

## ***Chapter 8***

### **The Little Wall Lake Area, Central Iowa**

LITTLE WALL LAKE is a marsh of about 270 acres, largely state-owned and administered by the Iowa State Conservation Commission. It lies two miles south of Jewell, Hamilton County, Iowa, and three miles south of the Goose Lake to be treated in the next chapter (Fig. 8.1).

I saw Little Wall Lake for the first time shortly after coming to live in Iowa in the summer of 1932. The water level was then rather high. With its extensive stands and patches of cattails and bulrushes, the marsh looked like ideal habitat for muskrats, waterfowl, and associated animal life. Rainfall varied greatly between 1932 and 1935, but a trend toward lowered water levels and massed cattail growths did not become pronounced until 1936, when only about 100 acres remained sufficiently wet to be attractive to muskrats. A dredging program that deepened some of the marsh in 1953 actually had little effect on the parts usually occupied by muskrats.

The State Conservation Commission gave me excellent cooperation in my work at Little Wall Lake, especially in connection with fur-refuge experiments; and I wish to single out Paul E. Leaverton and former Conservation Officer Kay Setchell for individual thanks. I also received valuable cooperation from trappers, including Wayne Clayton, Palmer and Dean Erickson, Lee Kramer, Keith Larson, John and Herbert Egenes, Leigh and Morris Johnson, Torkell Hill, Harley Doolittle, M. Boyd, O. Boyd, Robert Sowers, Frank Batman, Mike Olson, James Thorson, and Gary Severson.

#### **THE YEARS OF ACUTE LOCAL DROUGHTS, 1936-41**

Highly intensive work was begun at Little Wall Lake in late fall, 1936, as the imminence of a drought crisis became apparent. Notes taken in early spring were inadequate but suggest, so far as they may be relied upon, a breeding population the equivalent of 67 to 72 pairs,

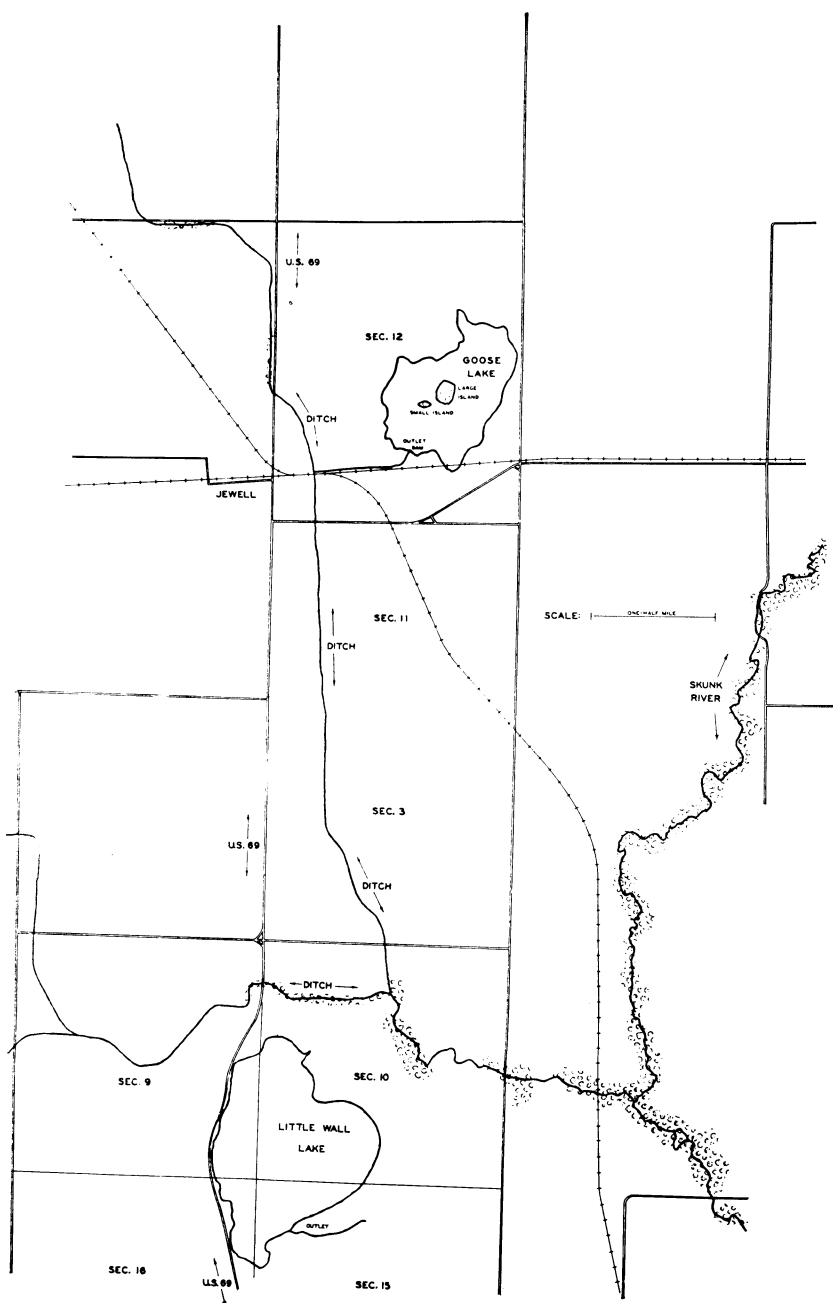


Fig. 8.1. Map of Little Wall Lake, Goose Lake, and environs, near Jewell, central Iowa.

probably nearer the latter, of which 30 pairs occupied the wetter 100 acres. The muskrats were on the whole uniformly distributed over the marsh, in the shallower as well as the deeper parts. It is now suspected but not definitely known that many of these left before the spring dispersal was over.

By October 27, the bottom was exposed except for a tract of about 10 acres in the southeast corner and another of similar size in the north central part. Numerous occupied lodges could be seen, but losses obviously had been severe. The presence of five intact skeletons in an area of 1,400 square feet probably represented disease mortality earlier in the month or in late September.

On November 29, when freezing permitted a thorough checkup, practically no water was left on the surface. The muskrat population was estimated at 40 for the approximately 100-acre tract still occupied. This was done on the basis of the known trappers' catch of 42 from the 100-acre dry end of another marsh (Mud Lake, Chapter 5) that had similar signs before trapping.

The marsh bottom was solidly frozen by December 4. Muskrats gnawed out of their underground quarters to forage amid the cattails on the surface and then retired, to plug their passageways with fresh mud. As the weather became colder, the sinking of the frost line into the mud forced the muskrats to forage on the surface, often exposing their sensitive tails, feet, and eyes to air temperatures that were sometimes around zero Fahrenheit even during the warmer hours of the day. Moreover, the dead vegetation available on top of the frozen mud afforded little of the heat and energy that muskrats need for cold weather subsistence (Errington, 1941a). Certain animals obtained some protection from snowdrifts, and their survival may have been prolonged for a few weeks. No evidence of any being alive was found after February 4, 1937.

Of the late fall population, some (perhaps a dozen) were illegally trapped in December, at a time when Little Wall Lake was a wildlife refuge. Three others were collected for specimens. Thirteen dead were found during the winter, including one positive and another probable victim of outright cannibalistic predation. Muskrat remains were found in quantity in 4 of 16 stomachs and fecal deposits of the muskrats themselves and in 21 of 41 mink scats examined from the marsh between December 5 and February 23. Three muskrats were definitely known to have left during December and January, but it was undetermined whether they were residents or had previously wandered into the area.

A mink scat found February 23, 1937, contained remains of a muskrat that was probably a newcomer. About a foot of water from melting snow lay over the central bottom, and the marsh again looked fairly habitable for muskrats by March 17, with numerous unused though suitable lodges. The first indubitable sign of reoccupation was seen on March 27. As late as May 9, it was judged that there might be no more than the equivalent of two pairs on Little Wall Lake. Soon

after, more animals came in, until by the last week of May the territorial settling seemed completed. The area of the habitable part of the marsh was now about 90 acres.

Very detailed field work in the breeding months of 1937 proved the existence of 7 females having young, together with associated males and an isolated adult, probably an unbred female. With one exception, the foci of activity of the family groups or territories were rather uniformly distributed in the shape of an irregular oval of about 500 x 700 yards. This arrangement was interesting in that it reflected unusual freedom of choice on the part of the immigrant muskrats. Having numerous vacant lodges and excellent food resources scattered over the wet area, the muskrats appeared to be influenced chiefly by their own densities in their selection of permanent quarters for the breeding season.

Thirteen litters were handled, and these were believed to have been all litters born on the marsh in 1937. Of these, one litter was born to each of 3 females; two litters to each of 3 females; and four litters to one female. Marking of 35 of the young by toe-clipping failed to yield information because of nearly annihilative drought losses later in the summer. The possibility of disease losses should also be considered, as a decomposing adult with what could have been hemorrhagic lesions was found floating in the water on June 2. All of the young of one of the two-litter females became emaciated and surely died. Remains of three adults eaten by minks were listed; these could have been disease victims. A bona fide mink victim was a fairly large young that took up residence in a drought-exposed lodge. Two young aged 32 days were found freshly killed by other muskrats. Two of 73 mink scats from April and May contained remains of adult muskrats; one of 19 scats from July to the middle of August contained remains of the large young from the drought-exposed lodge; there were no muskrat remains in 56 scats from September and October.

Little Wall Lake was dry by September, when evidence of activity by muskrats was seen only in the vicinity of the summer retreats. Abandonment of two former territories had occurred by late October, with no indications that their occupants stayed on the marsh. Two original territories continued to be used, and the animals of three other family groups moved into a previously vacant tract. The population remnant converged into the latter tract by November. When the legal status of the marsh was changed from a wildlife refuge to that of a public shooting ground, the remnant was completely trapped out—sixteen muskrats, according to a farmer who lived nearby.

The 1938 spring repopulation of Little Wall Lake involved far fewer animals, presumably because of lower densities overwintering in surrounding streams and lessened tendencies for cross-country movements. A fresh track of a stump-footed animal was seen on, but not after, March 12. No further muskrat sign was seen up to April 5, when about eight inches of water covered the bottom in the deepest places. By April 18, the water was about as high as in the previous

spring; by May 7, nearly the entire marsh bottom was covered. Muskrat cuttings were seen on April 28, but no fresh sign could be found on May 9, nor on May 24. No muskrat remains were found in 180 mink scats deposited from late January through April.

I was absent from central Iowa from June through August, 1938, so made no checkups of Little Wall Lake during that summer. Ex post facto evidence indicated that a female arrived in midsummer, found a mate, and gave birth to two litters in July and August. About 13 animals were in the vicinity of the natal lodge by late fall. Trapping by persons unknown to me eliminated nearly all of these. A sign of a living animal was seen during the winter of 1938–39, but, by March 4, the marsh was again depopulated.

The water level in the spring of 1939 was high, and the dense stand of cattails furnished inviting habitat for muskrats. The first recognized evidence of a muskrat appeared May 18, but no signs could be made out during careful searches in mid-July and mid-September. By the latter time, considerable overland movement of muskrats was resulting from a drought crisis along the local streams. An animal was killed by highway traffic just west of Little Wall Lake, September 30, and, by October 18, what appeared to be a newly-arrived individual was found at a part of the marsh that had been deepened by experimental blasting (Scott and Dever, 1940); it departed within 10 days. In late October, three or four muskrats built small lodges in two parts of the approximately 10 acres of marsh then remaining habitable. By November 12, the marsh had no surface water other than a few puddles, and the muskrats had moved on, except one that stayed until early December.

By April 9, 1940, water again covered the marsh bottom, much as in the previous three springs. Two territories were established in widely separated places, one in April, the other in early summer. A single litter born in one of these territories in late May apparently died of starvation at the age of about six days, and no new sign of adult muskrats was thereafter laid down in the vicinity. My guess is that a lone female had come in pregnant and died after giving birth to the litter. Despite drying up of the marsh during the summer, the other territory had a few animals maintaining themselves through August, until rains put water in the deeper places. The last muskrats abandoned the marsh, once again dry, about the first of November. Minks did not seem to take advantage of the drought-exposed muskrats in this instance, though they generally frequented the same places that the muskrats did. None of 210 spring and summer mink scats contained muskrat remains.

