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**Effects of Regulated Lake Levels on Muskrats
in Voyageurs National Park, Minnesota**



United States Department of the Interior

**National Park Service
Midwest Region**

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EFFECTS OF REGULATED LAKE LEVELS ON MUSKRATS
IN VOYAGEURS NATIONAL PARK, MINNESOTA

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Abstract.

Muskrats (*Ondatra zibethicus*) were studied as part of a comprehensive project by the National Park Service to determine effects of current water management programs on the aquatic biota of Voyageurs National Park. Water levels in Rainy Lake (minimal drawdown) are fairly stable with average fluctuations of one meter annually. Namakan Reservoir (significant drawdown) experiences fluctuations averaging 2.7 meters annually with high water through summer and early fall and a winter drawdown. Muskrat habitat and population characteristics in the two water regimes were compared from 1985-1987. Radiotelemetry was used to assess differences in mortality and long distance dispersal (1984-1987). Standard body measurements did not differ between areas. Significantly greater muskrat density was indicated in the minimal drawdown area for spring 1986 sign survey, fall 1986 trapnight success and house counts for 1985-86 and 1986-87. All other density estimates indicate greater numbers in the minimal drawdown area, although findings were not statistically significant. Overwinter survival of radioed muskrats was very low in both areas, especially during freeze-up in early winter. Impacts on muskrats would be reduced if a fluctuation schedule was implemented that has a more natural amplitude, a partial drawdown of about 1 m in early fall, and a further drawdown occurring over a short time in winter similar to that now occurring in Rainy Lake. This would allow time for muskrat houses to be constructed in deeper water, keep food shortage time to a minimum, and thus decrease above-ice foraging time and exposure to predators.

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INTRODUCTION

Muskrats are known to be adversely affected by severe water level fluctuations (Errington 1939; Bellrose and Brown 1941; Bellrose 1950; Donahoe 1966; Proulx and Gilbert 1983). In Voyageurs National Park, Minnesota (Fig. 1), a population of muskrats has historically been supported. Water levels on the park's major lakes are controlled by privately-owned dams located outside park boundaries. A dam on Rainy River, the outlet for Rainy Lake, has been in operation since 1909, while the dams regulating the levels of Namakan Reservoir (Kabetogama, Namakan, and Sand Point lakes) have been operating since 1914. The lake levels are regulated by the International Joint Commission (IJC) for the authorized purposes of navigation, hydroelectric power, fish spawning, flood control, and pollution abatement (Kallemeyn 1987).

Before the dams were built, natural annual fluctuations were probably 1.9 meters throughout this chain of lakes (Flug 1986). Currently, Rainy Lake water levels fluctuate one meter annually (minimal drawdown), while Namakan Reservoir fluctuates approximately 2.7 meters (Flug 1986). The significant drawdown in Namakan Reservoir occurs during winter with progressive declines continuing through February and March (Fig. 2). Food sources of the muskrat, including cattail (Typha sp.), burreed (Sparganium sp.), sedges (Carex sp.), grass (Gramineae), smartweed (Polygonum sp.), horsetail (Equisetum sp.), bulrush (Scirpus, sp.), and wild rice (Zizania aquatica), are left dry and frozen at the harshest time of year. Water rises quickly in late April and May when northern muskrats are having their first litters of the year (Errington 1963; Willner et al. 1980). The highest water levels are maintained from June through September. Flug (1986) estimated that natural water fluctuations in Namakan Reservoir would have less amplitude, with highest water in June and lowest water throughout the fall and winter (Fig. 3).

The mandate of the National Park Service is to conserve in an unimpaired state the scenery, natural and historic objects, and wildlife within National Park lands for the benefit of future generations (Organic Act of 1916, 39 Stat. 535). In 1983, Voyageurs National Park began a broad-based research project to determine the effects of the regulated lake levels on the aquatic biota of the park. The information obtained would be used to formulate recommendations for alternate regulatory systems and serve as baseline data for future studies (Kallemeyn 1983).

