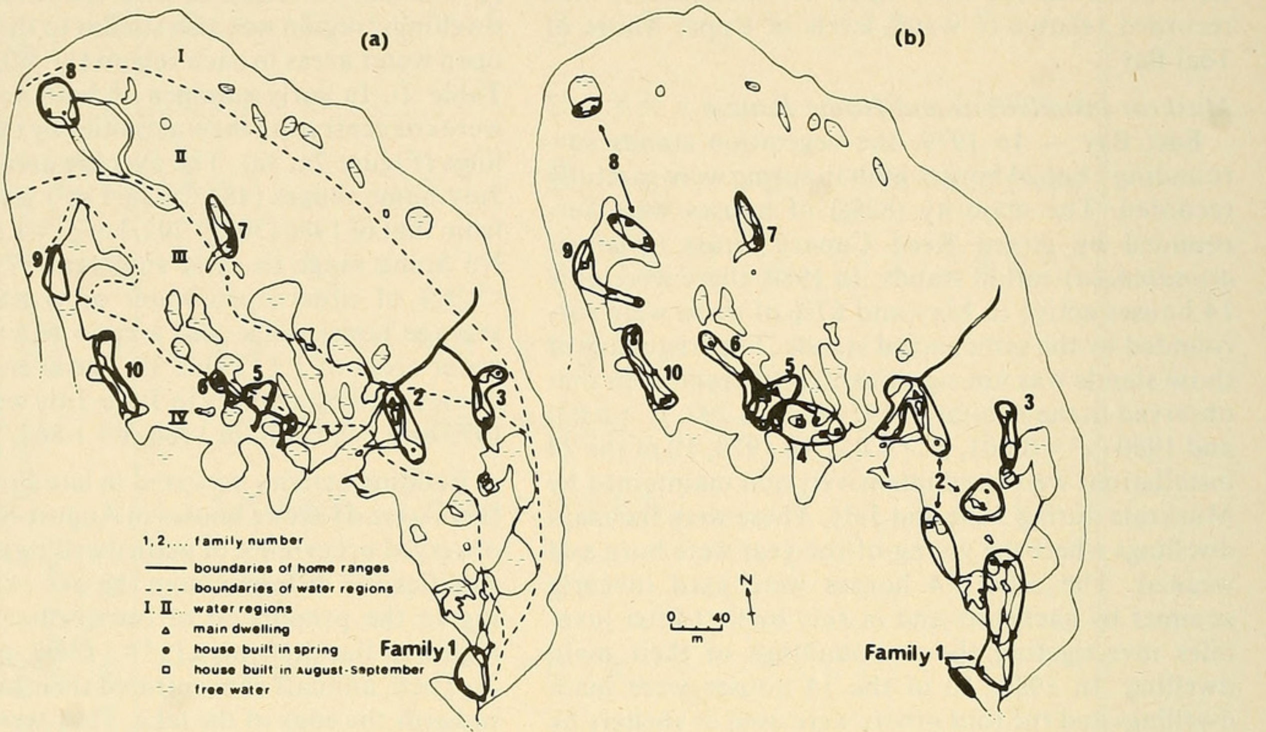

FIGURE 2. Home ranges of families inhabiting East Bay in summer 1979: a) June-July home ranges; b) August-September home ranges.