The water started coming back early in the winter of 1940–41 and, by the spring of 1941, was about at the level usually to be observed. But no breeding muskrats established themselves, and the marsh was again dry between midsummer and November, 1941. What were judged to have been lone animals appeared about the middle of July in one place and in early September in another. These stayed a few weeks at most. Eighty-eight mink scats deposited mainly in September

and October about the places used by the muskrats contained no muskrat remains.

#### **THE RECOVERY YEARS, 1942-43, AND UP TO THE SPRING OF 1944**

The water level, as of March 22, 1942, was up to, or exceeding, the maxima for the springs 1937-41. The plant successions favored by the recurrent exposures and floodings of the marsh bottom had by now culminated in a nearly solid stand of broad-leaved cattails, with scattered rushes and a few shrunken openings dominated by wild rice and yellow water lily. The marsh was in exceptionally good condition for muskrats.

On May 8, two freshly built lodges were seen, of which both were considered territorial foci. Four more territories were later established. These six territories were widely separated, three being in the wettest 100 acres of the east side and the others being in the northwest and southwest corners and the west center.

Water continued to rise on Little Wall Lake as a result of heavy summer rains, and, by early winter, a well situated (and legally protected) population was manifested by 35 large and medium-sized lodges, occupied by probably between 150 and 200 muskrats. Many of the lodges that were assiduously dug into by at least two minks were abandoned by the muskrats; many others were repeatedly plugged after the minks left them; and scarcely a lodge on the whole marsh escaped attention of the minks for more than a few weeks at a time during the winter months. Despite this close association between predators and prospective prey, no muskrat remains were found in 103 mink scats deposited from December, 1942, to mid-February, 1943, nor was other contemporary evidence seen of the minks successfully attacking the local muskrats.

Then, 153 of 208 mink scats from the last half of February to the middle of March contained muskrat remains, the calculated equivalent of up to 10 or 12 individual muskrats (see p. 923 of Errington, 1943). This period of vulnerability to the minks coincided with the beginning of the spring dispersal of stream-dwelling muskrats, though the muskrats of ice-covered Little Wall Lake showed few signs of dispersing or of outside activity. The one carcass examined was that of an old male. After the elimination by the minks of what appeared to be the vulnerable individuals, muskrat representations dropped to 5 in 69 mink scats for the second half of March. No further evidence of mink predation upon the muskrats was found during two visits in April.

The 1943 breeding density, as of May 20, was calculated at the equivalent of between 61 and 67 pairs, probably nearer the latter figure. The territories were patchily distributed — rather crowded together in places, with other places being nearly muskrat-vacant. The water level was the highest yet noted and sufficient to make the entire marsh habitable for muskrats. By June 7, growths of cattails covered the marsh so thickly that only the lodges near shore could be seen from land. A mid-August checkup showed the muskrat population to be thriving in the midst of a nearly perfect environmental combination,

and a fall population of about 1,300 was arrived at on the basis of sample counts. Only 2 dead muskrats (both young) were found during four visits in October; one of 12 mink scats contained remains of an adult.

Legal protection of the Little Wall Lake muskrats was extended for another trapping season. Although some evidence of probable illegal activity was seen, it is doubtful that much successful poaching was done. Considerable signs of restless or transient muskrats were visible on the ice during the winter of 1943-44, and the greater part of the detected predation upon muskrats by the dozen or more minks frequenting the marsh was borne either by such individuals or by some that were patently immature. Eight of 101 mink scats examined from November to the middle of January, 1944, contained muskrat remains. Despite the extensive mink intrusions into the lodges, the muskrat population as a whole lived with much security.

For the second half of January, 27 of 49 mink scats contained muskrat remains, as did 52 of 65 scats for February, a month of obviously increasing tensions among the muskrats. On a 16-acre sample of densely populated marsh, nine places were noted where apparently different muskrats habitually worked over the surface of the ice during thaws. The sample represented about one-tenth of the marsh showing this type of sign, from which an estimate of around 90 restless muskrats may be made. For early March, one of 5 mink scats contained muskrat remains, by which time the less favored muskrats seemed to have been eliminated. The great majority of the muskrats of the marsh (perhaps 1,200) were then left comfortably and securely situated.

Particular attention was paid to responses of muskrats to the activities of the minks. By midwinter, hardly a lodge in large tracts failed to show evidence of mink intrusion, but even many of those known to be repeatedly entered were retained by the muskrats as regular dwellings. Some of the mink holes were plugged so close to the lodge chambers that from an outside view they appeared to have been unrepaired; others were plugged so neatly at the outer surfaces that, except where marked for recognition, the former locations of the holes could easily have been overlooked.

The 1944 spring dispersal of muskrats at slow-thawing Little Wall Lake did not get under way until late March, about a month later than in ice-free small streams. During the dispersal, and up to May 9, 16 muskrats were found dead about the marsh, 13 being victims of highway traffic on U.S. 69, which skirts the west side. The figure arrived at for the breeding population, as of May 9, was the equivalent of 437 pairs, or about 900 adults, with a certain amount of dispersal continuing to be in progress and some surplus males still frequenting the marsh border.

#### THE GREAT CRISIS OF 1944

So far as it can be dated, the decline of Little Wall Lake as first-class muskrat habitat was assured by the rise of the water to an over-

flow level in consequence of rains on the nights of May 18 and 19, 1944. This killed the once-lush stand of broad-leaved cattails, and, with the advance of summer, Little Wall Lake took on some of the aspects of a body of open water, with little except rotting stalks of last year's cattails holding the lodges in place. The few small remaining clumps of live cattails (mostly narrow-leaved) were severely exploited by the muskrats. The high water did not wholly eliminate muskrat food from the marsh, for fairly extensive growths of hardstem bulrushes remained in the south center by July, and duckweeds, smartweeds, and submerged plants (especially coontail and bladderwort) were locally prominent. But hundreds of adults and thousands of young muskrats were confronted by an ecological crisis, of the sort illustrating what can happen in a large population of muskrats when many things go wrong.

The tragic consequences of the crisis were carefully followed through a program of intensive study. Up to June 10, breeding was progressing in a normal way in the deep-water lodges of the north and west parts, though animals were conspicuously spreading along the north and west shores. In the northeast corner and the east central part, green vegetation could hardly be found at all, and the lodges generally had an unmaintained appearance. A very few young, however, were still being born in the east central lodges as late as the third week in June, but this part was the site of lethal intraspecific strife. Ten dead young (mostly slashed by adults) and a dead adult were examined here on two visits, compared with two slashed dead young and a dead adult for a larger area of the west side. By late June, intraspecific strife was becoming more noticeable among the relatively better situated populations of the west part. Hostile displays between muskrats could be witnessed at any time of day, and slashed victims were seen dead in the water, on and in the lodges, and on rush rafts and shore.

Shortly before the middle of July, a storm blew ashore the lodges and muskrats of the east central part. Many animals of different ages and sizes thus found themselves suddenly transplanted into a strange environment already occupied by viciously intolerant residents. Minks took advantage of young muskrats that were marooned on shore during the hours of greatest vulnerability; 16 bodies (all killed about the same time and mostly uneaten) were counted outside the den used by a mother mink and her young. Twenty-two of 149 mink scats deposited in the first half of July contained remains of young muskrats, and it could be fairly well ascertained that the eating of most of these occurred during or just after the storm. None of 25 mink scats for May and only one of 60 June scats contained muskrat remains.

Some of the displaced east central muskrats continued to live in lodges that blew ashore without disintegrating. Some displaced muskrats stayed where they could in holes and other retreats on land, or in nests on mats of drifted debris. Most of them seemed to move cross-country eastward, over grain fields and pastures. A field of ripening



oats had eight major trails leading into it, and, after the shocking of the oats, many muskrats lived in the shocks, to be exposed by the threshers.

Over those tracts of Little Wall Lake on which habitability for muskrats remained fair, litters continued to be born into July and August. These conclusions, which were arrived at from the field data of spring and summer, agreed well with the seasonal distribution of litters indicated by the placental scars of the adult females examined in the trappers' catches of mid-November.

Although the survival of the early litters was high, survival of the late-born was low. The latter is reflected by recovery during the trapping season of only one of 126 tagged young, the majority of which (all but a May litter of six) were born in June. The very dubious life expectancy of this age class is emphasized by the successful over-all rearing of about half of the total number of young conceived by Little Wall Lake breeding females in 1944. The high rate of survival of the early-born might naturally be expected to doom many of the late-born even under better living conditions (Errington, 1946; 1951), but, with the marsh being subject to acute and progressive damage from the standpoint of the muskrats anyway, the handicaps of the late-born were sharply increased.

Manifestations of biological unbalance grew more pronounced in midsummer, and, if anything, more so as autumn came on. By the end of July, the marsh was almost lakelike except for the bulrushes of the south center, and increasing signs of muskrat activity could be seen along shore. Not only was there much random drifting of animals shoreward but there was also some mass moving.

On August 12, around 450 muskrats of mixed sizes were concentrated in the south central bulrush tract, whereas probably fewer than 100 had worked here only a few days before. On August 14, exceptional numbers were sitting along the south shore nearest the bulrushes; by September 2, the animals of this stretch of shore almost disappeared, and the population of the bulrushes was down to about 190.

Starting about August 21, another concentration of shore-dwellers or transients located a corn field, which they reached by crossing the busy highway, U.S. 69. An effort was made to record all traffic victims for sample 24-hour periods as long as the raiding of this corn field continued. In 20 days, 48 fresh victims were counted — as many as 12 killed in a single day — which, on a prorata basis, would total about 90 highway victims for the 38 days that the situation existed. Many other Little Wall Lake muskrats died on U.S. highway 69 throughout the summer and fall of 1944, but the above mortality fell in a special category.

The late-summer clearing of practically all of the emergent vegetation by the muskrats hardly signified, in itself, any uniformly desperate hunger crisis, for extensive growths of submerged plants remained available in many places. Nevertheless, hazardous feeding on shore continued on a large scale. Aside from some degree of undernutrition

of the young after midsummer, the population effect of deterioration of the food supply seemed chiefly a matter of heightened intraspecific tensions. Fighting was especially prevalent in shore zones invaded by the inhabitants of lodges disintegrating through action of waves and wind.

On October 7, 121 muskrats were counted sitting out a windstorm along a quarter-mile of shore line. These included many strife-torn and bewildered transients, but many animals plainly were acquainted with each other and displayed tendencies to huddle and move in groups. After the storm, some of the shore-sitters returned to the much damaged bulrush tract of the south center and there rebuilt lodges and nests; others improvised nests on debris floating out from shore or lived in badger diggings, and the like on a hillside; probably others simply drifted along the shore line (three were marked by toe-clipping but never found again); and others moved into the damp swale comprising the outlet. Nests with muskrats in them were seen — 9 adults and subadults in a single nest — in the outlet near the marsh until October 9, after which they moved about 140 yards down the outlet to establish new quarters in a hummocky bog. Some were still living in the hummocks when the trapping season opened on November 10.

From the middle of June through September, 150 dead muskrats were recorded, and it is likely that the actual mortality was considerably higher. Most of the interspecific predation upon the vulnerable shore-dwellers occurred through the agency of minks, although dogs killed some; one kill was attributed to a red-tailed hawk, and it is to be expected that red foxes living in the vicinity picked up at least a few (Errington and Scott, 1945). Muskrat remains (especially of young) were found in 42 of 112 mink scats for the second half of July.

Throughout August and September, the minks still preyed especially upon the young among the muskrats living on shore. Muskrat representations in mink droppings were in 24 of 111 for the first half of August; in 15 of 56 for the second half of August; in 16 of 61 for the first half of September; and in 15 of 41 for the second half of September. These muskrats, too, reacted according to patterns shown by transients, living in nests in the grass and in dry bank holes, excavating shallow burrows and then abandoning them, and otherwise betraying their restlessness and unfamiliarity with their surroundings. Besides suffering the usual mink predation and intraspecific strife, they were killed on a substantial scale by hunters' dogs after the hunting season for waterfowl opened on September 20. Sign of a juvenile great horned owl was found on the hilltop just south of the marsh, and evidence was seen October 8 of its scavenging upon a dead muskrat. This species of owl could be expected to take a certain advantage of vulnerably situated muskrats, though a juvenile might not be very successful as a muskrat predator (Errington, Hamerstrom, and Hamerstrom, 1940).