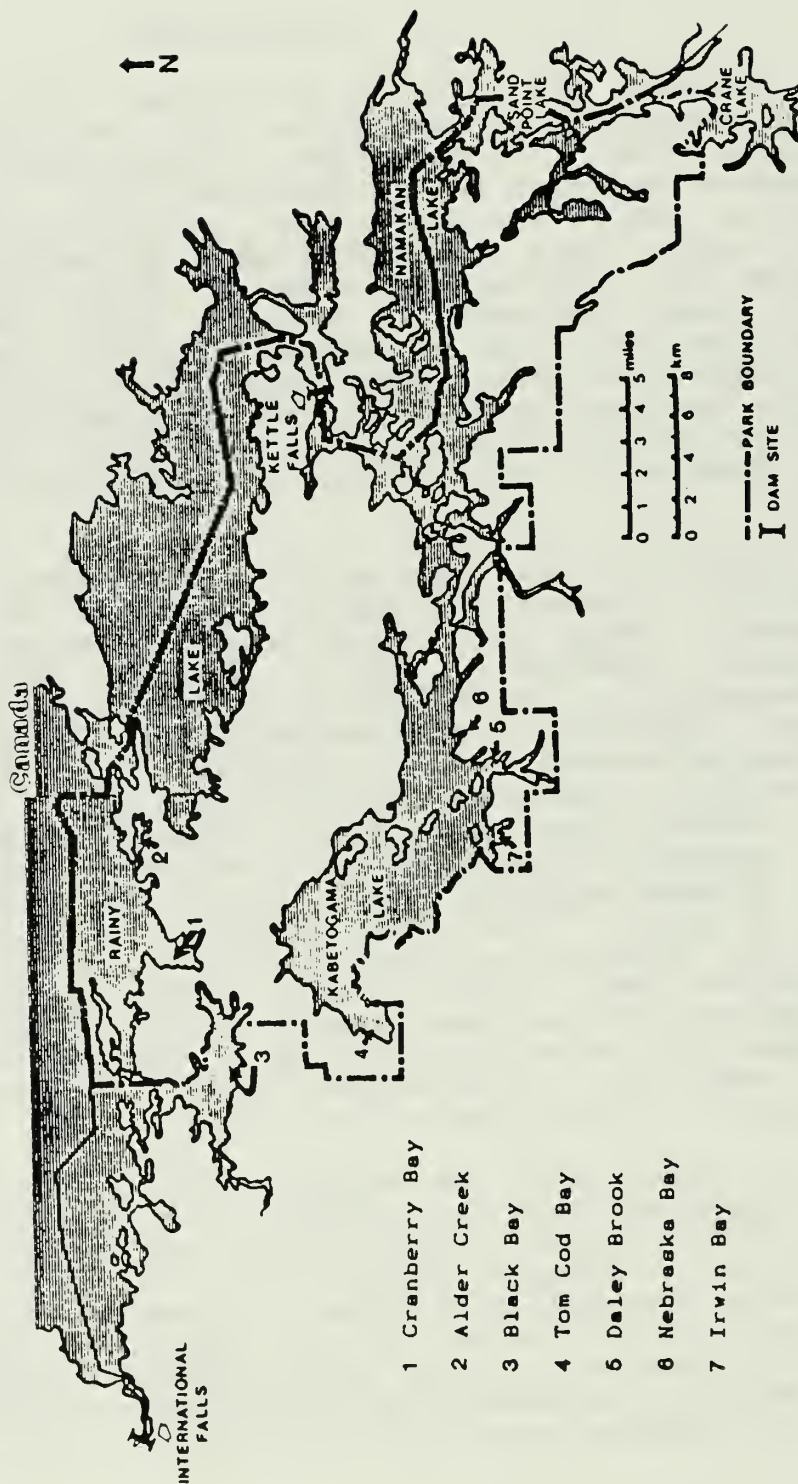


Fig. 1. Voyageurs National Park and study site locations for evaluating the effects of regulated lake levels on the park's muskrat population.

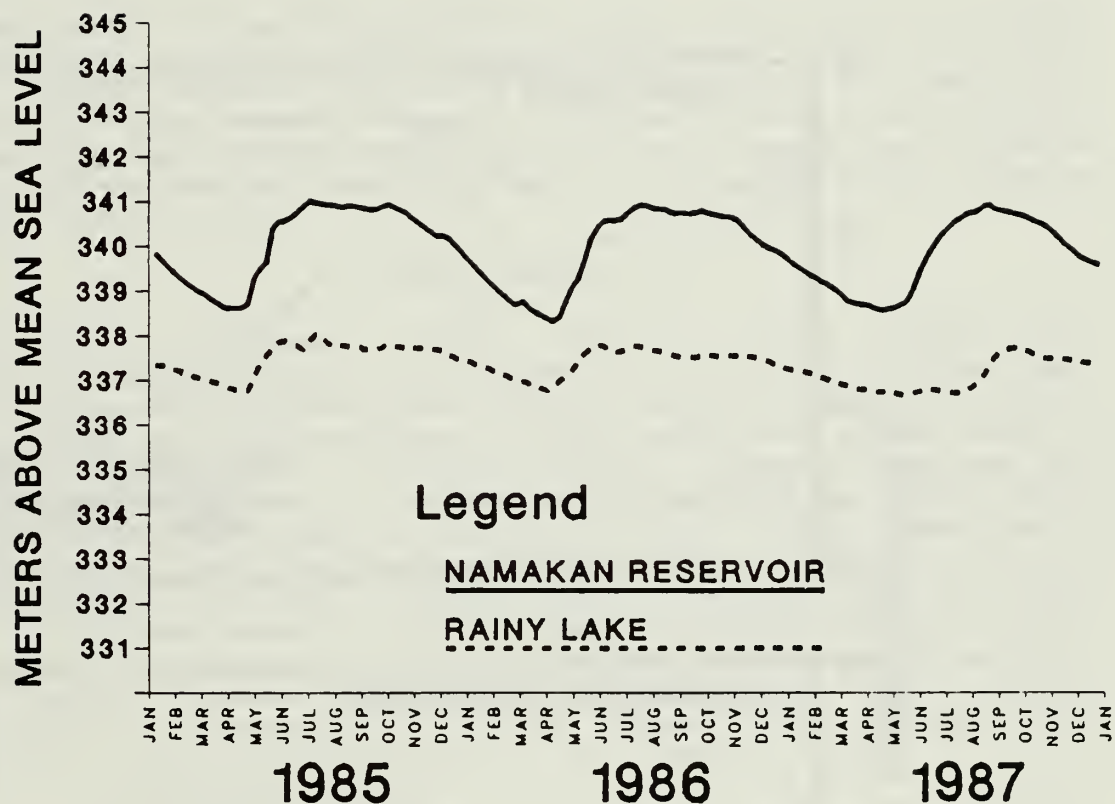


Fig. 2. Weekly average water levels for Namakan Reservoir and Rainy Lake, Voyageurs National Park for 1985 - 1987 (Data from Lake of the Woods Control Board).