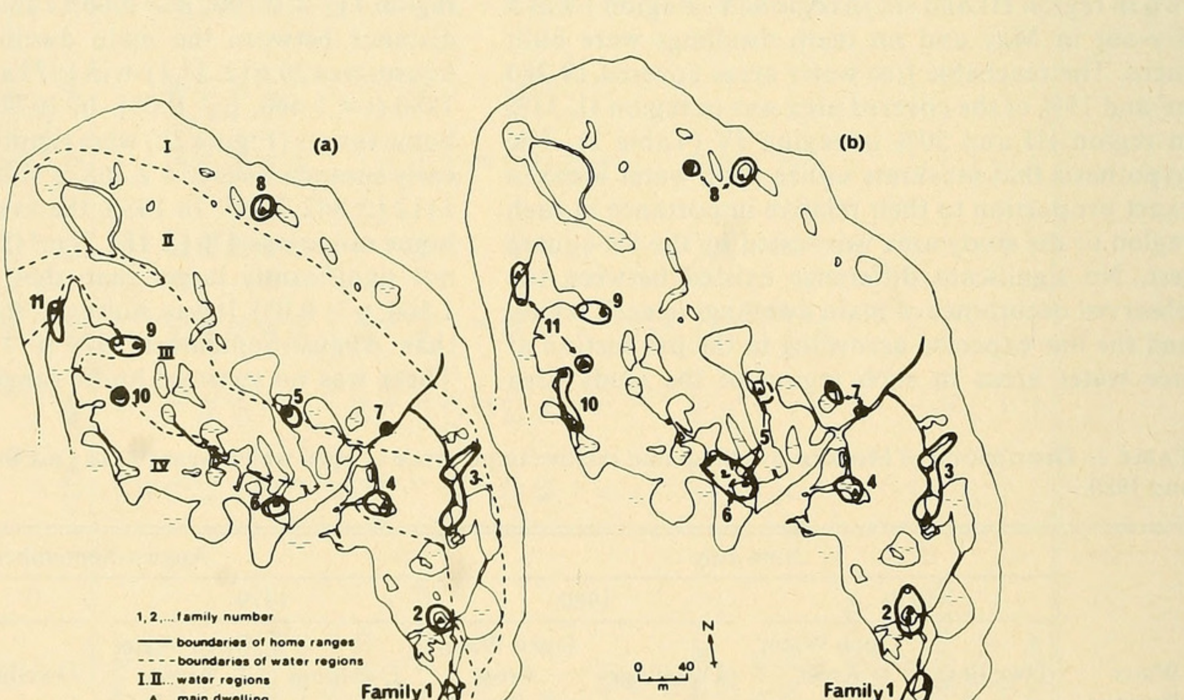

FIGURE 3. Home ranges of families inhabiting East Bay in summer 1980: a) June-July home ranges; b) August-September home ranges.

TABLE 3. Average composition of early and late summer Muskrat home ranges in East Bay in 1979 and 1980.

	June-July				August-September			
	1979		1980		1979		1980	
	Average Area (m^2)	S.D.	Average Area (m^2)	S.D.	Average Area (m^2)	S.D.	Average Area (m^2)	S.D.
Vegetation Stands	213.1	121.8	154.3	119.3	599.4	493.3	244.6	113.0
Open Water Areas	270.9	185.0	148.4	104.1	512.9	368.3	225.2	100.0

with < 25% of either open water or vegetation. In August-September of both years, water covered 50% of the area of the average home range (Table 3). There were 3.9 (± 1.7) houses/family in late summer 1979. This average was significantly higher than in early summer 1979 ($t' = 4.128$, $p < 0.005$). In late summer 1980, there were 2.2 (± 0.7) houses/family. This average was significantly higher than in early summer 1980 ($t = 3.382$, $p < 0.005$) but significantly lower than in late summer 1979 ($t' = 2.943$, $p < 0.005$).

Western Shore — Three of four installations built in spring 1979 were main dwellings: one house in the cattail stands, and two burrows in the horsetail stands. At the end of July, the surroundings of the burrows were dried out and animals relocated in houses built approximately 40 m from shore, in water > 70 cm deep. During summer 1979, two captures occurred in the sedge belt, nine in the cattail belt and 16 in the horsetail belt. The observed occurrence of captures in each vegetation belt was not different from the expected occurrence of captures for each vegetation belt ($\chi^2 = 0.415$, $p > 0.05$) and Muskrat appeared to use the belts at random. The summer home ranges averaged 2283 (± 816) m^2 (Figure 4b).

In spring 1980, four of five installations were main dwellings: three houses in the cattail belt and one burrow in the horsetail belt. New building occurred in August and a total of nine installations were used by Muskrats: six in the cattail belt and three in the horsetail belt. The number of installations in each vegetation belt was not distributed proportionately to occurrence of vegetation belts ($\chi^2 = 5.577$, $p < 0.05$) which implies that the cattail belt was "over-used." However, no significant difference existed between the observed occurrence of installations in each water region and the one expected according to the proportion of water regions in the study area ($\chi^2 = 1.153$, $p > 0.05$). Two of 17 captures prior to August occurred in the horsetail belt and 15 in the cattail belt. The observed occurrence of captures in each vegetation belt was different from the expected occurrence of captures in each belt and Muskrat captures were not distributed proportionately to occurrence of vegetation belts ($\chi^2 = 30.547$, $p < 0.005$). In August and September, 31 of 46 captures occurred in the cattail belt, 13 in the horsetail belt, and two in the sedge belt. Again, Muskrat captures were not distributed proportionately to occurrence of vegetation belts ($\chi^2 = 34.203$, $p < 0.005$) and Muskrat were concentrating more their activities in the cattail belt than in the others. Trapping results and field observations occurred in the vegetative portion of the habitat and the proportion of free water areas used by muskrats in their movements from one site to another is unknown. However, using an estimate of 50% water and 50% vegetation based on East Bay data, home range averaged 1682 (± 783) m^2 (Figure 4c).