Close watch, meanwhile, was kept for the hemorrhagic disease, but lesions were not recognized in any of the post-mortems made of dead

muskrats from Little Wall Lake until October, 1944. In the early part of that month, the disease appeared along the west central shore. Two probable disease victims (both decayed) were here seen floating near shore on October 6, but the first clearly diagnosed one was found on October 16. Between October 16 and 28, 21 certain and probable victims were found, all dead along 70 yards of shore at the focus of infection. From October 29 to November 2, the known zone of infection extended 840 yards north and northeast and 365 yards south of the set of burrows about which the unquestionably diseased animals were first discovered. By November 14, the zone was further extended about 50 yards to the northeast but was still largely restricted to the vicinity of the shore, despite the presence of a lodge-dwelling population less than 100 yards out in the marsh. By this time, the muskrats had been so reduced by public fur trapping that no further disease victims were found during the fall. Diligent searching produced no specimens showing the disease from outside the designated zone, but the origin of a trapped carcass having a few small liver lesions could not be traced.

The original focus of infection was, to all appearances, completely devoid of live muskrats by November 1. Then a strong wind and waves tore some deep water lodges apart, and the occupants came to shore and established themselves in the undefended burrows. The first of these newcomers known to die of the disease was found on November 9. A dead muskrat that proved to be diseased was washed in, November 2, near a shore lodge in a place where no evidence of the disease had been seen earlier; after the muskrat was examined, on the same day, it was returned to the water and anchored as an experiment; and, on November 9, the first of the muskrats at this new place was found dead of the disease.

Altogether, 97 dead muskrats from Little Wall Lake were examined between the first of October and the beginning of the trapping season, November 10. Forty-three of these definitely or very probably had died of the epizootic disease, and undoubtedly several times as many more had died underground in the burrows. (Once, I quartered over a piece of ground trying to locate the source of an odor by nose, finally dug through the sod and unearthed the putrid animal lying toward the end of a shallow burrow.)

The disease itself now became the main factor underlying the availability of Little Wall Lake muskrats to minks. Of 32 mink scats deposited during the second half of October along the stretch of shore where the epizootic was most lethal, 17 contained muskrat remains, compared with 7 of 83 scats from disease-free shores and 6 of 72 scats from the first half of the month, prior to the outbreak stage of the disease. At the same time, the symptoms of population unbalance continued up to the trapping, with evidences of vicious strife where strangers and residents came in contact.

The recorded trappers' catch at Little Wall Lake for the 1944-45 season was 1,346 muskrats — mostly taken by three parties of trappers.

Allowing for some muskrats caught by other or by unknown persons, it should be safe to fix the season's catch at about 1,400. On November 28, after the muskrat trapping ceased and during a period favorable for observation through thin ice, signs of considerable numbers of muskrats could be made out in the vicinity of burrows of the north-central and northeast shores. Possibly as many as 200 survived the trapping on the whole marsh.

Working backward from an early winter population figure of about 1,600, I think it possible to trace the course of numbers in the muskrats from the May population of about 900.

In a 1,000-carass sample obtained for examination from the fur trappers at Little Wall Lake in November, 1944, there were 78 adult males, 110 adult females, 440 young males, and 372 young females. From these ratios, it may be computed that a population of 1,600 on November 10 would consist, in round numbers, of about 125 adult males and 175 adult females, or a total of 300 adults; 700 young males and 600 young females, or a total of 1,300 young. Assuming that the ingress from surrounding habitats was inconsequential — which is surely to be expected, in view of the critical situation — about 600 or two-thirds of the adults had been lost from Little Wall Lake in one way or another since May.

If the 437 May territories be accepted as the equivalent of females among 900 adults, the May to November reduction of adult males and females would figure out at about 340 and 260, respectively. Part of the differential mortality suffered by the adult males would be in keeping with that commonly taking place during the warmer months (Errington, 1943), but the known ratio of only 42 per cent males in the adults alive by fall indicates, moreover, exceptionally severe differential mortality.

In the sample of 90 adult females the uteri of which contributed data on the 1944 breeding at Little Wall Lake, 9 (10.0 per cent) had not conceived during that breeding season. Eight (8.9 per cent) had conceived one litter each; 35 (38.9 per cent), two litters each; another 35, three litters each; and 3 (3.3 per cent), four litters each. The mean number of litters was 2.17 per adult female and 2.41 per breeding female. The recognized placental scars in 195 sets, or litters, averaged 6.68. Of the 81 breeding females in the trapped sample, 61 were judged to have given birth to their last young in June or earlier, 17 in July, and 3 in August.

The 90 adult females had totals of 761 placental scars assignable to 114 litters judged to have been born prior to the month of June and 541 scars corresponding to 81 litters born in June or later. Prorata computations from the May base of 437 females would give a figure of nearly 3,700 young conceived if not born for the high-survival part of the season. For June, the count was 407 scars in 59 sets; the females giving birth to and caring for these young suffered light enough known loss so that a 425-female base would seem reasonable; and, using this, we get a total of over 1,900 June young conceived or born. The late

summer losses of adults, including females, were sufficient to lower the base of adult females to about 300 for the July and August young, which, for 134 placental scars in the 90-female sample, would give a total figure of nearly 450 conceived or born. The totals for young conceived or born on Little Wall Lake during the breeding season of 1944, as thus figured, would come to about 6,060, or in rounder numbers, about 6,000.

The muskrats alive on the marsh at one time doubtless reached maximum numbers early in June, before losses of either adults or young became excessive. The previously indicated rearing of about half of the total numbers of young conceived would afford grounds for estimating that about 3,000 of the early young were alive and reared up to stages of relative independence by early June. To these we may add the June-born, alive as of the middle of the month, though largely doomed to be lost later — perhaps about 1,500. The July and August young may here be ignored, as their births chiefly constituted wastage in an accelerating decline. Counting about 850 adults, Little Wall Lake should have had a grand total of about 5,350 muskrats of all ages at the peak of the 1944 population.

In mid-August, conditions for study were such that quite accurate counts of lodge-dwelling populations were possible on about half of the area where lodges remained, and, on the other half, estimates were made from sample counts. The total arrived at for the lodge-dwellers was 1,240. By the end of the month, the muskrats regularly living in lodges were drastically lowered through destruction of lodges and shoreward movements, until the sample counts gave a figure scarcely in excess of 400. In early September, the lodge-dwellers were reduced to probably between 200 and 300 — then, their numbers seemed to remain rather stabilized for about a month. Further reduction resulted from storms in October and early November. Trappers' catches suggested a lodge-dwelling population of about 250 as of November 10.

The true bank-dwellers could not be satisfactorily counted in life, though frequent attempts were made to do so by watching sample stretches of shore and adjacent water at hours of the day most conducive to muskrat activity. Except along the disease-depopulated shores, however, the numbers of animals resident in the banks were not believed to have changed a great deal between mid-August and November 10. Approximately 1,150 were taken by trappers from the bank population, which number added to about 200 bank-dwellers surviving the trapping would give a total of about 1,350. The mid-August population of bank dwellers should have been perhaps about 1,400, plus the number of resident animals that died from epizootic disease in October and early November.

The disease victims — ignoring those scattered along lightly-affected shores — made up the equivalent of the entire bank population of about 600 yards of the very heavily populated west shore. From what is known of nearly annihilative trappers' catches along and out from stretches that had comparable densities before the epizootic, the late

fall disease loss may be estimated at about 350. The 350 that died from disease added to 1,400 would give a total of about 1,750 bank dwellers, as of mid-August, which added to 1,240 lodge muskrats would give a postbreeding population of about 3,000.

In recapitulation, the available figures for the Little Wall Lake population in 1944 may be listed according to certain periods: early March, about 1,200 adults; mid-April, about 1,000 adults, plus some of the earliest young; mid-June, about 5,350 of all ages, including about 850 adults; mid-August, about 3,000, including probably not more than 600 adults; November 10, about 1,600, including about 300 adults; late November, possibly 200 after the trapping.

#### **THE YEARS OF SUSPECTED CYCLIC LOW, 1945-47**

General evidence suggests that the low phase of the 10-year cycle operated in north central United States somewhere during the years 1945 to 1947 (Errington, 1954a; 1957). No attempt will be made in this chapter to discuss fully the phenomenon with respect to the muskrat; rather, the Little Wall Lake case history will be continued as a presentation of data, and the cyclic aspects thereof will be reserved for more nearly adequate treatment later. The mere fact of low densities should not necessarily be construed as evidence of cyclic depression, nor should overmuch significance be laid to epizootic disease, *per se*, as a mechanism.

Following the melting of the ice and disintegration of deep water lodges through wave action in the middle of March, 1945, 21 specimens of dead muskrats were retrieved. Judging from the appearance of their internal sex organs, these victims had died in late November or early December. Despite the partly decomposed state of the specimens, their viscera remained sufficiently unchanged to show disease lesions in nine, and it is likely that most of the others died from the same cause. The spring distribution of the victims and the last information obtained on the spread of the disease in November make it reasonably certain that an epizootic took place after freeze-up in the north part of the marsh, where the most muskrats survived the trapping. The muskrats of this part, however, were by no means completely eliminated by the disease during the winter.

On March 29, 1945, a recently dead specimen was found near the north shore with a bloody anus suggesting the disease, but visceral decay was too far advanced to permit clearer diagnosis.

Minks were scarce, if present at all, on Little Wall Lake in December, 1944, and early January, 1945. Toward the middle of January, coincident with a pronounced acceleration of mink movements on central Iowa observational areas generally, one mink appeared and lived in or near some muskrat burrows that had been depopulated by the epizootic in October. The frozen bodies of disease victims were apparently the principal attraction for the mink, and the only mink scat found here for this period consisted of muskrat remains. A fragmentary mink-eaten carcass also was found in a snow tunnel leading

into one of the burrows. From late January to the middle of February, a single muskrat representation occurred in 35 mink scats.

Shortly after the middle of February, a mink — probably the above-mentioned — moved into an enormous snowdrift across the lake to the northeast. On March 16, after the drift melted, four mink-eaten carcasses of muskrats were distinguished in the debris at the site, and 38 of 44 of the associated mink scats contained muskrat remains. The one carcass complete enough to indicate the status of a victim had had the end of its tail frozen off during the winter — a sure mark of a wanderer or of an otherwise ill-situated individual. Muskrat remains were found in two of 14 mink scats deposited elsewhere about the marsh in the first half of March.

On March 19, 1945, at least a dozen muskrats were seen along the west side of Little Wall Lake, which suggests a fair winter survival, the disease loss notwithstanding. The best estimate I could make was of between 100 and 125 alive on the whole marsh, as of early April. In consequence of the spring dispersal and a sweeping epizootic getting underway in late April (after months of no detected disease losses), the population was reduced to the equivalent of eight pairs and enough extra animals to bring the total of resident muskrats up to about 20. Seven dead were found between April 23 and June 20, of which 4 were surely or probably diseased.

Young were known to have been born at only four places (including one at which the mother died), but postbreeding ingress introduced such a big variable that the significance of November data on placental scars cannot be clearly judged. Three of 11 adult females examined had conceived 3 or 4 litters each in 1945, and 2 other females had conceived 2 litters each — which should be considered along with the evidence on very poor reproductive success obtained through the 1945 field studies at Little Wall Lake. Of the other 6 adult females examined from Little Wall Lake in November, 4 had not conceived in 1945, and 2 had conceived a single late litter each — which looks more like what had been the performance of the local stock. Of 83 trapped carcasses examined, 4 were adult males, 10 adult females, 43 young males, and 26 young females.

From August to the opening of the trapping season, November 10, 8 dead were found. These included 2 old animals with multiple abscesses in their viscera but no recognized victims of the hemorrhagic disease nor of predation. No muskrat remains were found in 309 mink scats deposited between late March and the middle of August. Nor did the local muskrats suffer observed intraspecific strife even when an estimated 200 to 250 newcomers appeared at the marsh in late summer, to bring the pre-trapping population up to about 300.

The reported trappers' catch was 184, and an early December checkup (after the muskrat trapping and while the ice was clear enough to allow an excellent view beneath) gave the basis for population estimates of about 100. The marsh was in highly satisfactory condition for the existing muskrats, as fine growths of river bulrushes dominated the previously lakelike west half.