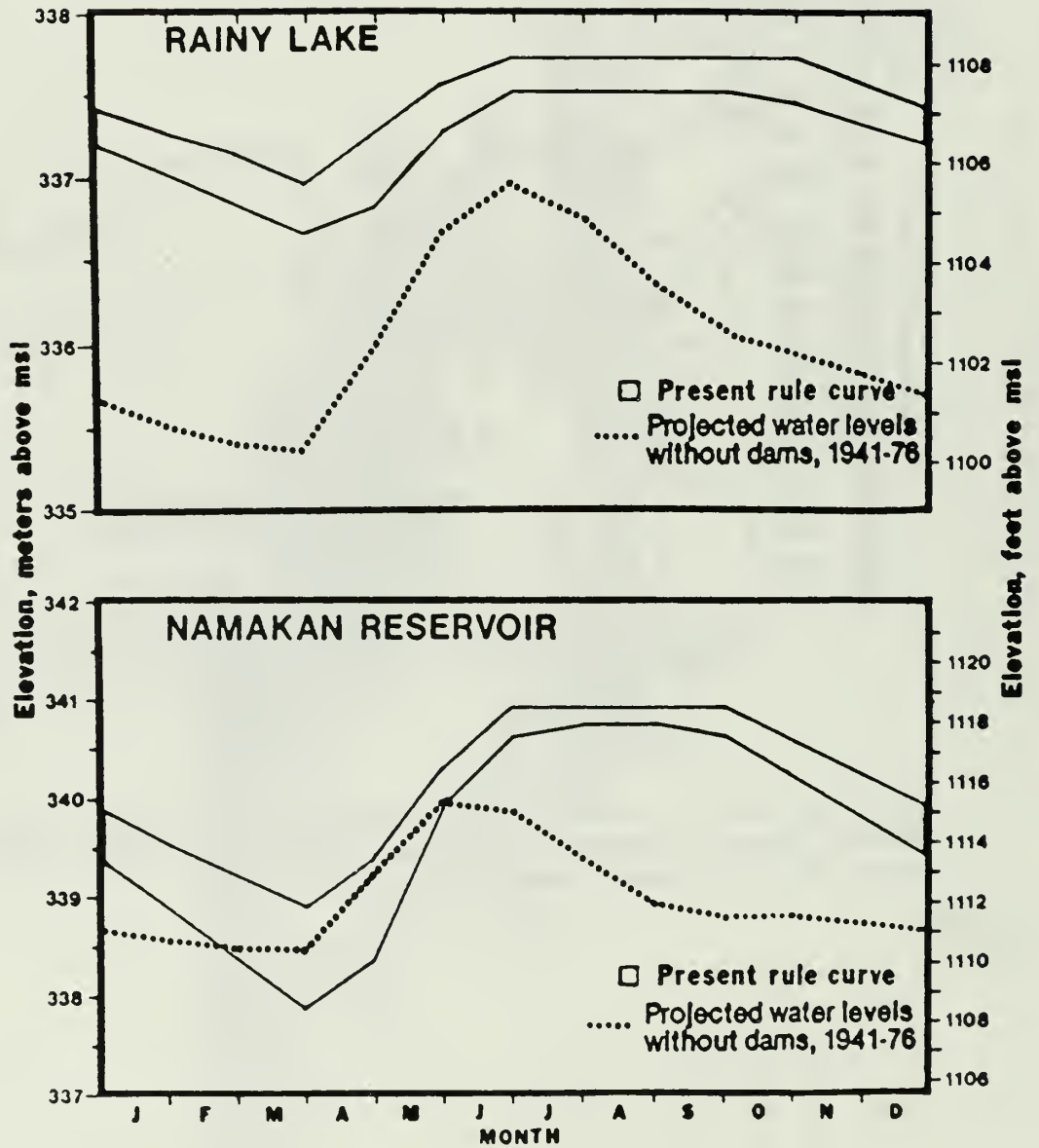


Fig. 3. Present rule curves and projected water levels without dams for 1941 - 1976 (Adapted from Flug, 1986).

This portion of the research project was designed to test the hypothesis that muskrat densities and morphology in suitable habitats of the park are influenced by the water level management regime. Study methods included comparisons of standard body measurements and several density indices between significant drawdown and minimal drawdown areas. An attempt was made to document individual movements and mortality using radiotelemetry and field observations.

STUDY AREA

Voyageurs National Park (Fig.1) lies along the Minnesota-Canadian border and is part of a chain of lakes that stretches from the Boundary Waters Canoe Area in the east to Lake of the Woods in the northwest. The park was established in 1971 (Pub. Law 91-661) to preserve the scenery, geology and waterway system used by the voyageurs of the 1700 and 1800s. This nearly 89,000-hectare park is 39% water with 4 large lakes and 26 small interior lakes (Kallemeyn 1983). It is underlain by the Canadian Shield and has numerous small islands in the larger lakes. Middle and eastern portions have rocky shorelines, while the western end flattens out enough to allow broad marshes. Average annual snowfall is about 140 cm with daily average temperatures in January of -16.1°C (Cole 1987). Temperature extremes are -40° to 36°C (Kurmish et al. 1986).

The park lies in the southern boreal region (Cole 1987). Kurmish et al. (1986) found forests consisted of quaking aspen (Populus tremuloides), paperbirch (Betula papyrifera) and other hardwoods, jack pine (Pinus banksiana), balsam fir (Abies balsamea), white spruce (Picea glauca), black spruce (P. mariana) and scattered stands of white pine (P. strobus) and red pine (P. resinosa). Marshes and streams contained cattail, burreed, bulrush, sedges, smartweed, horsetail, wild rice, pondweeds (Potamogeton sp.), flowering rush (Butomus umbellatus), and sweet flag (Acorus calamus).

MATERIALS AND METHODS

Site selection

Topographic maps and field surveys were used to select 5 bays and 2 creeks in the park as study sites. Areas were chosen that had at least some expanses of cattail and shores that were not too steep and rocky for suitable muskrat habitat. Study sites (Fig. 1) were located in areas experiencing minimal drawdown (Rainy Lake) and significant drawdown (Kabetogama Lake). In Rainy Lake, study sites were located in Cranberry Bay, Black Bay, and Alder Creek. Sites on Kabetogama Lake were located in Daley Brook and Tom Cod, Nebraska and Irwin bays.

Cranberry and Tom Cod bays are both large shallow bays (4 m and 3 m maximum depths, respectively) with large expanses of cattail. Black Bay in Rainy Lake is also a large shallow bay with cattail, but was only used for house counts due to low accessibility and time constraints. Muskrat trapping is allowed on one side of Black Bay which lies outside the park. Alder Creek joins Cranberry Bay on the northeast edge; the creek's mouth has the characteristics of a small bay with a few cattail beds. The south portion of Alder Creek forms a slow stream with sedges and other forbs lining the edge. Daley Brook is a similar stream that empties into Kabetogama Lake. Nebraska Bay has small areas of cattail and is exposed to wind. Irwin Bay has large beds of cattail, some of which are too thick to be prime muskrat habitat (Proulx and Gilbert 1983; Allen and Hoffman 1984).

Trapping

Musk rats were live-trapped in fall (September, October, and November) 1985, spring (May and June) 1986, and fall 1986 with Tomahawk traps (National Trap Co., Tomahawk, Wisconsin) baited with apples. Traps were placed on or near muskrat houses, runways, feeding platforms and scatting sites. Captured muskrats were weighed and standard body measurements (zygomatic breadth, body length, tail length, and right hind foot length) taken. Anus to urinary papilla (AP) measurements were also taken to aid sex determination. Monel #1 ear tags (National Band and Tag Co., Newport, Kentucky) were attached to one ear on all trapped muskrats.