Teal Bay, Creek and Upper Shore of Teal Bay: In 1979, Teal Bay and Creek were used by only one family which established its house in the cattail stands of the creek. The same house was used in 1980 by one family and another main dwelling was found in Teal Bay, in a clump of willows (*Salix* sp.) at the junction of the cattail and spike rush belts. In Upper Shore of Teal Bay, three main dwellings were found among cattail stands. One of them was found destroyed in July and Muskrats built a new one among cattail and bulrush stands. Captures and feeding platforms were restricted to the immediate site of the houses and the area covered by the movements of the animals was not determined in any of these habitats.

Ponds: In early summer 1979, seven burrows were found in Pond 1 but only two were still active in August. All others were abandoned as soon as their entrances became exposed by the drop in water level. In August, two more burrows were built in the shore of the island. Muskrats were using trails up to 10 m long leading from their burrows to feeding grounds. The home range was estimated at 3900 m^2. It had 2100 m^2 (54%) of vegetation stands and 1800 m^2 (46%) open water.

In 1979, in Pond 2, two burrows, located on the only shore well supplied with water, were used during all summer months. Muskrats were using trails up to 8 m long leading from their burrows to feeding grounds. Their home range was estimated at 3200 m^2. Vegetation stands covered 1700 m^2 (53%) and open water, 1500 m^2 (47%).

In 1980, Ponds 1 and 2 were used by the same family. Burrows that had been used from May to