The population wintered with no detected loss from December, 1945, to early March, 1946. No muskrat remains were found in 64 mink scats deposited in January and February. When the ice receded from the shore in early March, muskrats came out in all places where their presence could have been expected from the December signs. The spring signs also indicated a Little Wall Lake population in the vicinity of 100 animals.

The mink-eaten remains of an undersized muskrat were traced to about this time, and 1 of 6 similarly dated mink scats picked up nearby consisted of muskrat remains. Of 26 mink scats examined during the rest of March, none contained muskrat remains, and muskrats were seen to be getting along in a normal manner for this season, with the exception of two specimens dying about March 19 from the hemorrhagic disease. No epizootic materialized, however.

The perfect 1945-46 winter survival at Little Wall Lake contrasts with an approximately 80 per cent loss for Goose Lake (see Chapter 9). The rain and thaw, which temporarily flooded out the muskrats from their dry burrows under the ice at Goose Lake, merely deepened the water and raised the ice a few inches at Little Wall Lake. This rise was without complications for the Little Wall Lake muskrats, though both they and the Goose Lake muskrats were essentially restricted to shore zones, and were roughly comparable in per-acre densities for the tracts occupied. Seemingly about the same number of minks (three or four?) hunted the muskrat-occupied tracts of each marsh, and almost certainly individual minks visited both places. The minks also entered the water by penetrating muskrat habitations at Little Wall Lake as at Goose Lake; and, at both lakes, they had similarly convenient access to similar types of food other than muskrats. The muskrats at Little Wall Lake were patently secure, living disease-free in moderate abundance and in habitat characterized by satisfactory food, water depths, and burrow systems.

The 1946 spring population of Little Wall Lake had, by May, leveled off through dispersal to the equivalent of about 22 pairs, or about 50 adults. This number was further reduced to about 19 pairs or possibly 40 adults during the summer. Nevertheless, only 4 dead (including a five-weeks victim of a mink and a large young that someone wantonly had shot) were found from April through October. The only muskrat remains in 554 contemporaneously dated mink scats were apparently of the one five-weeks victim, represented in 5 scats.

The marsh remained in good condition for muskrats throughout summer and fall of 1946. It attracted many immigrants, as in 1945, and this ingress followed the same chronology in 1946 as in 1945. The 1946 breeding season at Little Wall Lake, however, was one of sufficient local reproduction so that a much greater proportion of the animals present by the November trapping was of resident adults and their progeny than had been the case in 1945.

Prior to the 1946 trapping, the marsh had been divided into two parts. One part, on the west side, was a breeding stock refuge for fur animals. The other part, larger but not so well populated, was open



to public exploitation. The total reported trappers' catch of muskrats was 227, and it is unlikely that the actual catch exceeded 250. By March 22, 1947, just before the spring dispersal began here, the signs of muskrats surviving on the trapped part became rather evident, and, from this, an estimate of about 30 animals was made on the basis of personal trapping experience. On the refuge side, the muskrat population was estimated, in a similar way, at about 345, as of November 27, 1946. These figures suggest an early November (pre-trapping) population of about 625.

A sample of 140 carcasses trapped at Little Wall Lake in 1946 consisted of 8 adult males, 9 adult females, 70 young males and 53 young females. The age ratio from the sample applied to a total of 625 animals would give a fall population of about 75 adults and about 550 young. The Little Wall Lake ratio of 12.1 per cent adults differs only insignificantly from the 12.5 per cent obtained from 438 carcasses from all central Iowa sources in 1946 (28 adult males, 27 adult females, 203 young males, 175 young females, and 5 young of undetermined sex). The Little Wall Lake age ratio would give a figure of about 290 young for 40 resident adults or 330 animals all together; if this be close to the number of true residents, then it would seem that about 300 animals might represent postbreeding immigrants. The field evidence suggested that most of the newcomers established themselves in centrally located growths of bulrushes — at least a great many of them did, in places a quarter-mile or farther from any of the shore zones dominated by residents of the summer's breeding territories.

The 1946 data from placental scars suggest more irregularity in breeding among 10 adult females examined from Little Wall Lake than among 17 females examined from central Iowa streams. Four of the 10 females from Little Wall Lake either had not conceived in 1946 or had conceived but a single litter, whereas only 2 of the 17 stream females had conceived but single litters. The other 6 of the Little Wall Lake females averaged 3 litters each, and the other 15 of the stream females averaged slightly under 2.9 litters each. Of 20 litters conceived by Little Wall Lake females, 9 had been due for birth before June, as had 22 of 43 litters of stream females. Differences in the reproductive performances of the two groups of females may be ascribed in part to isolation of certain territories interfering with the mating of some of the females living at Little Wall Lake.

The detected wintering loss for 1946–47 was three animals, which doubtless does not represent all that died; but the loss was surely low, especially in view of the continued frequency of signs on the refuge tract. Of these dead, one was recognized as a victim of the hemorrhagic disease, dying about the middle of February near what had been the old west central focus of infection of October, 1944. A new epizootic slowly made headway from here as spring progressed.

Another correlation between winter feeding by minks upon muskrats locally suffering from disease was shown by the 1946–47 data from

Little Wall Lake. No muskrat remains were found in 320 fall scats deposited before the November trapping, despite the presence of hundreds of muskrats. Neither were muskrat remains found in 47 scats deposited from the middle of January to early February. Then, the first muskrat known to have died from the disease during the winter died about the time that the first muskrat remains began to appear in the mink scats. Eight of 30 scats deposited from the middle of February to early March contained muskrat remains, and all of the muskrat-containing scats came from the site of the disease flare-up. For the middle of March to late March, only one of 33 scats contained this item; at the very end of the month, all of 6 scattered droppings were made up of muskrat remains, but this was probably associated with dispersal vulnerability more than with the disease. No muskrat remains were found in 5 April scats.

It may be mentioned that central Iowa minks had been so nearly annihilated by the 1946-47 fur trapping that untrapped Goose Lake was almost the only one of my observational areas that harbored any minks at all by January, 1947. Of the four minks that were distinguishable more or less satisfactorily on the basis of tracks or trails at Goose Lake, the biggest seemingly started visiting Little Wall Lake in early January, finally frequenting Little Wall Lake regularly after the middle of February. This big mink was most probably one of the principal exploiters of a stricken muskrat population at Goose Lake (see Chapter 9), yet its depredations upon uninfected muskrats at Little Wall Lake were surely negligible.

Between the middle of March and the fore part of July, 1947, 53 dead muskrats were examined from Little Wall Lake. Thirty-eight of these were certainly or very probably victims of the epizootic disease, 7 were transients killed by a dog near a lake-side set of farm buildings, one was found shot, and 7 (including 5 weaned young) died from undetermined causes.

Before the middle of April, the epizootic nearly depopulated about 300 yards of the shore zone having the most muskrats, possibly killing up to 100 during this time in a strip totaling about two acres in area. It was judged that most of the resident victims died out of sight in the bank burrows and were not seen. Only two lodges were situated here, and these, when opened, had three victims inside compared with one outside. Of five February and March victims the sexes of which were recorded, only two were males; then, as newcomers made up an increasing proportion of the victims in early April, the ratio of males changed to seven out of eight. Except for a corner of the marsh where victims were known to die 600 to 750 yards north of the focus of infection in mid-April, evidences of the epizootic were restricted to the vicinity of the original west central focus until late April.

Starting about the last week of April, muskrats died conspicuously in places along the northeast and southwest shores for a couple of weeks. A ratio of 11 males to 10 females in the dead would seem rep-

representative of the local residents. After this, a few more diseased or probably diseased dead were found: a female dying about May 18, a male on May 21, and another male about June 21. By the time that the epizootic subsided, after killing an estimated 200 muskrats, all sites where disease victims had not been found were in the south part of the marsh, and the apparently uninfected shore zone constituted roughly a third of the total muskrat-occupied periphery.

A remaining population of 29 adult females and associated males, or a total of about 60 adults, was arrived at through the field studies after the epizootic subsided, or as of late May to the middle of June. One breeding female was found dead for this period, but she had given birth to two litters before dying.

The heavy June rains of 1947 actually filled Little Wall Lake to overflowing, the water running off into the outlet over a wide flat depression. The deep-water bulrush stands covered a good half of the marsh but they seemed thinner than at midsummer, 1946. The bulrushes still comprised excellent habitat for muskrats, which, however, were making but limited use of them on July 22, when fewer than half a dozen individuals — all adults — were seen far out from shore. Even by the middle of September, relatively few muskrats were living out of convenient reach of the bank burrows.

During July, August, and early September, 1947, the survivors of the epizootic and their offspring seemed to be getting along well. Four of 587 late June to early September mink scats contained muskrat remains, one representation being of a young muskrat of about five weeks killed about early July. In this particular case, a female mink took over an isolated burrow system (the only muskrat-occupied one in the whole east shore) for her own family, and the muskrats resident there responded to the mink intrusion by excavating another set of burrows about five yards away. In their new quarters, this family group of muskrats seemed to live securely after the earlier loss of a member. The other muskrat remains were of an animal possibly two months of age judged to have been eaten in late June and two representations of an animal of three to three and one-half months, eaten in late August. Remains of an adult muskrat were also found in a raccoon scat deposited about mid-August, and a dead muskrat was found corresponding to the fecal contents. A female muskrat that had given birth to two early litters died from probable hemorrhagic disease on September 3.

The saturating rains of June were followed by a long, dry period, much of which was also very hot, but the water level of the marsh dropped only about 10 inches by August 13. On that date, a local thunderstorm brought up the level about five inches, but this gain was lost during the next four weeks. The signs continued to suggest a favorably situated population. As of September 10, no evidence of animals drifting to Little Wall Lake from outside was recognizable, though the flows of muskrat-occupied streams in the vicinity were becoming much diminished, and many of the residents at Goose Lake

were experiencing a drought crisis accompanied by extensive readjustments and a certain amount of mortality. On September 15, one of the season's young tagged at Goose Lake was found dead of the hemorrhagic disease on the southeast shore of Little Wall Lake. Later in the fall, two recognized transients were seen working the south and west shores.

By early October, there were about 16 muskrat lodges of habitable sizes in the central bulrushes, 7 of which were clumped together in an area of about an acre lying about 60 yards out from a series of abandoned bank burrows. It was quite apparent in the latter case that the muskrats had simply withdrawn to deeper waters of their regular home ranges. A few other lodges built in shallow water were clearly associated with bank burrows. What seemed to be an infected burrow system along the west side had the aspect of having been little used and was near the site where the dead muskrat was found on September 3, as well as near the raccoon-eaten body of mid-August. Still another possible disease victim was found near the burrow system on October 4.

There was other detected 1947 fall mortality at Little Wall Lake. Fragments of a subadult were found October 6 along the east shore, and contemporaneous remains of what looked like the same animal were found in 3 of 136 mink scats deposited from mid-September through November. On November 3, a subadult male was found that had been killed by a charge of shot and then scavenged upon by a mink.

The muskrats of Little Wall Lake were never seriously affected by drought in 1947, and rains in late October improved their situation still more. In view of a closed trapping season on muskrats in the fall of 1947, the best I could do to obtain representative sex and age ratios was to compile data from animals found dead, excluding suspected victims of old age. The Little Wall Lake specimens actually handled were 7 adults (4 males, 3 females) and 25 young (16 males, 9 females), but, because of the smallness of the sample, more nearly representative ratios would probably be obtained by considering along with these data those from other central Iowa areas. The Little Wall Lake series added to 58 specimens from neighboring Goose Lake and 11 from Keigley's Branch and Squaw Creek drainages, would give totals of 19 adults (7 males, 8 females, and 4 of undetermined sex) and 82 young (36 males, 20 females, and 26 of undetermined sex).

From available data, we may judge that about 24 of the original breeding females of Little Wall Lake for 1947 were still alive and present in the fall. Application of the over-all central Iowa sex and age data to 24 adult females at Little Wall Lake would give a figure of about 243, which might be assumed to represent essentially the truly resident fall population. Allowing for about 50 animals coming in — which I think should be ample allowance, considering the scarcity of muskrats in the central bulrushes — the total fall population should be around 300.

This population wintered with little loss until March, 1948. Only

two winter dead were found, of which one was an old male suspected of having died from age. None of 10 mink scats deposited, December through February, contained muskrat remains.