Trapnight success (total captures/total trapnights, excluding recaptures and their respective trap nights) and population estimates were determined from trapping data. The study bays and streams were subdivided for statistical comparison into discrete areas with no capture overlap. Estimates of the number of muskrats/house were obtained from trapping seven houses in each lake in fall 1986 until no new muskrats were captured for at least two consecutive nights.

Sign Surveys

Sign surveys provided indices of muskrat density in spring and fall 1986 and fall 1987. All feeding platforms, tracks, and scatting sites were counted as sign. Spring surveys were done on foot after the lake ice melted. The survey lines were either subdivided into portions hiked in a day (1986) or marked into equal sections with alternate portions counted (1987). The fall surveys were done by canoe and subdivided for analysis into portions done each day.

House Counts

As an additional index of population levels, muskrat houses were counted in winter from skis or snowmobile. In 1984-85, counts were made in Daley Brook and Black, Cranberry, and Irwin bays. In 1985-86, Irwin Bay was omitted, but Tom Cod and Alder Creek were added. In 1986-87, all of the above areas were counted. Subdivisions within these areas were identical to those used for analysis of capture data.

Radiotelemetry

In 1984, eleven muskrats were implanted with radio transmitters (Custom Telemetry and Consulting, Athens, Georgia; 5.6 x 2.0 cm) using ketamine hydrochloride as an anesthetic. Seven of these died soon after release, apparently from diving reflex inhibition (drowning) caused by the drug (pers. commun., U. S. Fish and Wildlife Health Lab., Madison). The fate of the other four was unknown because of radio failure soon after release.

In September and October 1985, temperature-sensitive transmitters (Telonics, Inc., Mesa, Arizona; IMP/200/L, 5.8 x 2.0 cm., 22 - 27 gm.) were surgically implanted in ten muskrats using methoxyflurane (Metafane) as an inhalant anesthesia. Two animals died during surgery. Three more died within 2 weeks; exact cause of death is not known, but we assume mortality resulted from lingering stress or infection. Five muskrats survived longer than 2 weeks, and one of these survived through February.

In September and October 1986, activity-sensitive radio collars (Wildlife Materials, Inc. HLP-1140-LDA) were utilized in an attempt to reduce handling mortality. Eleven muskrats were anesthetized with methoxyflurane while being collared. Animals were held at least six hours, but released on the day of capture. There were no mortalities related to handling.

All radioed muskrats were located at least twice weekly until the signal could not be found for three consecutive attempts or the muskrat died. Death was assumed when radios registered a constant body temperature less than 38°C (1985) or there was no activity for 3 location attempts (1986). An effort was made to recover all carcasses to determine cause of death.

Data analyses

A multivariate analysis of variance (MANOVA) was used to compare standard body and AP measurements between genders, lakes, and bays within lakes (Statistical Analysis System [SAS]). Significant differences found through MANOVA were investigated further with analysis of variance (ANOVA) to

determine which dependant variables were responsible. The ANOVA was used for comparing trapnight success, sign survey results and house counts between lakes and bays within lakes (SAS); the areas and distances for these indices and the population estimates were computed with a digitizer. Chi-square tests (SAS) were used to determine if sex ratios differed from 50:50 and if gender proportions differed between lakes and bays within lakes. Other tests were used where noted. Significance levels used were $\alpha = 0.05$.

A modified Lincoln/Peterson estimator (Seber 1986) was used for population estimates using capture-recapture information. The capture data were grouped into two trapping occasions as follows; initial captures were defined as those occurring in the first 2-4 days of a trapping period, which varied from 4 to 10 days in length. Captures occurring after this period were grouped in the second trapping occasion. Only sub-areas with sufficient recapture data were used for density estimates. Results were analyzed using the Mann-Whitney test (Conover 1971).

RESULTS

Sex ratios and body measurements

Proportions of males and females did not differ significantly between lakes. In spring 1986, 67% (n=21) of the muskrats captured were males; in fall 1986, 62% (n=143) were males. The fall ratio (both lakes) differed significantly from 50:50 ($p < 0.01$). The sample size from spring was too small to detect differences.

Based on the MANOVA, no significant differences were found in any standard body measurement between lakes, bays or gender. Kabetogama Lake muskrats were slightly heavier than Rainy Lake muskrats in the fall and slightly lighter in spring (Table 1).

Anus to urinary papilla (AP) measurements were significantly greater in males than females ($p < 0.0005$) in spring and fall 1986 (Table 2). Males and females differed more in Kabetogama Lake than in Rainy Lake ($p < 0.001$) in the fall. Tukey's pairwise comparison procedure with unequal sample sizes (Zar 1984) showed that males differed ($p < 0.001$), but females did not ($p > 0.20$). Spring 1986 measurements did not differ between lakes, but spring males have an obviously longer AP measurement than fall males.

Density estimates

Population density for Rainy Lake muskrats (based on mark-recapture) was more than twice that in Kabetogama in both 1985 and 1986 (Table 3). Differences were not significant,

Table 1. Weights (g) of muskrats from Kabetogama and Rainy lakes, Voyageurs National Park, from Fall 1985, Spring 1986, and Fall 1986.

	Fall 1985			Spring 1986			Fall 1986		
	$\bar{X}$	SE	n	$\bar{X}$	SE	n	$\bar{X}$	SE	n
Kabetogama	911	28.1	56	951	34.2	8	872	26.8	45
Rainy	902	38.8	29	1081	31.2	13	828	22.9	100

Table 2. Anus to urinary papilla measurement (mm) of muskrats from Kabetogama and Rainy lakes, Voyageurs National Park, from Spring and Fall 1986.

	Male ^a			Female		
	$\bar{X}$	SE	n	$\bar{X}$	SE	n
Spring 1986						
Kabetogama	30.5	2.36	6	16.0	1.00	2
Rainy	31.5	1.75	8	16.6	0.75	5
Fall 1986						
Kabetogama ^b	20.4	0.56	25	14.4	0.41	19
Rainy ^b	18.3	0.29	61	15.6	0.32	36

^aMales and females differed significantly at $p < 0.0005$.