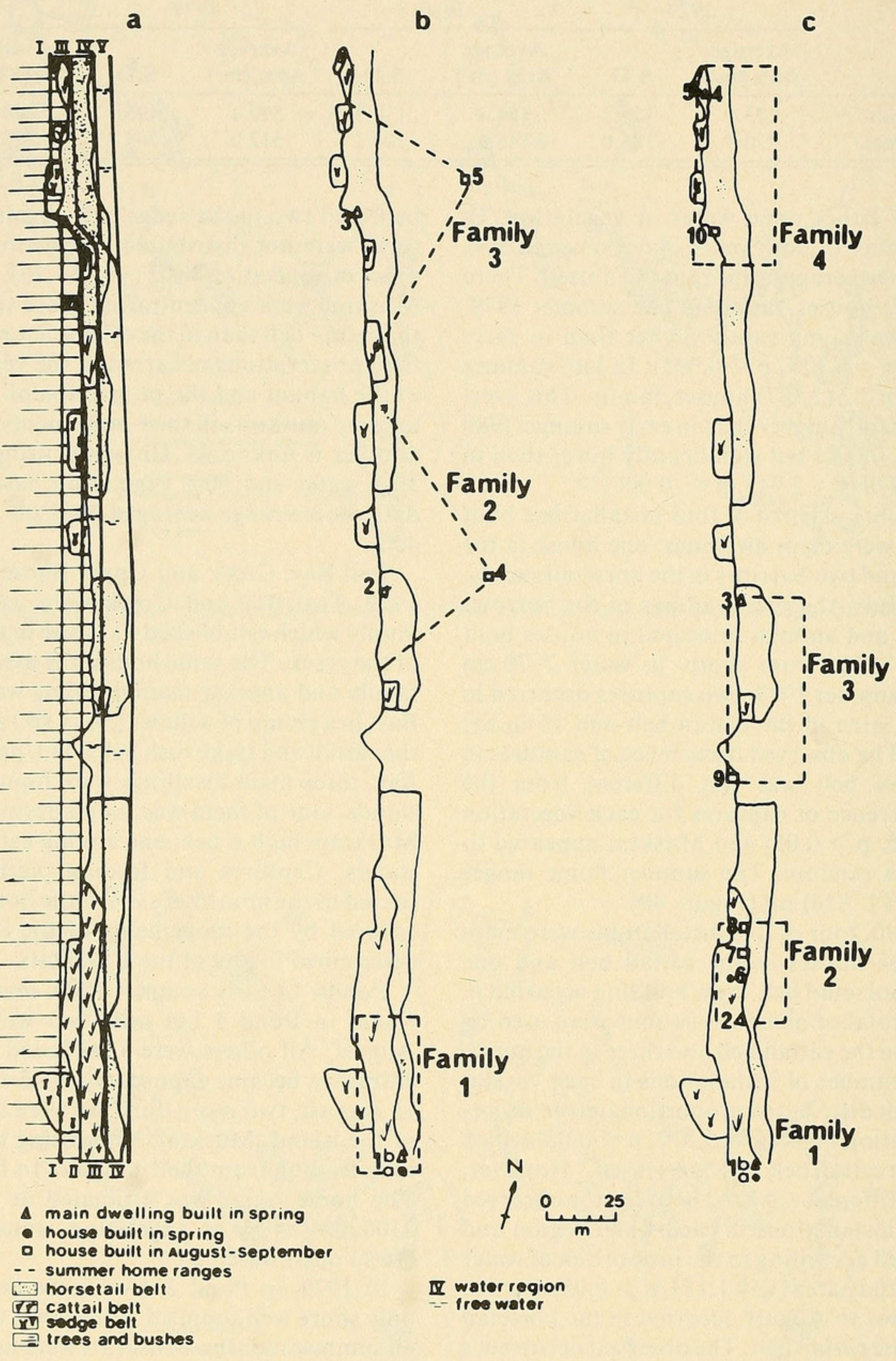

FIGURE 4. Vegetation belts and water regions (a) and location of muskrat installations and home ranges of families inhabiting Western Shore in summers 1979(b) and 1980(c).

September 1979 were used again. The home range was estimated at 7100 m². Vegetation stands covered 3800 m² (54%), and open water, 3300 m² (46%).

Food Habits

Sufficient information to study Muskrat food habits was obtained from East Bay and Western Shore. In East Bay, cattail and Reed Canary Grass (*Graminae*) had the highest frequency indices and were also important Muskrat food items (Table 4). Cattail was always abundant on the feeding platforms but its forage ratio decreased from May to August (Table 4).

In Western Shore, in 1979, all species, except bulrush, were in proportions lower than their availability (Table 4). In 1980, Muskrat food habits were also diversified but the frequency of cattail on feeding platforms at different periods of the year was always very high and the species was used in proportions greater than its availability (Table 4).

Muskrat Populations

In 1979 and 1980, most females in each habitat had two litters. In 1979, the number of first litter juveniles captured per female averaged 5.7(± 2.3) in East Bay (10 families) and 5.0(± 2.0) in Western Shore (three families). No significant difference existed between these two values (t = 0.473, $p > 0.05$). It appeared that females which had a second litter in East Bay (six families) produced more young than in Western Shore (three families) and the averaged number of second litter juveniles captured per family was 3.8(± 2.5) and 1.3(± 1.5) respectively (t = 1.564, $p > 0.05$). In 1980, an average of 6.6 (± 2.4) first litter young were captured per family in East Bay (11 families), 5.7(± 2.9) in Western Shore (four families) and 5.7 (± 0.6) in Upper Shore of Teal Bay (three families). These values were not significantly ($p > 0.05$) different from each other. The average number of second litter juveniles captured per family in East Bay (eight families) and Western Shore (three families) was 5.4 (± 2.5) and 5.3 (± 4.0) respectively (t = 0.049, $p > 0.05$). Few second juveniles were captured in Upper Shore of Teal Bay because of a lack of favorable trap sites in late summer 1980 and the trapping results relative to this age were not considered for that habitat.

Juveniles represented between 66 and 92% of all trapped populations (Table 5). When all muskrat populations of all habitats were grouped together, juveniles comprised 74.4% of the trapped population in 1979 and 85.5% in 1980. The sex ratio of most population segments was even. When all populations were grouped together, adult sex ratios favored males ($\chi^2 = 5.333$, $p < 0.05$) in 1979 but were even in 1980. First litter sex ratios were even in 1979 ($\chi^2 = 2.539$, $p > 0.05$) but departed significantly from a 1:1 ratio in 1980 ($\chi^2 = 6.931$, $p < 0.05$). Second litter juveniles had

TABLE 4. Muskrat food habits in East Bay and Western Shore in 1979 and 1980 (A = % availability in the habitat; 0 = % occurrence on the feeding platforms; FR = forage ratio).