#### **THE BREEDING AND POSTBREEDING MONTHS OF 1948 AND 1949, TWO YEARS OF SPORADIC DISEASE LOSSES AND LOWERING WATER LEVELS**

From March well into May, 1948, intraspecific tensions among the Little Wall Lake muskrats were manifested by shore-wandering, fighting, and mortality from predation — particularly along the west shore, which was frequented by a disproportionate number of the total population of some 300 muskrats. That the minks responded is shown by the incidence of muskrat remains in 14 of 21 scats examined for March and early April. Beginning about the middle of March, as more and more dispersing animals and territory seekers worked the shore, a farm dog largely took the place of the minks as a lethal agent, until it lost interest in the muskrats and stopped its deliberate hunting of them soon after the middle of April. Thirteen victims of the dog were examined between March 18 and April 15: two old males, one old female, eight immature or newly mature males, and two immature females. These specimens probably comprised a fair cross-section of the shore-dwelling population of transients, but they may also have included a few true residents.

Muskrat victims of motor traffic were found on U.S. highway 69, at the west side of Little Wall Lake, on March 3 and April 25. An adult female, dead from unknown cause, was found April 5. A local epizootic of the hemorrhagic disease started killing muskrats toward the middle of March; this die-off coincided in time and place (the northwest corner of the marsh) with the dog killings, but the dog victims showed no recognized disease lesions.

The epizootic “smoldered” for the next two months, killing a known two or three muskrats a week between early April and early May in the northwest corner. On May 5, a disease victim (dead about two days) was found along the west central shore, several hundreds of yards to the south of the sites of dying earlier in the spring, and a second victim was found, freshly dead, at the new place on May 10. Of the 13 verified or highly probable disease victims examined, the sexes and age classes of 11 were recorded: two old males, two old females, and two and five of immature or maturing males and females, respectively — presumably a cross-section of a largely settled population.

After May 10, the epizootic seemed to subside, and no muskrat remains were found in 70 early-summer mink scats. But, for August, a time when certain burrow sets along the west central shore became mysteriously muskrat-vacant, eight of 39 scats contained muskrat remains, as did three of five scats deposited in late October and early November at a well-known old infection focus. Remains were found of only a single animal that may have died of disease between June and September, that one also dying along the west central shore.

The 1948 breeding population was the equivalent of 89 pairs, or, using the previous winter's sex ratios, a total of about 225 adults, as of early and into mid-May. The territories were massed along the more attractive parts of the west and south shores and especially in places having burrow systems of previous years. There was, nevertheless, sufficient crowding to result in considerable establishment of breeding territories in some of the less habitable stretches of shore along the north and east sides. Substantial emigration took place in late May and early June, but 50 territories were still being maintained by August. By the end of August, four territories had been lost from disease. In view of the lack of evidence of cross-country movement in late summer and fall, even as central Iowa streams dried up, I am sure that little emigration from Little Wall Lake occurred during the months immediately preceding September. By then, the upper parts of numerous burrow systems were exposed but not enough, on the whole, to cause their occupants any real inconvenience or danger. Indeed, the latter made easy adjustments as the water continued to recede slowly until November rains came.

Of five muskrats dying about freeze-up in 1948 and prior to the opening of the trapping season on December 1, two (an adult and a young male) were found dead of shot wounds, two were adult females dying from unknown causes (possibly disease and old age), and the fifth was a large young male having a very severe strife wound across hindquarters and abdomen. Two subadults lay freshly dead, November 29, on the shore of a private impoundment east of the marsh; these evidently had been killed by a dog, their wounds suggesting powerful bites and "mouthing." The same area of Little Wall Lake that served as a fur refuge in the fall of 1946 was also reserved for the same purpose in 1948, and the known legal catch from the parts open to trapping totaled 93, of which the carcasses of 84 were examined. All together, counting animals dying from disease and predation, we have 97 specimens that we may regard as a nearly random sample for the winter of 1948-49: 9 adult males, 12 adult females, 52 young males, and 24 young females. The latter sex and age ratios applied to the 46 of the 1948 adult females judged to have been still present in the fall at Little Wall Lake would give a fall population of about 370, including about 290 young of the year.

After the trapping, excellent current signs were to be seen about one burrow system in the part of the marsh that had been open to trapping, and nine other places of that part also showed evidences of living muskrats. Nearly half of the shore zone had been depopulated by the trapping, and my estimate of the number of muskrats that escaped the trapping on the trapped area was about 40. On the refuge tract were 25 major sets of burrows and 31 more or less independent minor ones; if an average of six muskrats apiece be assigned to the major burrows and three to the minor ones, the early winter population of the refuge would amount to nearly 245. This figure added to the known trapping catch of 93 and the estimated 40 escap-

ing the trapping off the refuge would give a grand total of about 375, which is not far from the 370 computed through sex and age ratios and the fall territorial data.

Ten of the adult females examined from fall, 1948, to spring, 1949, were in good enough condition to permit counting and aging of placental scars. One had not conceived in 1948; 2 had conceived two litters each; 5, three litters; and 2, four litters. Four of the 27 litters indicated by the placental scars were assigned to the early part of the breeding season; 19 to a mid-season (May-June-July) grouping; and four were late litters, including one probably born about the first of September. Three of the four females conceiving late litters had also conceived early ones and then apparently passed through about two months without conceiving until the times of their late pregnancies.

The muskrats surviving the trapping at Little Wall Lake wintered very well, 1948-49, both on and off the refuge tract, except for a single known transient frequenting the south shore and the occupants of a single burrow at the southwest corner of the marsh. During the first half of the winter, five of nine mink scats picked up near this burrow (the chamber of which had been opened by a mink) contained muskrat remains, compared with no muskrat representations in eight winter scats found away from this site. Such a high incidence in scat samples for a period of several weeks between mid-December and February was considered most suggestive, though not fully appraisable at the time. The possible presence of dead muskrats in or about this particular burrow was kept in mind, and, when the ice went out, six water-rotted but otherwise nearly intact bodies came to shore nearby. The four best-preserved specimens of these were young animals having charactersitic liver lesions and appearances, despite post-mortem changes, of acute enteritis. Deaths of all six were dated back to about December, 1948, on the basis of their sexual states.

The vicinity of the burrow was watched in the spring for evidence of recurrence of the local die-off. However, the upper part of the burrow, along with whatever muskrat remains were in it, became effectually buried by the push of the midwinter ice, and later wave action erased the external evidences of former muskrat activity. In the course of the spring and summer of 1949, muskrats rehabilitated another old burrow system some yards from the infected one, but they did not seem to get into the latter.

Miscellaneous spring mortality recorded in 1949 at Little Wall Lake included a muskrat killed on the highway on May 9, an adult female killed by a .22 caliber bullet in late March, and two dog victims (both newly-mature males) examined March 28 and May 26. On May 24, an old male muskrat, dead about two days, was found outside one of the west central burrows where late spring and early summer disease mortality had occurred in 1948; its disease syndrome was chiefly pneumonic, but it had liver and intestinal lesions as well.

The settled breeding population at Little Wall Lake in 1949 was the equivalent of 35 pairs as of May 26, 3 pairs lower than at the first census of early May. The sex ratio of 62.0 per cent males obtained for the winter specimens applied to 35 territories would give a calculated total population of about 95 adults.

The water had receded enough from the shoreline ice ridges by June to expose the upper parts of some of the channels leading to the muskrat chambers in the banks. During a dry summer, it receded still more until, by early October, it was down well over two feet below the 1944 overflow level. The muskrats of the one stretch of shore having good bulrush stands within easy reach abandoned the shore burrows to build lodges in the bulrushes. Elsewhere about Little Wall Lake in 1949, the muskrats responded by deepening burrows and channels, plugging caved-in parts of chambers, improvising nests under root tangles of trees, building shoreline lodges or small structures out in shallow water, on floating logs, boats, and other floating objects.

Summer mortality appeared to be quite heavy. The incidence of muskrat remains in mink scats was high — 11 in 24 scats examined for that season, compared with one in 29 for September — and some of this surely could have represented mink predation upon occupants of exposed burrows. The remains of the muskrat in the September scat were of a "kit," whereas those in the summer scats ranged from "kits" to adults — mostly adults and subadults. Mink-eaten remains of an adult were also dated to the middle of September. Several burrow systems retaining plenty of water and appearing to be entirely habitable took on unused aspects suggestive of a continuing summer epizootic. The majority of these dead burrow systems were restricted to that part of the marsh (the northwest shore) where dying from disease had occurred during the spring and summer of 1948. The hemorrhagic disease was almost certainly the agency of much of the 1959 summer loss at Little Wall Lake.

There were a good many signs of activity along the west shore in early October, but, by the latter part of that month the patently regular residents were living in small to medium-sized, off-shore lodges, and such few animals as continued to frequent the shore were suspected of being transients. Fifteen of 82 October mink scats contained muskrat remains. One scat deposited about October 26 consisted of remains of a "kit." The October scats with muskrat representations were found scattered about the periphery of the marsh, hence were not indicative of any particularly localized availability of muskrats.

Numerous muskrats were reported as having been wantonly shot by duck hunters in the central bulrushes shortly before freeze-up, but, although I worked this area several times as soon as the ice would hold me, I did not succeed in finding them. There remains the question of whether a group of several said to have been floating in one part of the marsh might have been disease victims instead. An adult



male turned in by a trapper in early December had dozens of liver lesions that did not look quite typical for the hemorrhagic disease.

The experimental fur refuge area was changed in 1949 to give legal protection from trapping to the muskrats of about the south third of the marsh. Fifty-six December-caught carcasses from Little Wall Lake were examined, along with 21 others from a neighboring drainage ditch. Sex and age ratios for the Little Wall Lake sample were 9 adult males, 8 adult females, 18 young males (including 6 "kits"), and 21 young females (including 8 "kits"). For the Little Wall Lake and ditch samples combined, the ratios were 12 adult males, 10 adult females, 27 young males (including seven "kits"), and 28 young females (including 10 "kits"). Of the 8 adult females from Little Wall Lake, one had not conceived in 1949, one had conceived two litters, and 6 had conceived three litters each; 4 of 20 sets of placental scars represented young born later than late July. The two adult females from the ditch had conceived 45 young in five litters between them, including one litter assigned to August.

The variables introduced by disease, partial drought exposure, and ingress make calculating the fall population a very tricky matter. Splendid visibility under new ice in December, 1949 (after the trapping had practically ceased) permitted counts of 7 heavily used lodges or burrow systems in the refuge area and 2 more outside of it; about 8 muskrats may be provisionally assigned to each. There were also 27 moderately well-used lodges or burrows on the refuge and 20 more outside; perhaps 5 muskrats may be assigned to each of these. Thirteen places having few signs but at least a single muskrat were counted on the refuge and 29 more outside; assignment of a single muskrat to each of these would result in underestimation, but, since the assignment of 5 muskrats to each of the moderately used habitations may result in some overestimation, the two errors may tend to counterbalance.

Allowing for 14 muskrats caught after the census counts, the above bases would give a total of about 205 muskrats alive on the refuge and about 130 on the trapped part after the trapping. The trapping itself was of very moderate intensity, with no known loss from wringing, and the 56 muskrats examined may be regarded as the total catch. The catch, added to the post-trapping estimates, would give a pre-trapping total of about 390, with more than half of these being on the refuge.

The data for early September, 1949, indicate that perhaps three of the adult females had been lost during the summer at Little Wall Lake, plus adult males and large numbers of the season's young. The losses of young, in fact, seemed to have been disproportionately heavy. Fourteen "kits" were listed among the 39 young of the trappers' catches, and, in actuality, the proportions of late-born young were still higher, as five other of the 39 young were plainly small, yet not quite small enough to have been graded as "kits." When

nearly half of the total sample of young of the year trapped in December turn out to have been late-born, compared with only a fifth of the season's known litters having being born as late as this, something must have happened to many of the early-born young. The high percentage of late litters among the total conceived may in itself be regarded as evidence of compensatory breeding in response to unusual losses of early and mid-season young.

A fall figure of 32 adult females used as a base for calculating the resident population at Little Wall Lake would give a total of about 225, whether through application of the sex and age ratios of the trapped specimens from that marsh alone, or the ratios from the marsh specimens plus those of the ditch nearby. The pre-trapping total of about 390 minus 225 residents would then make it appear that numbers in excess of 165 may have come into the marsh in October, when so much evidence (shore signs and mink predation) of transients was seen, especially early in the month.