^bKabetogama and Rainy lake males differed significantly at $p < 0.001$.

Table 3. Muskrat density estimates (muskrats/hectare of vegetation) for Kabetogama and Rainy lakes, Voyageurs National Park, Fall 1985 and 1986.

	1985			1986		
	$\bar{X}$	SE	n ^a	$\bar{X}$	SE	n
Kabetogama	0.25	0.046	2	0.59	0.273	3
Rainy	0.93	0.139	2	1.45	0.289	5

^an = number of sub-areas.

Table 4. Trapnight success (total captures/total trapnights) for Kabetogama and Rainy lakes, Voyageurs National Park, for Fall 1985, Spring 1986, and Fall 1986.

	$\bar{X}$	SE	n ^a	TR ^b	T ^c
Kabetogama					
Fall 1985	0.218	0.059	17	16.94	288
Spring 1986	0.039	0.013	10	22.80	228
Fall 1986 ^d	0.144	0.026	9	32.22	290
Rainy					
Fall 1985	0.260	0.077	7	14.57	102
Spring 1986	0.081	0.033	7	24.43	171
Fall 1986 ^d	0.346	0.041	16	20.88	334

^an = number of sub-areas.

^bTR = mean trapnights per sub-area.

^cT = total trapnights.

^dDifferences between Kabetogama and Rainy lakes were significant at $p < 0.005$.

however ($p > 0.10$), because of the small sample sizes and large variance.

Trapnight success also indicated greater muskrat numbers in Rainy Lake (Table 4). Trapping success in Kabetogama ranged from 42 to 84% of the Rainy Lake level. Based on the ANOVA, differences were statistically significant in fall 1986 ($p < 0.005$).

Lake differences in muskrat sign abundance (Table 5) were significant in spring 1986 ($p < 0.025$), when almost no sign could be found in Kabetogama Lake. Again, the trend in fall 1986 was for more muskrat sign in Rainy Lake. In spring 1987, both lakes were exceptionally dry through June (Fig. 2) and very little sign could be found in either area.

Rainy Lake had greater densities of muskrat houses in all three winters (Table 6). Differences between the two lakes were not statistically significant, although in the winter of 1984-85 the difference approached significance ($p < 0.069$). However, houses were significantly more abundant in large, marshy bays of Rainy Lake than in comparable bays in Kabetogama Lake (Table 7). House counts in Cranberry Bay (Rainy) were greater than those in Tom Cod Bay (Kabetogama) in both years (T-test, $p < 0.05$ in both years).

Radiotelemetry

A total of twenty-one muskrats were radioed in 1985 and 1986 (Appendix). In 1985, five out of ten survived longer than two weeks and 2 of those survived at least into January of the following year. In fall 1986, ten muskrats survived longer than two weeks. Three of these signals could not be located after early November, and the remaining 7 did not survive beyond December.

Four of the surviving radio implanted muskrats in 1985 were in Kabetogama Lake; one was in Rainy Lake. One of the Kabetogama Lake muskrats died in mid-November of unknown causes. Two animals remained active near their capture sites until mid-December (shortly after freeze-up) when the radio pulse rate indicated they were dead. One was recovered on 23 January from a dry burrow system with only skull, hair and radio remaining. The other was located on 14 December in another dry burrow, but the carcass could not be recovered until May, when only hair and a hind leg were found. Cause of death could not be determined. One other Kabetogama Lake muskrat remained active near its capture location until 20 January, when it suddenly moved upstream and remained there for three locations. It was found downstream of

Table 5. Muskrat sign survey results (sign/km) for Kabetogama and Rainy lakes, Voyageurs National Park, from Spring and Fall 1986 and Spring 1987.

	$\bar{X}$	SE	n ^a	K ^b	T ^c
Kabetogama					
Spring 1986 ^d	0.14	1.182	21	0.467	9.81
Fall 1986	19.79	6.230	16	0.794	12.70
Spring 1987	0.00	0.000	9	0.683	6.15
Rainy					
Spring 1986 ^d	0.35	1.932	15	0.401	6.02
Fall 1986	27.67	4.792	15	0.863	12.95
Spring 1987	1.15	5.769	5	0.368	1.84

^an = number of intervals hiked.

^bK = average kilometers/interval

^cT = total kilometers.

^dDifferences between Kabetogama and Rainy lakes were significant at $p < .025$.

Table 6. Muskrat house counts (houses/hectare of emergent vegetation) for Kabetogama and Rainy lakes, Voyageurs National Park, from 1984-85, 1985-86, and 1986-87.

	$\bar{X}$	SE	n ^a	A ^b	T ^c
Kabetogama					
1984-85 ^d	0.06	0.030	12	20.17	242
1985-86	0.05	0.017	23	17.89	411
1986-87	0.14	0.025	32	23.78	761
Rainy					
1984-85 ^d	0.23	0.043	27	15.03	406
1985-86	0.09	0.021	43	12.14	522
1986-87	0.19	0.036	41	13.53	555

^an = number of sub-areas counted.

^bA = mean hectares per sub-area.

^cT = total hectares counted.

^dDifferences between Kabetogama and Rainy lakes were close to significance at $p = 0.069$ for 1984-85.

Table 7. Muskrat house counts (houses/hectare of vegetation) for Tom Cod and Cranberry bays, Voyageurs National Park, for 1985-86 and 1986-87.

	$\bar{X}$	SE	n ^a	A ^b	T ^c
Tom Cod ^d (Kabetogama)					
1985-86	0.05	0.017	13	14.78	192
1986-87	0.21	0.048	13	14.78	192
Cranberry ^d (Rainy)					
1985-86	0.14	0.033	24	10.75	258
1986-87	0.33	0.059	19	12.68	241

^an = number of sub-areas counted.

^bA = mean hectares per sub-area.

^cT = total hectares counted.

^dDifferences between bays significant at $p < 0.05$ for both years.

its original area on 29 January. The animal could not be located after this date.

The implanted muskrat in Rainy Lake was active near its capture location until 10 January. It was located on 13 January about 2 km inland in a beaver drainage where it remained active at least through 28 March, the last attempt to locate the animal.