	28 May- 6 June 1979 24 Platforms			25 June 29 July 1979 51 Platforms			28 May- 10 June 1980 32 Platforms			16 June- 22 July 1980 48 Platforms			29 July- 27 August 1980 33 Platforms			12 June- 12 August 1979 14 Platforms			16 May- 16 June 1980 9 Platforms			23 June- 17 July 1980 9 Platforms		
	A	O	FR	A	O	FR	A	O	FR	A	O	FR	A	O	FR	A	O	FR	A	O	FR	A	O	FR
Typha sp.	85	100	1.2	80	74	0.9	61	44	1.5	86	81	1.0	81	64	0.8	32	21	0.7	26	78	3.1	31	33	1.1
Equisetum sp.	9	8	0.9										5	6	1.2	84	28	0.3	88	67	0.8	94	62	0.7
Graminae	78	29	1.4	87	59	0.7	92	69	0.7	87	52	0.6	88	21	0.2	41	14	0.3	63	67	1.1	58	22	0.7
Eleocharis sp.	37	33	0.9	7	23	3.3	7	16	2.2	30	29	1.0	22	27	1.2	68	7	0.1	17	33	1.8	45	22	0.5
Sagittaria sp.				15	2	0.1				16	2	0.1				46	21	0.4						
Sparganium sp.				13	2	0.1							28	21	0.8									
Scirpus sp.				2	2	1.0				6	2	0.4				41	50	1.2	23	11	0.4	43	78	1.8
Carex sp.																			15	11	0.7	13	11	0.8
Polygonum sp.																						13	11	0.8

TABLE 5. Muskrat captures in Luther Marsh study areas in summers 1979 and 1980.

Age and Sex Classes	East Bay		Western Shore		Teal Bay & Creek	Teal Bay	Creek	Upper Shore of Teal Bay	Pond 1		Pond 2
	1979	1980	1979	1980	1979	1980	1980	1980	1979	1980	1979
Adults	36	23	6	6	2	1	1	3	2	2	2
Male	*25	12	4	4	1	—	—	1	1	1	1
Female	11	11	2	2	1	1	1	2	1	1	1
First Litter	57	73	15	22	3	9	3	18	6	9	8
Male	33	*49	*12	7	2	5	2	10	2	7	3
Female	24	24	3	13	1	4	1	6	4	2	5
Unknown	—	—	—	2	—	—	—	2	—	—	—
Second Litter	22	38	4	15	1	3	—	5	—	4	4
Male	12	23	3	9	1	2	—	3	—	2	1
Female	10	15	1	6	—	1	—	2	—	2	3
Third Litter	—	9	—	—	—	—	—	—	—	—	—
Male	—	7	—	—	—	—	—	—	—	—	—
Female	—	2	—	—	—	—	—	—	—	—	—

*Sex ratio significantly different ($P<0.05$) from 1:1.

an even sex ratio in 1979 ($\chi^2 = 0.322$, $p > 0.05$) and 1980 ($\chi^2 = 2.615$, $p > 0.05$).

Estimates of Population Size and Density

In fall 1978, 15 female adults were autopsied and 186 placental scars were counted (12.4 scars per female). In fall 1979, 424 scars were counted for 33 breeding females (12.8 scars per female). Since most of the females of the studied habitats had two litters, these results indicate that female Muskrats produced an average of 6.3 embryos per litter. This average was applied to the live-trapping results to estimate population size in each habitat. The population of East Bay was the largest, followed by the populations of Western Shore and Upper Shore of Teal Bay, Teal Bay and Creek and Ponds (Table 6).

These population estimates were used in a determination of maximum relative densities which would have occurred if all animals were alive (Table 6). The relative densities were calculated with respect to the habitable portion of the habitats, according to water levels and open water areas. With the exception of Pond 2, there were between 19.3 and 22.4 animals/ha in 1979 and between 18.1 and 22.6 animals/ha in 1980.

Population densities can also be estimated by the areas covered by the home range (Table 6). East Bay populations had markedly more animals/ha of home range (> 100 animals) than in any other populations (< 80 animals).

Yearly Muskrat Population Changes

From spring 1979 to spring 1980, growth rates of 1.1., 1.3, 2.0, and 1.0 were obtained for breeding muskrat populations of East Bay, Western Shore, Teal Bay and Creek, and Pond 1 respectively. The

TABLE 6. Estimates of Muskrat population size and density in Luther Marsh study areas in summers 1979 and 1980.