The population of around 335 muskrats calculated to have survived the 1949 trapping wintered securely and comfortably despite the low water level and the presence of only fair food resources about the shore zone. The ice in no case thickened to the extent of completely cutting off the food of any wintering group of muskrats, and there was always water in the channels even of the partly exposed burrow systems. Two bodies of young muskrats datable to early winter were found after the ice went out along the west central shore; these were suspected of having been diseased. No muskrat remains were found in five midwinter mink scats.

#### **THE BREEDING AND POSTBREEDING MONTHS OF 1950-52**

In late February and March, 1950, some mortality of the muskrats of lodges in the central bulrushes became apparent, as two of five locally deposited mink scats contained muskrat remains. Both of these two scats having muskrat representations were from repeatedly "bored" lodges of the south center. They were believed to have reflected increasing intraspecific tensions of late February in the most densely populated part of the marsh, for it was on the nearest shore that the signs of dispersal and land activity first became pronounced after the ice melted around the margins in late March. Fifty-two mink scats of similar dating from elsewhere about Little Wall Lake contained no muskrat remains. Nine muskrats dying in late March and April were found: five traffic and four disease victims. Three of the traffic victims — and later associated with them the body of a mink, presumably killed while scavenging — appeared to have been struck as a group.

The spring dispersal occurred in two big movements, the first following the shore activities on the refuge tract in March and involving possibly as many as 100 animals. This was no doubt hastened by wind action breaking up all the lodges in the south central bulrushes,

thus evicting their occupants from the part of the marsh in which they may be said to have had property rights. The second big movement culminated in mid-April, and evidences thereof were most pronounced about the rest of the heavily populated refuge tract, particularly that of the southwest corner of Little Wall Lake. Food shortage may well have had something to do with the magnitude of the dispersal here, for animals that I watched feeding seemed to eat about everything that was at all edible, searching the drift for particles of green vegetation, etc. The majority did not have ready access to any choice foods, such as bulrush rootstocks.

Of the 335 muskrats calculated to have survived the fur trapping, fewer than 100 remained as the breeding population, as of the first of May, 1950. At this time, 33 breeding territories were distinguished. There were three main sets of burrows that might be considered as infected with the hemorrhagic disease in the winter and spring of 1949–50 and in which more muskrats may have died concealed underground than were retrieved; and these had had a total early winter population estimated at about 25. If it be assumed that the occupants of these burrows died out before spring, and if an allowance be made for about 15 dying from miscellaneous causes in late winter and early spring (11 individuals were accounted for), then about 200 of the spring decline of 1950 might be chargeable to dispersal.

As in early May, the late May checkup gave 33 breeding territories, but the sites of three territories had been shifted considerable distances in the meantime. In all three cases involving big territorial shifts, the animals later abandoned their late May sites as well as those earlier maintained. By late June, one breeding territory was established in the central bulrushes, about 500 yards from one of the ephemeral shore-zone territories abandoned about this time; and the total number of maintained territories dropped to 29. Then, by late July, four more shore territories (in the southeast corner) disappeared, but with a corresponding increase of muskrats in the south part of the central bulrushes lying out from the vacated shore. By mid-August, the marsh seemed to have about the equivalent of 29 maintained territories, including four that were productive of few if any young.

Of the four unproductive territories, three were situated in partial isolation along the most sparsely populated stretches of the shore zone — the north end and the east central side. Along a stretch comprising about 2,000 yards, or about half of the shore zone of the marsh, there were, along with these three unproductive territories, only four productive ones. The sole territory of the better-populated shore that proved to be noticeably unproductive was adjacent to a territory of which the occupants were found to be dying of disease in late August and early September.

The latter disease victims were the only ones actually found at Little Wall Lake between late spring and midautumn, 1950, but two of the four territories becoming nonfunctional without compensating

gain elsewhere in early June were at sites of infection foci of the spring. The loss of one of the other territories in June may have been associated with the washing away of a shore lodge by high waves of a storm; this, though not attended by death of any adults (it probably did drown a litter of young), is thought to have been followed by departure of a female from the marsh.

Water levels of the marsh had been restored by May and June rains to within about a foot of overflowing into the outlet, and the water receded only to a moderate degree during the dry weather of late summer and early fall of 1950.

In early and mid-September, considerable local readjustment of the Little Wall Lake muskrats was in progress. Newcomers rehabilitated two of the previously abandoned territorial sites, and a group of animals established itself at one place about 150 yards away from any earlier 1950 retreat of muskrats. On September 21, signs of transient animals were recognizable along two other long-vacant stretches of shore.

Mid-November population estimates at Little Wall Lake, made with the aid of good bubble signs under clear ice, totaled about 435. The sample of 125 carcasses examined consisted of 8 adult males, 9 adult females, and 108 young of the year. These ratios, applied to the 29 adult females judged to have been alive and present in maintained territories (including four territories that were productive of few or no young) by mid-August, would give a total fall figure of about 400. The latter figure should be very close to the actual pre-trapping population, distributed as about 160 in a fur refuge area in the south part of the marsh and about 240 in the north part open to trapping.

Two adult females in addition to the above 9 yielded reproductive data for Little Wall Lake in the fall of 1950. Two of the total of 11 examined had not conceived in 1950 — which fits in with the field data obtained from the summer's territorial studies — but 7 females had conceived 3 litters each and 2 females had conceived 4 litters each in 1950. A single small female judged to have been born in May, 1950, herself gave birth to a litter of 4 young in August. The nine 1950 breeders among the 11 adult females conceived a mean of 24 young; and, of the 29 litters conceived, the births of 4 were dated to May, 9 to June, 9 to July, and 7 to August and September.

The main event affecting the Little Wall Lake muskrats before the trapping was a northwest windstorm reaching its height on November 9. It washed away the lodges of a centrally located tract of hardstem bulrushes. Individuals that had merely extended their home ranges from bank burrows to deep water lodges returned to the familiar banks when their lodges disintegrated, but many of those living far out in the marsh came ashore as evicted strangers, and the behavior of these latter was repeatedly observed.

Four homeless muskrats (two big ones, one of medium size, and a rather small one) were seen sitting out the storm along the wave-

beaten southeast shore on November 9, and a mink scat from the night consisted of muskrat remains. One mink scat deposited before the storm and seven deposited some days afterward were without muskrat remains. Two dead muskrats — old and young males — found intact in the rushy drift showed no disease lesions and were thought to have drowned in the violent waters. Four evidently wandering muskrats were reported by a hunter as taking refuge under a boat on the southwest shore, and other animals worked along the east shore. On November 14, three new superficial burrows were examined along the east central shore, of which one burrow had about three muskrats and the others single animals. Between these burrows and the part of the southeast shore where the four evicted ones had been seen on November 9 were at least six land holes that showed sign of temporary occupancy.

Land activities attributed to storm-evicted newcomers could be seen along most of the shore of Little Wall Lake up to the beginning of the trapping on November 25, and, in the refuge part, past the end of December in those places drawing the greater proportion of the homeless ones. One of the young females taken by a trapper was suspected of having been an animal trying to make late adjustments. It had a very severe, recently healed muskrat bite near the base of its tail.

The hemorrhagic disease, though still at Little Wall Lake in the fall of 1950, had almost no significance as a population depressant. Eight or 13.6 per cent of a lot of 59 trapped mostly from the west central shore — the deadliest part of the marsh from the standpoint of epizootiology — had liver lesions, an exceedingly high incidence in animals active enough to be caught in traps. But the post-mortem appearance of many of the lesions suggested good progress in natural healing. A single disease victim was found dead under the ice, and two others were examined from a privately-owned impoundment northeast of the marsh.

Water conditions were favorable on Little Wall Lake during the fall and winter of 1950–51, but the food supply was really good only in such places — mainly the central part — as were dominated by bulrushes. Elsewhere on the marsh, the muskrats subsisted upon rather inferior foods, particularly yellow water lily. During cold weather, this diet was supplemented by some feeding on the flesh of painted turtles and fishes. Nothing resembling a hunger crisis was noted, but, from the feeding behavior of the animals and the condition of specimens found dead through different agencies of mortality, it may be judged that the population on the whole tended to be somewhat undernourished.

The apparent food limitations were considered partly responsible for conspicuous unrest and movements away from the marsh in early April, 1951. Approximately 250 muskrats (nearly the whole population remaining after the fur trapping in early winter) had survived the

winter; yet by early May, only about 100 muskrats seemed to remain, these living in 41 fairly well recognized territories. Up to this time, little winter or spring mortality had occurred—7 dead from miscellaneous causes were found after the ice went out. However, by early June, the number of functional territories had been reduced to 24; by early July, to 15, plus 6 places having probably lone animals in residence, thus giving a total of perhaps 40 adults alive on the marsh. One stretch of shore zone having 9 original territories had a probably lone animal in residence by July 5. Another stretch having 12 original territories had 3 territories and 4 adults judged to be living alone by July 2. Only along 7 short stretches of shore could muskrats be said to be thriving by July. The losses continued, and, by mid-July, the east half of the marsh and most of the west half had almost no muskrats. Two groups of thriving muskrats were left, both groups living in the midst of superior food resources.

For many weeks it was not satisfactorily demonstrated that the 1951 population actually was being reduced to the extent indicated. Some stretches of shore had abundant signs and others, inexplicably, hardly any or none at all. The over-all pattern suggested an epizootic, but the muskrats had not died in important numbers during the preceding fall and winter, despite the very high incidence of sublethal cases of hemorrhagic disease; nor were more than a few found dead during the period of greatest decline in the spring and summer. The problem was met by watching closely the obviously functional territories, to see whether something diagnostic might happen and be recognized before the signs became obliterated through weather, wave action, scavengers, or decay.

The reduction proved indeed to have been due to an epizootic—apparently of the hemorrhagic disease, as usual, though of the deadly pneumonic syndrome. The fresher of 14 dead found in the course of special searches between mid-May and September showed extreme congestion of blood not only in the lungs but about the whole thorax. Virtually no other lesions were seen in the victims except for occasional more- or less-healed necrotic foci in some of the livers. Many animals appeared to be dying out of sight in the burrows. In two instances, I smelled odors of decay through the ground over the chambers of muskrat burrows. The 1951 epizootic seemed to be almost confined early in its course to the vicinities of old infection foci, spreading slowly as the season advanced until, by June, it got around the shore zone except for the two places mentioned. By August, it may well have covered all of the muskrat-occupied part. Then the dying slackened by fall. Six animals were found that died in October of which three had been shot by hunters, and the other three were not certain victims of the disease.

Little Wall Lake was minkless during the spring and summer of 1951 until one appeared in August. One of 72 mink scats deposited, August–October, contained muskrat remains. This muskrat-containing scat was found under circumstances suggesting that the victim had

newly arrived in a place that had been muskrat-vacant for months. A quite substantial (but local) movement occurred in late August and September along the shore away from the northwest part. Animals moved both southward along the west shore, and eastward and then southward along the north shore, to repopulate to a varying extent many of the vacant burrow systems.

From the first of November to the middle of that month, clear ice afforded good opportunities to read bubble signs in the vicinities of most of the used burrow systems of Little Wall Lake. It soon became apparent that a tremendous amount of variation in bubble signs was occurring between visits at the sites of some of the burrow systems. The latter variation was partly due to different intensities of muskrat activities along a given stretch of shore. Sometimes the muskrats would be mainly frequenting one set of burrows and then they would be frequenting one of the neighboring sets for a few days.

The state-owned area of Little Wall Lake was closed to trapping, but Leigh Johnson, the owner of the north end, was encouraged to trap his private holdings during the general open season so as to provide some definite population data that could be used as an index for estimating numbers of muskrats in untrapped parts. His catch of seven muskrats from the extreme northwest corner seemed to reduce by about a third the amount of bubble signs being laid down there; and the amounts of pre-trapping signs of that corner were compared with signs recorded on the same days and under comparable conditions along other stretches of shore. The shore habitat was blocked off for study according to similarities usually to be noted in quantities and distribution of bubble signs, not only on specific days but also for periods of days. From all of the data, one set checked against another, a final estimate of about 160 muskrats was arrived at, representing the population of Little Wall Lake as of early November.