In 1986, five muskrats were radio-collared in Rainy Lake, one in Alder Creek and 4 in Cranberry Bay. The Alder Creek muskrat was active through 7 October; its collar was recovered 9 December, but no other remains were found. Predation is assumed to be the cause of death because the collar was bent and chewed. The first mortality in Cranberry Bay occurred between 3 and 8 October. Cause of death was trauma, probably by predation by a large canid or felid (pers. comm., Fish and Wildlife Service Health Lab., Madison, Wi.). The three other Cranberry Bay muskrats remained active through early November. One Cranberry Bay collar was recovered 18 December from a house near its original capture location. Mink had dug into the house, and while no remains were found, mink scats with muskrat hair were present. Another collar was located on 9 December in a muskrat house with mink sign, but was not recovered until May when the hair, skull, and other bones were found in the dry house. The remaining muskrat was located 9 December about 150 meters inland from its capture location in an aspen tree cavity at a height of 10 meters. When it was recovered (frozen) in February, no external marks were evident, but avian predation is assumed to have been the cause of death.

Six muskrats were radio-collared in 1986 in Kabetogama Lake; five in Tom Cod Bay and one in Daley Brook. All of these were active in their capture areas until early November, when the bays became inaccessible by boat because of ice conditions. In late November the Daley Brook muskrat was located under water (inactive), but could not be recovered until spring when the area was dry. Only the collar was found; it may have slipped off the animal. Three signals in Tom Cod Bay could not be found after freeze-up in November, even from aircraft. One of the remaining signals was located 14 December (inactive) in a dry burrow about one kilometer upstream from its capture site, but the carcass could not be recovered. The other was found 10 December in a patch of dry cattails. Snow and ice hampered recovery until May, when the skull, hair, a few bones, and the collar were recovered. The cause of death was uncertain, but predation was suspected; no mink sign was found, but otters were seen several times at that location in the fall. Otter scats with muskrat hair were also observed at other Tom Cod Bay locations.

DISCUSSION

Sex ratio and body measurements

Muskrat sex ratios frequently favor males in both kill and live-trapped populations, although usually not to the extent found in this study (Baumgartner and Bellrose 1943; McCann 1944; Dozier et al. 1948; Beer and Traux 1950; Alexander and Radway 1951; Sather 1958; Errington 1963; Donahoe 1966; Clough 1987). Long-term studies at the Blackwater National Wildlife Refuge, Maryland ruled out sex bias from kill traps (Dozier et al. 1948). Because live-trapping allows some choice on the part of the muskrat, it is possible that males are more easily caught, especially in the spring when the animals are actively seeking mates. A few workers have not found a skewed sex ratio in live-trapping (Proulx and Gilbert 1983), but it is sufficiently common that the observed sex ratios at Voyageurs do not seem unusual. The ratios also do not appear to be affected by the differing drawdown regimes.

The drawdown of Namakan Reservoir did not appear to significantly affect individual growth of muskrats, as shown by standard body measurements. It may, however, explain the slightly heavier fall and lighter spring weights of Kabetogama Lake muskrats compared to Rainy Lake muskrats. Boyce (1978) found muskrat weights were positively correlated with areas experiencing seasonality of food supply. He theorized that animals living with a seasonal food shortage would have lower population levels, thus less competition and faster growth when food was available. Larger animals are then selected for during shortages because they are able to survive longer without food (Morrison 1960). Dozier (1948) found muskrats had lower weights in spring and theorized it was because of harsh weather and onset of breeding condition. In February, water levels in Kabetogama Lake drop well below the emergent vegetation line. With extremely cold conditions and little snow, it is difficult for muskrats to move to a food source and they are vulnerable to predation when they do (Errington 1939). Muskrats in Rainy Lake usually have water around at least part of their food supply all winter and do not experience such seasonal extremes in conditions, especially in late winter. Although the weight differences between the two lakes were not significant, the trend toward greater fall weights in Kabetogama Lake may be due to less competition when food is abundant in summer. Lower spring weights may be due to the harsh conditions (coupled with the onset of breeding season) that usually do not occur in Rainy Lake.

Alternatively, the lower fall weights of Rainy Lake muskrats may be due to a greater abundance of juveniles in the population

compared to the Kabetogama Lake population. Donahoe (1966) found more and heavier juveniles in controlled (stable) water level units than in uncontrolled (fluctuating) water level units. Kabetogama Lake muskrats showed a 4% gain in weight from fall 1985 to spring 1986, with a subsequent 8% loss by fall 1986. For the same periods, Rainy Lake muskrats gained 20% and lost 23%, respectively. It seems unlikely that the larger change in Rainy Lake muskrats, especially the overwinter gain, would be due only to food supply. A large proportion of juveniles in the population, reaching adulthood over the winter, could increase the average weight of the population. A smaller proportion of juveniles in the Kabetogama Lake population could account for the much smaller overwinter weight gain.

Sex differences in AP measurement have not been reported elsewhere, but informal communication with others indicate it may be typical. Beer and Meyer's (1951) study at Horicon Marsh, Wisconsin may shed some light on why there may be seasonal or area differences among males (fall 1986). They found that adult male testes reached a maximum weight in May, receded during August to November, and were quiescent from December to February. Ovaries changed weight on a similar schedule, but not as dramatically. The larger testis size in spring is probably responsible for the longer measurement in males at this time, when the genital region was swollen. Males are not likely to differ between lakes in the spring because all are reproductively active. In fall, however, male AP measurements in Kabetogama Lake averaged 2.1 mm. longer than those in Rainy Lake. Errington (1951, 1961) found females had more litters at lower densities and/or when early litters were unsuccessful. The longer fall AP measurements may indicate that Kabetogama Lake muskrats are remaining in breeding condition longer and compensating somewhat for lower densities.

Studies correlating testis size with AP distance are needed to confirm the hypothesis that Kabetogama Lake animals are staying in reproductive condition longer. A summer study could be done in Voyageurs National Park to determine how many litters are produced in each area. Techniques, however, are intrusive, involving either kill trapping to count placental scars (Errington 1963), or taking apart houses throughout the season to count number and size of litters (Olsen 1959).