Study Area	Maximum Population Estimate	Muskrat/ha of Habitat	Muskrat/ha of Home Range
1979			
East Bay	121*(137)	21.2	109
Western Shore	44	19.3	65
Teal Bay + Creek	15	22.4	—
Pond 1	8	20.5	20
Pond 2	15	46.9	47
1980			
East Bay	148	23.5	287
Western Shore	52	22.6	77
Teal Bay	15	18.1	—
Creek	8	—	—
Pond 1	15	21.1	21
Upper Shore of Teal Bay	44	—	—

*Value obtained when one considers that thae adult population was made up of only 10 breeding pairs. The value within brackets includes adult male bachelors.

Muskrat population of Pond 2 was completely exterminated from 1979 to 1980. Considering that all populations had a large number of juveniles in 1979, a considerable reduction of the densities occurred over winter 1979-80.

In fall 1978, 159 carcasses were analysed and there were 8.6 juveniles per female adult. Considering that there were 12.4 placental scars per female, the juvenile mortality rate from birth to the fall trapping season was estimated at 30.6%. In fall 1979, there were 8.1 young and 12.8 placental scars per adult female in a sample of 338 carcasses, which give an estimate of mortality between birth and the fall trapping season of 36.7%. The juvenile mortality over the two summers averaged 33.6%.

The reduction of Muskrat populations over winter was calculated according to the maximal summer population estimates (Table 6), the sex ratio of each population segment and the average summer survival rate of the juveniles. A 10% adult mortality during summer (Errington, personal communication *in* Olsen 1959), an equal mortality for males and females and an immigration rate equalled to the emigration rate were also assumed. In East Bay, the surplus of male adults in summer 1979 consisted of bachelors which left the study area over summer. Thus, only 10 males were considered as part of the summer adult population. Also, the winter natural mortality rate in this habitat was calculated according to a potential of 12 breeding pairs in East Bay in spring 1980 (one female died in early summer from Tyzzer's disease). The winter reduction ranged from 60 to 75% in East Bay, Western Shore, Teal Bay and Creek, and Pond 1 (Table 7). The average was 68.2(± 6.4)%. Reduction of male and female populations averaged 65.3(± 13.1)% and 68.3(± 6.5)% respectively. Male populations were not reduced significantly more than female populations ($t = 0.407$, $p > 0.05$).

Life Table

If the summer mortality rates of adults and juveniles are fixed at constant rates of 10 and 33.6% respectively, and the winter kill is 68.2%, a hypothetical life table can be built for a cohort of 1000 juveniles (Table 8). More than half the animals would die during the fall and winter months following their birth and only 21.1% would be present during the first breeding season. Maximum longevity would be 60 months. A survivorship curve for such a population would be characterized by a high mortality during the summer months of the first year and during each winter season (Figure 5).

TABLE 7. Winter reduction (%) of fall muskrat populations in Luther Marsh study areas in 1979-80.

Habitat	% Reduction		
	Male Population	Female Population	Total Population
East Bay	71.4	71.4	71.4
Western Shore	66.7	80.0	75.0
Teal Bay + Creek	60.0	60.0	60.0
Pond 1	50.0	75.0	66.7

TABLE 8. Hypothetical muskrat life table for a cohort of 1000 juveniles at Luther Marsh.

Age (months) x	Survival lx	Mortality dx	Mortality Rate qx	Survival Rate px
5	1000	336	0.336	0.664
5	664	453	0.681	0.319
12	211	21	0.099	0.901
17	190	130	0.684	0.316
24	60	6	0.100	0.900
29	54	37	0.685	0.315
36	17	2	0.118	0.882
41	15	11	0.733	0.267
48	5	1	0.200	0.800
53	4	3	0.750	0.250
60	1	—	—	—
65	—	—	—	—

Discussion

Muskrat houses were found in areas affording two essential constituents: 1) heavy building material and 2) enough water to cover house channels and provide Muskrats with access to their house beneath the water's surface. According to water conditions which prevailed in regions where intensive building occurred and those where abandonment of houses was observed, a minimum of 15 cm of water was necessary to accomodate lodge-building Muskrats. This estimate is in agreement with the findings of Bellrose and Brown (1941). Abandonment of houses was observed with a decrease in water level (Coulter 1948; Westworth 1974; Danell 1978). Therefore, water plays the role of a dispersion factor. However, the selection of cattail stands by Muskrats in Western Shore 1980 suggests that, when water levels are > 15 cm deep everywhere within a habitat, vegetation stands become a dispersion factor. Therefore, the suitability of a site for Muskrat building activities depends on the simultaneous presence of heavy emergent vegetation and water. Although previous studies pointed out that muskrats intensively use burrows in summer (Dilworth 1966; Philips 1979), the present study indicates that Muskrats used such structures as an alternative to houses only when heavy emergent vegetation was absent and/or water depths were < 15 cm.