The above population was evidently composed of the few survivors remaining of the spring and summer adults, plus the young reared in five highly productive territories, plus what young may have been reared in two other territories that may have been productive to some extent. No significant ingress of animals was believed to have increased the population of the marsh during the late summer and fall period of adjustment. All adjustments described at Little Wall Lake in detailed notes in 1951 were manifested by diminished signs in formerly occupied places, as animals established new quarters elsewhere. All fall, only one animal was noted that behaved like a footloose wanderer. This one lived by itself in the central bulrushes until forced ashore by a storm, after which it returned to the center. The marsh was outside of any known routes traveled by adjusting muskrats of the neighborhood in 1951.

Wintering losses, 1951-52, were fairly light and all but confined to a stretch of the south shore that had the greatest concentration of muskrats on the marsh. For the above stretch of shore, a population

of about 25 was estimated from signs after freeze-up, and this would seem to have been about the correct number. As spring approached, as many as 14 could be seen sitting together about a small patch of open water lying out from the best-used burrow system; six others were in sight at the same time, and there were at least three muskrats at other places in this stretch. In this group, remains of six dead were found. All had been fed upon by predators in mid- and late February and March, but the muskrats evidently had been dead since earlier in the winter. One of these had been dug out of a deep snowdrift by a fox. Another had suffered loss of some of its toes and tail through freezing before being eaten upon by minks, foxes, and crows. None of 78 mink scats deposited from late fall to early February contained muskrat remains, but 19 of 47 scats for the middle and latter part of February did, as did one of 50 March scats.

On March 31, a muskrat was found killed by highway traffic south of Little Wall Lake, and considerable breeding-season adjustment was by then in progress. The first evidence of animals dispersing from wintering quarters was seen on March 13. The best figures obtained for the late April to June period gave a total of about 42 breeding territories or, following a central Iowa sex ratio of 53.0 per cent males for the winter of 1951-52, about 90 adults. The greatest breeding concentration on the marsh was in the northwest corner, where four territories were found along a 140-yard stretch of food-rich shore. No further dying from disease was noted during the spring and early summer of 1952.

However, about late June, some dying from the pneumonic syndrome began at one place along the west shore, at one of the sites of mortality of previous years. This epizootic gained headway by mid-July, when dying was occurring in at least three widely separated places, including the old focus mentioned above. No muskrat remains were found in 48 mink scats for June, compared with remains in 5 of 161 July scats. By early and mid-August, animals were dying in several places along the west and south shores; and this continued to be the situation into late August and early September, when some very good specimens of pneumonic victims were examined. Of 24 mink scats recorded for August, 5 contained muskrat remains.

By mid-September, the dying seemed almost over. One animal having massive liver abscesses — these amounting to about two-thirds of the volume of the liver — was found dead on September 17 at one focus at which only pneumonic victims had previously been found in 1952. Dr. Paul C. Bennett, of the Iowa Veterinary Diagnostic Laboratory, obtained from these abscesses a pure culture of the pus-forming *Aerobacter aerogenes*, well known as a secondary invader. On October 15, another animal having massive multiple abscesses in the liver and other viscera was found at the same place, but it really had died of a terrific case of pneumonitis. A typical pneumonic victim was found on September 25 in the sparsely-populated hardstem bulrushes



of the center, well away from any known site of previous disease mortality.

The 22 dead (14 from newly-weaned to "kit" sizes, 4 subadults, and 4 adults) that were accounted for as individuals during the summer and early fall epizootic doubtless represented only a fairly small fraction of the total dying. Only 3 dead were found, for example, outside the burrow where the first dying was noted; yet this burrow had taken on a lifeless appearance by September, despite the fact that at least two and probably three litters of young had been born and reared there up to the time of dying. But, as a rule, not many of the burrow systems where animals were known to have died in 1952 showed evidence of annihilative or even severe losses. A burrow system, outside of which 4 dead had been found between late August and mid-September, was heavily used by muskrats through September. Another dead muskrat was found here on November 1.

Few mink scats were obtained in midfall, only nine (none with muskrat remains) for early October. There were, in fact, very few minks around after midyear, 1952, and one of those few was found dead in late summer.

The over-all muskrat sign in late September, after the dying largely had ceased, indicated a near-saturation population for the marsh in the condition that had been characteristic of it since 1945. Although there may have been some ingress from a neighboring ditch, the population seemed essentially self-contained up to mid-October. (A total of about a dozen muskrats, including the pneumonic victim found dead on September 25, stationed themselves in the center and north-center somewhat after the manner of strangers.) The second week of September was a time of extensive readjustment at Little Wall Lake, with all adjustments seeming to be on a very local scale. In four instances, the sources of animals rehabilitating old burrows or establishing quarters along previously vacant places were convincingly traced to parts known to have been highly productive of young during the summer. Trapping was legally restricted to the west part of the marsh in the fall of 1952, and only 42 carcasses (2 adult females, 17 young males, and 23 young females) were obtained for examination. The smallness of this series, combined with the effects of the pneumonic losses of late summer, introduced many uncertainties into population calculations. From data obtained in late July, it could be judged that only 25 of the original 42 territories were productive of young, and, by late August and early September (before the big population adjustments), only 21 were being maintained by what had the appearance of substantial family groups. Of the 21 territories that remained unproductive or were lost during the summer, 5 were along a sparsely populated stretch of shore (hence probably maintained by unbred females), 3 were clearly depopulated through disease, and the causes of failure were not specifically ascertained for the 13 others. Of the 21 functional territories of late summer, 3 were sites of severe though

not annihilative disease mortality. If 19 territories be used as a base for calculations, for application of the sex and age ratios of the trapped carcasses, the total late fall population should have been in the vicinity of 425 muskrats, or somewhat above the usual fall saturation levels of late years. This figure would be fairly consistent with the impression gained from the earlier "reading of sign."

The 1952 disease losses at Little Wall Lake therefore seemed to have been well compensated. Certainly to some extent, the mechanism was a near-maximal rate of breeding on the part of such adults as were in position to breed: both of the trapped specimens of adult females had conceived 4 litters, totaling 73 young, in 1952. One of the 23 young females examined in November had conceived a litter of 7 — an exceptionally large litter for a precocious breeder.

About 60 muskrats were accounted for as taken by trappers during the fur season. Continued signs of probably twice that number could be made out after the trapping had terminated on the part open to trapping. In addition, there were considerable concentrations of muskrats in two main tracts of the refuge area. All together, at least 300 muskrats entered the winter at Little Wall Lake, and these wintered very well, despite moderate lowering of water levels as a result of the dry weather of summer and fall.

The marsh was devoid of minks from early winter up to mid-February, 1953, but red foxes systematically sniffed the lodges and push-ups and worked the shore zone throughout the winter. About February 10, a mink appeared, to remain until spring. It was remarkable how soon this mink found and established itself at the two infectious burrow systems of the summer and fall epizootic that still had live muskrats after the trapping season. From one of these, the mink dug out the bodies of at least two muskrats, and all of 10 mink scats deposited between mid-February and March contained muskrat remains. At the second burrow, the mink found at least one muskrat, and 17 of 33 of its scats for late February contained muskrat remains, compared with none in 32 deposited in the first half of March at the same place. Away from these two known foci, only one dead muskrat was recorded in the field notes for this period, and that one decayed without having been utilized by scavenging mammals or birds.

#### **THE BREEDING AND POSTBREEDING MONTHS OF 1953-55**

A big reduction in the Little Wall Lake muskrat population occurred between the break-up of the ice and mid-April, 1953, which may be ascribed to ordinary spring dispersal. As of early May, the settled muskrat population figured out at about 80 adults maintaining 47 territories. By mid-June, only 37 territories remained functional. Most losses of territories were along the west side, and so was nearly all evidence of actual disease mortality. Six disease victims were handled.

In addition to the disease losses taking place before the breeding

season gained headway in June, there was more loss by late July, especially in about five burrow systems at which mortality from disease had been recorded in preceding years. Annihilative losses were noted at two of these five burrow systems. In one case, a raccoon did much of the scavenging upon the dead in an exposed burrow system, though muskrat remains were recorded in two of 16 mink scats deposited near by. In another case, 25 of 239 mink scats for early and mid-July contained muskrat remains, whereas none of 172 scats deposited later (through October) contained muskrat remains — and all of the 25 muskrat-containing scats were datable to a period of less than two weeks, all traceable to one burrow system that suddenly went dead.

The continued exposure of the shore zone during a late-summer drought forced most of the muskrats to move toward the center, away from the really dangerous old foci of infection. There was very little dying from late summer through the fall of 1953. The deeper water offered the adjusting muskrats plenty of space and passably good habitat, and, generally, the local animals acted as if they belonged and knew what they were doing. A very few, wandering about the shore, were thought to have been strangers from the dry streams of surrounding areas.

As a conservation measure during a year of drastic reduction of central Iowa muskrats, Little Wall Lake, as a public-owned marsh, was closed to trapping in 1953. Because of the resulting lack of data from trapped carcasses, the only calculations of fall populations that could be made were on the basis of lodge counts and signs — a task made easier than usual by the abandonment of bank burrows forced by the drought. The population, as of early December, was calculated at between 350 and 400, probably nearer the former.

The water level, though conspicuously reduced by the drought, still was not reduced to the point of crisis. An estimated 300 — after some illegal trapping — wintered well despite mediocre food resources. However, the marsh was almost abandoned by muskrats in early April, 1954. The migrants moved out of here, cross-country, in response both to population pressures and to the over-all unattractiveness of the place for muskrats. With the coming of spring, the continued low water level left the bank burrows exposed along the periphery of most of the marsh, and the deeper water was too wind-swept and lacking in emergent vegetation to encourage building or maintaining of lodges. After some milling about the shore zones, the restless and homeless ones took the alternative open to them.

A carefully estimated population of 30 remained on April 19. On June 4, a good census gave only 13 currently maintained territories, representing about as many muskrats as had been originally estimated. By late summer, it was clear that Little Wall Lake had a total of 17 maintained territories. The connection between clumping of territories and successful reproduction in a low-density population was pronounced. None of six territories scattered along the shore of the east

half produced young, whereas 10 of 11 in the west half (including eight territories arranged in three clumps) produced young.

Two territories were lost because of disease in early summer and two others also may have suffered considerable disease loss in late summer. A certain amount of territorial shifting occurred in the west half as the breeding season progressed, but very little evidence of wandering was noted. The more conspicuous of adjustments involved one family and probably no more than a half dozen individuals working into the most heavily vegetated central parts. All of five evidently lone animals staying alive along the east shore retained their territorial sites throughout the summer.

In late September and early October, many muskrats came into Little Wall Lake from a drainage ditch lying to the north, to settle in those parts having fairly attractive combinations of food and water and few or no muskrats already in residence. The locally reared young were judged to have been the offspring in about thirty-three litters having the following estimated birth periods: five litters in April, seven in May, nine in June, seven in July, four in August, and one in September. All together, the population of locally resident adults and their season's young was carefully estimated at slightly fewer than 200, as of early October. After the removal by trappers of at least 100, the signs to be seen through clear ice indicated a population still between 300 and 400. This would signify a 1954 fall ingress perhaps in the vicinity of 300.

After the trapping season, the population wintered with no detected loss, 1954-55. The population was nevertheless top-heavy for the nearly open-water marsh in the spring, and a pronounced egress occurred in early April. At the time of maximum restlessness, fox-eaten remains of two were found on shore.

By mid-May, 1955, the population remaining after the spring dispersal was well established in 31 territories, all in the shore zone and about half of them in a stretch representing less than a fourth of the shore zone. The favored stretch had been deepened near shore by dragline operations two years previously and was thus more protected from exposure during low-water stages. By mid- and late June, there were still 31 maintained territories, mostly located as before but with some outstanding exceptions. Four territories were then located in central stands of emergent vegetation and a corresponding number of earlier ones along relatively unattractive shore zones showed evidences of abandonment.

The 31 territories were maintained by about 50 adults. Most of the territories located in the more isolated positions were unproductive of young. The unproductive were nine of 12 territories scattered about the east and south two-thirds of the marsh. The 16 territories that were productive of young among the other 19 of the Little Wall Lake territories included nine territories of the northwest shore that were massed along a 500-yard stretch having the dragline trench.