Density estimates

Drawdown effects are indicated by the trend toward lower muskrat numbers in Kabetogama Lake for all density estimates, with significant effects in trapnight success (fall 1986), sign surveys (spring 1986), and house counts in the larger, marshy bays (1985-86, 1986-87). In 1987, both areas were dry in spring,

and conditions on Rainy Lake were similar to those occurring every year on Kabetogama Lake. The detrimental effect of this can be seen in the results of the sign survey for that season.

Population estimates in both lakes were low (0.25-1.45 muskrat/ha), but within ranges reported elsewhere. Errington (1939) found 4.94-7.40 muskrats/ha in wet areas, 2.47/ha in areas that had been dry at least a month, and 0.15/ha after a dry summer. Proulx and Gilbert (1983) had maximum estimates ranging from 18.1-46.9/ha for a variety of habitats, while Clay and Clark (1985) found 0.3-2.4/ha in areas with several kinds of emergent vegetation.

House counts in both areas (0.05-0.33/ha) were also lower than in other studies. Bellrose and Brown (1941) found 0.7/ha in areas of fluctuating water, 1.5/ha in semi-stable areas, and 8.6/ha in stable areas. Donahoe (1966) found 0.34-0.76/ha in uncontrolled water level units and 2.57-4.29/ha in controlled water level units. Relatively low muskrat densities in both study areas in the park may be due to the fact that marsh habitat is limited since most of the topography is steep and rocky.

Danell (1978) and Proulx (1984) found that muskrats abandoned houses and constructed new ones as water receded in summer and fall. This leads to an overestimation of active house numbers in winter counts (Proulx 1984). In both fall trapping seasons at the park, muskrats in Kabetogama Lake constructed new houses in deeper water as lake levels gradually lowered before freeze-up in October and November. This behavior was not seen in Rainy Lake. Therefore, the difference in number of active houses between the two areas may actually be greater than reported.

Muskrat colony size also contributed to greater muskrat density in Rainy Lake than in Kabetogama Lake. All individuals resident in a house were considered tagged if no additional captures were made for two or more consecutive nights. Colony size in Cranberry Bay on Rainy Lake (mean = 4.7 muskrats/house, SE = .62, n = 7) was substantially greater than in Kabetogama Lake (mean = 2.0 muskrats/house, SE = .34, n = 7). This indicates that even if Kabetogama Lake muskrats were having more litters annually, summer survival or litter size may be low. Only five recaptures were made in the fall of spring-caught muskrats, all in Rainy Lake, so survival could not be estimated.

General condition of Kabetogama Lake muskrats (fall 1986) did not seem as good as that of muskrats from Rainy Lake. Of 45 muskrats captured in Kabetogama Lake, 5 (11%) had abnormalities more severe than nicks and cuts; one had a leg that hung limp, one had a hard, swollen abscess in its cheek, 2 had cleft lips,

and one had an extra anus. Only one of 95 (1%) muskrats captured in Rainy Lake had this type of defect (abscess). Errington (1939) found dispersing muskrats were more likely to be in poor condition, which lends support to the idea the Kabetogama Lake population may largely be made up of new immigrants each year (see below).

No recaptures were made in spring of fall-caught muskrats in either Kabetogama or Rainy lakes, therefore overwinter survival could not be estimated (data from radio-collared animals indicate survival may be very low). Spring captures in Kabetogama Lake, however, appeared to be comprised of recent immigrants. Only one muskrat was caught in the first week of the trapping period when the water elevation was 339.86-340.21 meters above mean sea level (mmsl). Maximum summer elevation is 340.93 mmsl. Subsequent captures (7) occurred after the water had risen to 340.25 mmsl and cattail roots were submerged. Also, all houses were dry and muskrat sign was not found until the higher water levels were reached. In Rainy Lake, 8 captures were made during the first week of trapping (water elevation = 337.73-337.77 mmsl; maximum summer elevation = 337.78 mmsl) and all houses were in at least 0.45 meters of water at the start of the trapping period.

Other studies have shown that overwinter survival of muskrats is influenced by depth of water at houses. Optimum house depth was found to be 30-46 cm by Bellrose and Brown (1941), 30-80 cm by Danell (1978), and a minimum of 15 cm by Proulx and Gilbert (1983). Bellrose (1950) found that severe "freeze-outs" occurred when houses were in less than 15 cm of water. Systematic measurements of water depths were not made in Rainy Lake, but all houses trapped in the spring and fall were in water over knee deep (46 cm). In the dry spring of 1987, when only a sign survey was done, most Rainy Lake houses were dry or almost dry. In Kabetogama Lake, 3 water depth measurements were made at a distance of 50 cm from each of 4 permanent houses and two feeding houses in the fall of 1986. Average water depth was 43 cm at permanent houses and 17 cm at feeding houses. By ice-out in the spring of both 1986 (18 April) and 1987 (17 April), all of these houses were dry.

The cattail areas where houses were located were at water depths of < 1 m during summer (Kallemeyn 1987) and most submergent vegetation was at depths of < 1.2 m (Kallemeyn pers. comm.). Water levels in Kabetogama Lake began to decline in October and reached minimum levels from February to April (Fig. 2). In winter, water levels may drop to 338.30 mmsl, well below the submergent vegetation zone. This means that in the harshest part of winter muskrats cannot reach their food supply by water, are exposed to predation if they try to reach it overland, and

will most likely find the food source frozen under several centimeters of ice if they get there. It should be noted that Rainy Lake levels often drop one meter or more. The length of time the levels are below the cattail areas in Rainy Lake, however, is much shorter and muskrats can probably survive on submergent vegetation that is not exposed.

Radiotelemetry

Low survival of radioed muskrats in both Rainy and Kabetogama lakes precluded comparisons. The two instrumented muskrats surviving past freeze-up in 1985 (one in each area) both showed sudden long distance movements in mid-January. It may be postulated that the Daley Brook muskrat was responding to severely reduced water levels and consequent lack of food, but its ultimate fate is unknown. It is also not known if the Cranberry Bay muskrat was moving because of inaccessibility to food or for some other reason.

Freeze-up is apparently a vulnerable time for muskrats in both lakes. Push-up sites (domes of submergent vegetation piled over cracks or holes in the ice) are not made until persistent ice cover is well established, so this protection from predators for above ice activity would not be available during freeze-up (Dozier 1948). It is not known if the radio collars contributed to their vulnerability to predators at this time.