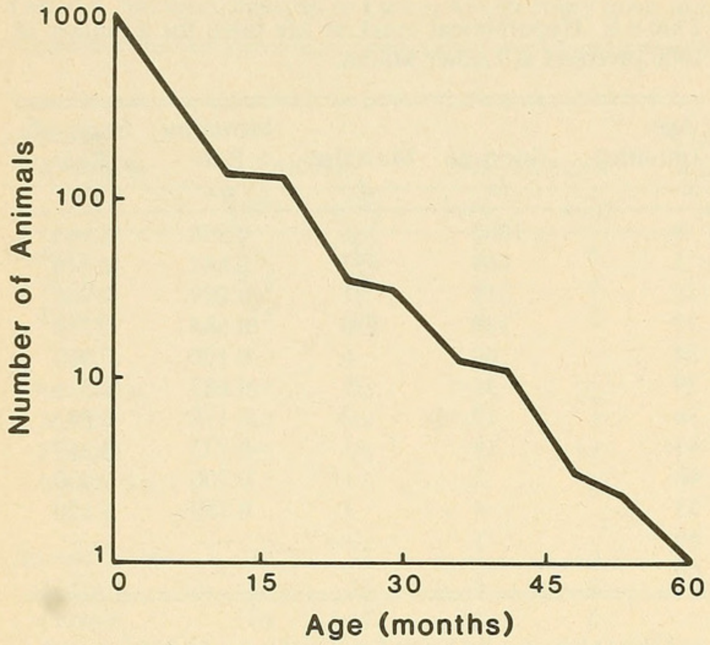

FIGURE 5. Hypothetical survivorship curve of a cohort of 1000 juveniles at Luther Marsh.

Until now, no one has ever quantified the proportions of a home range in water and vegetation stands and thus determined the composition of suitable Muskrat habitat. In this study, the average home range had a ratio of vegetation stands:open water areas of 1:1 and it is suggested that vegetation stands cannot be dissociated from water areas when one considers the composition of a suitable habitat. According to previous studies (Sather 1958; Erickson 1963; Neal 1968), summer home ranges can be enclosed by a circle 45 to 60 m in diameter. In this study, such a circle would have overestimated home range sizes by including areas unused by Muskrats, such as vegetation stands isolated from water areas and thus inaccessible. Furthermore, in this study, late summer home ranges often consisted of disconnected areas, each occupied by some family members concentrating their activities around the installations that they built. The minimum home range sizes determined in this study would appear to be realistic in that they measured areas intensively used by Muskrats and not areas traversed by animals in the re-establishment of their areas of daily activity.

Home range expansions during the summer could be due to juveniles which were forced to leave the breeding lodge before the birth of the next litter (Errington 1961). In this study, home range expansions occurred in late July. At this time of the year, second litter juveniles started to investigate the immediate surroundings of the main dwelling and first litter juveniles re-established themselves in new homes. However, with a decrease in the water level in late summer 1979, several vegetation stands became inaccessible. An expansion of the home ranges could have served to re-establish a balance of water to vegetation and to avoid frictions usually observed in degraded environments (Errington 1951, 1954; Neal 1968).

Muskrat food habits were related to three factors acting simultaneously: 1) diversity of the flora; 2) movements of the animals; and 3) preference of the animals. When possible, muskrats concentrated their activities near their installations. Also, food habits reflected the floristic composition of the surrounding stands. This explains the high occurrence of cattail on the feeding platforms. When the surroundings had a diversified floristic composition, as in Western Shore, there was a larger number of plants with a high percentage of occurrence on feeding platforms. When vegetation and water did not make up, together, the surroundings of Muskrat installations, Muskrat food habits became more diversified. Captures in Western Shore, 1979, showed that feeding activities there occurred far from the installations and animals used the different vegetation stands as they encountered them. Finally, a variation in the forage ratio of the plants, such as cattail, indicated that there was some seasonal preference in plant food. This was also noticed by Butler (1940) and Takos (1947).