It is likely that water drawdown led to increased predation pressure in Kabetogama Lake. Errington (1939) found that muskrats foraged much more on top of the ice when burrows and houses became dry, giving them more exposure to predators. They were also preyed upon when they tried to remain in exposed burrows. Bald eagle (Haliaeetus leucocephalus) predation on a muskrat above ice was documented once in Kabetogama Lake in January 1987. After ice-out in spring, wide mud flats with long exposed burrow systems were seen in Daley Brook and Tom Cod Bay. Several muskrat carcasses were found in small nests in these systems, a few with associated mink scats. A similar situation was not found in Rainy Lake until 1987, when both areas had exposed mud flats. There is no evidence that mink can limit muskrat populations in secure habitats (Errington 1939; Wilson 1954), but they can contribute to the demise of populations under stress from drought and/or freeze-out (Errington 1939; Proulx et al. 1987). Evidence of mink predation on some radio-collared muskrats and sign of entry into muskrat houses and burrows indicate this may be a major cause of mortality in drawdown areas of Voyageurs.

SUMMARY AND MANAGEMENT RECOMMENDATIONS

Artificially regulated water levels in Namakan and Kabetogama Lakes fluctuate approximately 2.7 meters annually, with lowest levels in late January through March. Levels in Rainy Lake are fairly stable, with fluctuations of about 1 meter annually on a similar schedule. Effects of these fluctuations on muskrat were studied as part of a broad-based effort by the National Park Service to find alternate water management regimes that would maintain naturally occurring aquatic plants and animals in Voyageurs National Park and meet the demands of other legitimate users of water in the Rainy Lake watershed.

Rainy Lake supported significantly greater densities of muskrats than Kabetogama Lake, based on trapnight success (fall 1986), sign surveys (spring 1986), and house counts in larger, marshy bays (1985-86, 1986-87). Although population estimates and density indices for other seasons do not show significant differences, the trend is consistent with greater densities in Rainy Lake, the minimal drawdown area. This indicates that the significant drawdown on the Namakan Reservoir lakes does adversely influence the muskrat populations.

Standard body measurements do not indicate any significant effect of water regime on the growth of muskrats. Slightly higher fall weights and lower spring weights of Kabetogama Lake vs. Rainy Lake muskrats may result from overwinter stress and reduced competition in summer. Alternatively, Rainy Lake may produce a greater proportion of juveniles (from either larger litters or more litters) that attain adulthood during winter. Sex ratios show a normal preponderance of males in both lakes. A difference in anus to urinary papilla measurement among males of Rainy and Kabetogama lakes (fall, 1986) may be indicative of continued breeding, suggesting that the drawdown population is compensating for lower densities with extended reproduction.

Telemetry results showed only that freeze-up was a vulnerable time for muskrats. As water levels dropped and before push-up sites provided cover, muskrats were forced to move on top of the ice and apparently became easy prey for predators.

This study confirmed that stable water is more favorable for muskrat populations than fluctuating levels. Rainy Lake, with its less than natural water level fluctuation, was found to provide the best habitat for muskrats in Voyageurs National Park. Natural fluctuations (estimated at 1.9 m) would not provide the stable water necessary for optimum muskrat habitat. Any drawdown over one meter exposes prime cattail areas needed for food and houses. Prime muskrat habitat, however, is not the goal of the park in

preserving the waterway system of the 1800s. Fluctuations closer to natural conditions would have drawdowns occurring with timing similar to conditions currently present in Rainy Lake. This would improve the situation for Kabetogama Lake muskrats, although an increased drawdown in Rainy Lake would be detrimental. Drawdown in Rainy Lake is already one meter; the muskrats there may be vulnerable to "freeze-outs" of food supply and houses in drier years. To make conditions for muskrats consistent throughout the park, while complying with stated park goals, fluctuations with an amplitude closer to natural conditions should be implemented. A water level change of 1.9 m is still fairly severe as it is well below cattail and submergent vegetation areas. To improve the situation, about 1 meter of the drawdown should occur gradually through September and October to give the muskrats time to build houses at lower levels before freeze-up. Continued drawdowns below the food source (cattail and submergent vegetation) should occur over a short time period, similar to the situation currently existing on Rainy Lake. If houses still have some water and the period of food scarcity is short, above ice foraging time and exposure to predators will be reduced. Increases in spring water levels should occur before the end of April to avoid flooding out muskrat houses while they are raising young.

With shelters in sufficient water and a minimal period of food shortage, enough muskrats should survive to provide both lakes with a healthy population. The resulting increased muskrat densities on the Namakan Reservoir lakes would increase opportunities for visitors to enjoy muskrats and their natural predators in a national park environment.

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APPENDIX.

Fates of radioed muskrats (1985-1986) in Kabetogama and Rainy lakes, Voyageurs National Park.

	Capture number	Date of release	Date of last live or active location	Fate of muskrat
1985				
Kabetogama	49	9/14		Died during surgery.
	52	9/15	1/29/86	Lost contact after sudden increase in movement.
	53	9/15	10/09/85	Died in bank burrow.
	56	9/18	10/03/85	Died in dry burrow.
	103	10/15		Died during surgery.
	116	10/25	11/10/85	Died in dry burrow.
Rainy	69	9/23	9/27/85	Died in burrow under house.
	75	9/24	3/26/86	Moved inland to beaver pond.
	77	9/25	9/26/85	Died of stress?
	86	9/29	9/30/85	Died of stress?

	Capture number	Date of release	Date of last live or active location	Fate of muskrat
1986				
Kabetogama	256	10/15	11/02/86	Lost radio contact.
	262	10/15	11/05/86	Died in house - preyed upon or scavenged.
	270	10/19	10/29/86	Died in dry burrow.
	275	10/21	10/29/86	Lost radio contact.
	278	10/22	10/29/86	Lost radio contact.
	292	10/31	11/01/86	No remains - possibly slipped collar.
Rainy	148	9/16	10/07/86	Probable predation.
	199	9/24	11/04/86	Died in house - preyed upon or scavenged.
	141	9/19	11/04/86	Found in aspen cavity; predation.
	139	9/27	10/08/86	Confirmed predation.
	244	10/06	10/13/86	Died in house - preyed upon or scavenged.



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