In 1979 and 1980, most females had two litters in all study areas. This agrees with other studies carried out in temperate Canada and the adjacent United States, e.g. McCann (1944) in Minnesota, Gashwiler (1950) in northern Maine, Fuller (1951) in the Athabasca-Peace Delta, MacLeod and Bondar (1952) in southern Manitoba and Stewart and Bider (1974) in southern Quebec. Bellrose and Low (1943) and Arata (1959) have suggested that litter size may vary with environmental conditions. At Luther Marsh, environmental conditions might have had an effect on the number of animals born alive or surviving during the few hours or days following their birth. Trapping results indicated that juveniles made up a larger portion of the population in 1980 than in 1979. In Western Shore, although no significant difference was observed between the average number of juveniles captured per family in 1979 and 1980 (because of small sample size), the fact remains that 1980 families produced four more second litter juveniles than the 1979 families. Considering that 1980 families were located in an environment more favorable with respect to vegetation type and water conditions, a higher productivity of juveniles would have been expected as an outcome. Also, the difference between captures of East Bay and Western Shore in 1979, although not found statistically significant, could be meaningful on a long term basis, if the same environmental situation was repeated over many years in each habitat. In 1980, the similarity between captures of juveniles of East Bay, Western Shore, and Upper Shore of Teal Bay appears to have been a result of families of all habitats having been subject to similar environmental conditions.

During summers 1979 and 1980, adult populations usually had an even sex ratio. This was also found by Aldous (1947), Coulter (1948), and Erickson (1963). An even sex ratio and the fact that only one adult male and one adult female were captured per main dwelling supports the idea of a monogamous breeding system (Stevens 1955; Sather 1958; Mathiak 1966). The general trend of the juvenile populations was also towards an even sex ratio. That result agrees with the findings of McDonnell (1979) and with the theory of Fisher (1930) who concluded that, at equilibrium, an optimal organism should allocate half its reproductive effort to progeny of each sex.

Very few publications concern Muskrat densities in summer. An average of 21 animals/ha was obtained in all habitats in 1979 and 1980. This is markedly smaller than the 123 and 55 Muskrats/ha reported by Lynch et al. (1944) and Vincent and Quéré (1972) respectively for more moderate climes, but is similar to 21.7 Muskrats/ha estimated by McDonnell (1979) for Luther Marsh. Previous studies correlated population densities to the type of vegetation present in a habitat (Bellrose and Brown 1941; Errington 1941, 1948; Alexander 1955). A vegetation-Muskrat density relationship becomes apparent when one considers the density of animals/ha of home range. In this respect, there were markedly more animals in East Bay per unit area than in any other habitat. This observation agrees with Smith and Jordan (1976) who associated the largest concentrations of Muskrats/ha with the habitat richest in cattails.

The summer survival rate was very high at Luther Marsh and was greater than the values reported by Baumgartner and Bellrose (1943), McCann (1944), Alexander (1955), Dorney and Rusch (1953) and Olsen (1959). On the other hand, the winter reductions estimated at Luther Marsh were very high, compared to 38 and 44% reported by Errington (1939) and Stewart and Bider (1974) respectively. Relatively low summer population densities could have favored a high summer survival rate of the juveniles and concurrently, allowed too high a concentration for the harsh winter environment at Luther Marsh. Intraspecific strife, starvation and disease might have occurred in animal groups subjected to restricted winter feeding grounds (Errington 1954, 1961).

According to the life table, 99.5% of a cohort of 1000 juveniles would not reach four years of age. Errington (1961) estimated the Muskrat life span to be three to four years but he had no numerical values to substantiate his conclusions. The shape of the survivorship curve implies a constant rate of mortality, independent of age. Although many Muskrats die in their first year of age, the reduction did not produce a concave survivorship curve as hypothesized by Giles (1978). Probably no real population has a constant survival rate throughout its whole life span and the sigmoid curve reported in studies of other rodents (Caughley 1966; Barkalow et al. 1970) might be applicable also to Muskrat populations. Animals in their prime might be more capable of coping with the environmental conditions than are older ones, and the slope of the corresponding portion of the survivorship curve might be less steep in the real world. Data collected in a minimum five-year study would provide a more reliable survivorship curve.

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