The latter was the place that still had an estimated three-fifths of the muskrats living at Little Wall Lake by the last of September. This was after two months of gradually increasing drought-exposure of the shore zones and a period of substantial population adjustments beginning well before the onset of the drought. A little dying was noted in the vicinity of a notorious old disease focus, but nothing serious developed from it, and few muskrats of the Little Wall Lake population were now living in places especially hazardous from the standpoint of disease. Neither was there much evidence of summer mortality from other causes, nor of summer movements to or away from the marsh. The muskrats present by late September represented essentially the population belonging there, irrespective of the considerable readjustment that occurred on a local scale.

By early October, evidence was noted of activities of probable newcomers, and, by freeze-up, considerable evidence of newcomers was to be seen. Many ill-situated individuals that behaved like strange wanderers remained active about the drought-exposed northwest shore (in the principal line of travel of wanderers from the drainage ditch lying to the north) throughout December.

The 1955 trapping catch of muskrats totaled about 90, and it did not conspicuously reduce the population entering the winter. The most carefully studied sample of marsh had an average of about four and one-third muskrats per medium-sized and large lodge, as calculated from trapping data. This ratio, applied to a total of 112 lodges of like sizes, would give a total late fall population of about 485.

Of the 85 muskrat carcasses representing the sample handled from Little Wall Lake in late November and early December, 4 were adult males, 11 were adult females, 48 were young males, and 22 were young females. The calculated total of adult females then on the marsh was 63, of which only about 30 could have been regular summer residents. Although only 19 of the territories maintained during the 1955 breeding season showed evidence of having been productive of young, most of these were obviously quite productive. From the above ratios, combined with data on population samples of the stream dwellers from which late fall immigrants were recruited (see Chapters 10 and 11 for 1955 stream data), it may be calculated that the 19 productive territories reared an average of nearly 15 young in each, or a total of about 280 of the young present in the fall. According to the same calculations, the fall immigrants consisted of about 33 adult females, a very few adult males, and about 120 young. The calculated late fall population may therefore be broken down into about 330 resident muskrats of all ages and about 155 immigrants of all ages.

The 11 adult females in the 1955 trapped sample from Little Wall Lake (which necessarily included immigrants as well as residents) had conceived a total of 35 litters during the breeding season. One of the 11 adult females examined had not conceived young in 1955.

**VARIABLE FORTUNES OF THE MUSKRAT POPULATIONS FROM  
JANUARY, 1956, THROUGH APRIL, 1958**

Nearly 400 muskrats survived a brief trapping season in late November and early December, 1955. Thereafter, the detected 1955-56 wintering mortality from all causes was practically confined to a sparse population of animals living or trying to live in one sizable tract of frozen shallows. Here, luckless animals commuted from bank holes out across the ice, or from holes in frozen mud lodges to the vegetation fringing the shore, or just worked around finding little to eat and much trouble. The marsh was minkless during the winter crisis of these muskrats, which seemingly prolonged by several weeks the time that some badly situated muskrats were able to stay alive; but hunger, cold, bleeding from gnawed-off frozen tails, and fighting among themselves finally accomplished much of the eliminating that the absent minks failed to do. Of 11 shallow-zone muskrats that could be fairly well distinguished as individuals on the basis of appearance or activities, 8 were known to have died by the middle of February.

Among the more informative victims of winter-killing was a sub-adult, which had been living in a bank hole and foraging on the exposed marsh bottom. It came out while the temperature was 23 degrees below zero (F.), worked over the snow in its accustomed way, turned over on its back, and died. Previously, it had gnawed off about half of its frozen tail. Another died in a hole in the side of a lodge, where one of its cannibalistic fellows was discovered feeding upon it. One muskrat continued to gnaw on its frozen tail until it had only a short stub left, and this stub kept bleeding conspicuously for a period of at least 11 days before the animal died. Much fighting took place between the desperate muskrats working on the surface of the ice, and several individuals caught by hand for superficial examination showed fight wounds as well as frost injuries.

The particular muskrats that managed to live the longest in the shallows were chiefly big strong ones that had access to substantial quantities of bulrush rootstocks mixed with rush stems in the material of which the lodges had been built. Although such rootstock-containing lodges were partly hollowed out by muskrats from within, the usual procedure of surface-feeding muskrats was to search for the rootstocks from the outside. This left proportionally more of the Little Wall Lake lodges with rumpled exteriors than at Wall Lake, where the presence of minks may have been making the muskrats more circumspect in their behavior (Chapter 7).

A pronounced exodus of muskrats from Little Wall Lake coincided with a period of local readjustment in late March and early April. Between March 29 and April 9, five traffic victims and one apparent example of a transient drowning during a windstorm were found at or near the marsh. By late April and early May, the remaining muskrat population was fairly well established in definite territories,

and later checkups confirmed most of these territories, besides adding a few more. As of mid-June, there were 67 recorded territories, of which 5 were judged to have been maintained by lone adults. From the winter and spring sex ratio of 62.2 per cent males in a sample of 91 specimens, the established mid-June population of adults may be calculated at about 170, or approximately half of the animals that had probably gotten through the winter on the marsh.

The population of mature animals, higher than usually remained on the marsh after the spring dispersal, may be largely attributed to an actual improvement of muskrat breeding habitat that resulted from partial drought exposure. Not only were the resident muskrats forced away from long stretches of shore zones — including the most dangerous old disease foci — but they also found the shallower central waters offering attractive sites for lodge building that had not been there at times of generally deeper water levels. By the end of June, however, the exposure of large tracts of marsh bottom was bringing about increasingly critical conditions for the muskrats resident in 20 of the maintained territories.

As at Wall Lake in 1956, something happened at Little Wall Lake that seemed inexplicable in terms of the usual patterns of climatic emergencies, mortality, and population behavior. Away from the drought-exposed territories at Little Wall Lake about 100 acres remained in attractive condition for muskrats throughout late summer and fall; yet only 22 of the total of 67 territories on the entire marsh were showing, or had shown, evidences of productive breeding by mid-July. The muskrats of only 2 of the 20 territories most affected by the drought seemed to make successful adjustments in the direction of deeper water. By early September, many of the formerly occupied parts of the marsh had been abandoned, without detected evidence of where their respective occupants went. As of late summer and early fall, the postbreeding population of muskrats was estimated at about 220.

One of the mid-June litters was seen to be preyed upon by a large muskrat. The only other mortality actually noted on the marsh during the warm-weather months was of two adults, both found dead on exposed marsh bottom near disease foci of previous years. Nevertheless, it is most doubtful that disease significantly contributed to the muskrat losses between early summer and fall. Nor was it merely a matter of drought, for, in most abandoned territories, abandonment occurred while some water still covered the marsh bottom about the territorial sites.

Times of birth of 23 litters were recorded from Little Wall Lake field data in 1956: sixteen from early April to early May, three for about mid-May, one for early June, two for mid-June, and one for early July. In addition, there was some evidence of late breeding on the east side of the marsh, where food and water conditions remained most favorable for the muskrats. It is of interest that the lone example

of a three-litter female recorded for Little Wall Lake during the summer of 1956 lived in an isolated dredge pool next to shore. Members of this family group were repeatedly observed, without finding any evidence of unusual irritability, restlessness, or inability to take care of themselves.

A heavy ingress of muskrats became apparent in the late fall of 1956, until a population of about 550 had been built up by the opening of the trapping season on December 1. Trappers took about 225 during a 15-day open season, and their catch rates were holding up well when the season closed. Ratios for 196 trapping season carcasses were 18 adult males, 25 adult females, 85 young males, and 68 young females. The 153 young of the year included 10 "kits," judged to have been born in August.

Two of the 25 adult females of these muskrats of mixed origin had not conceived in 1956, and one of the 23 productive females was in unsuitable condition for the counting and aging of placental scars. Of the other 22 adult females, 3 had conceived two litters each; 9, three litters; 9, four litters; and 1 a probable five litters. None of the 68 young females had bred precociously. The seasonal distribution of birth dates estimated from placental scars of the trapped sample showed 15 litters for April, 18 for May, 21 for June, 16 for July, and 4 for August. The differences between the above distribution and the seasonal distribution of litters observed during the summer's field work of course reflected in part the mixture of true residents and immigrant animals in the trappers' catches.

For the early part of the winter of 1956-57, the approximately 300 muskrats that survived the trapping season suffered little mortality, despite continued surface activities on the part of several groups living in drought-exposed and shallow-water zones. Even when minimal temperatures went as low as 30 degrees below zero in the first half of January, the surface-active muskrats were usually taking care of themselves. But, by the spring, most of the vulnerably situated muskrats were dead, as were the occupants of sizable tracts of marsh having fair to excellent wintering conditions.

The principal detected agency of loss was the hemorrhagic disease. Between freeze-up and spring, dying began at three places, at least, of which two had been sites of rather minor disease mortality during previous years. Then, the epizootic swept through a well-populated tract of about 10 acres, besides killing many muskrats on three additional smaller tracts. It subsided in late spring, just as it seemed ready to sweep the whole marsh.

Over some parts of Little Wall Lake that were not positively known to have been sites of disease mortality during the winter of 1956-57, the field evidence was not at all clear as to whether the wintering losses were due to disease, to hunger and cold, to mink and fox predation upon drought-exposed muskrats, or to all of these agencies in combination. One such site of imperfectly diagnosed mor-



tality in 1956–57 was adjacent to the only proven focus of the hemorrhagic disease at which muskrats had died during the winter of 1955–56.

Five distinguishable minks (three males and two females) were present on Little Wall Lake from mid-December through the next two months, but only three (an enormous male and the two females) remained from late February until break-up. The food habits of these minks reflected well the deteriorating fortunes of the muskrats as the winter progressed.

The first evidence of a local population collapse from disease was found in late January, and, thereafter, mink diets ran heavily to muskrats instead of to the mice and dead waterfowl upon which they had earlier subsisted. For late January and the first half of February, 4 of 14 mink scats contained muskrat remains; for the second half of February, all of 15 mink scats did, as did also 9 of 18 scats for March. Mink-eaten remains representing at least 14 individual muskrats were found, but the actual number scavenged upon was doubtless much higher. After the middle of March, the minks were no longer frequenting the tract of marsh most likely to have had dead muskrats lying about.

Of 21 disease victims found in suitable condition for post-mortem examination, 18 had lesions suggesting low resistance (Errington, 1957).

The 1957 summer rains improved the habitat for muskrats at Little Wall Lake, though most of the parts that had been drought-exposed for the previous year regained little water. As of late May, there were 30 territories maintained by about 65 adults. By the time that the epizootic subsided, or by late June, 26 maintained territories (representing about 60 adults) could be distinguished. Thereafter, losses of undetermined nature, but probably from disease, occurred at one territory — at the site of what had been bona fide disease losses in the spring. Remains of three young muskrats were recorded for the latter site, including one eaten upon by another muskrat and one eaten upon by a mink.

The muskrats surviving the epizootic may be considered to have had a normal breeding season in 1957. As the period of late summer adjustments came on, muskrats moved into places that were up to hundreds of yards distant from the season's breeding territories. It may be doubted, however, that these adjusting individuals represented newcomers from the surrounding countryside, for, in most cases, their spreading away from the local breeding territories could be traced from signs.

The reported trappers' catch at Little Wall Lake during a 15-day open season was 251, of which 190 specimens were posted: 10 adult males, 23 adult females, 92 young males, and 65 young females, including 2 breeding precociously in the calendar year of their birth.

Three of the 23 adult females had not conceived in 1957; 1 had conceived a single litter; 1, two litters; 10, three litters; and 8, four litters. Counting the 13 young conceived by the two precocious young, the number conceived by the breeders in the trapped sample totaled 500.

For purposes of computing the total late fall population, the marsh may be divided into four tracts, of which two were trapped hardly at all and two were trapped quite heavily. For the trapped tracts, consideration of the way that catches declined during the open season permits reasonably satisfactory estimates of the probable numbers of muskrats remaining at the close of the season. For one trapped tract, a catch of 44 represented a probable four-fifths of the population; for the other, a catch of about 207 represented a probable two-thirds of the population; and thus the fall population of the trapped tracts figured out at about 365. The untrapped tracts had lodges and other signs suggesting a population a little more than 50 per cent greater than that of the tract yielding the 44 animals judged to have represented four-fifths of the local group; hence, the populations of the virtually untrapped tracts should have been in the vicinity of 85. Adding 85 to 365 gives a total of about 450 as the pre-trapping population of Little Wall Lake.

Selective early-season trapping pressure upon adults is shown by the ratios of 3.4 young per adult in 80 specimens taken during the first few days of the trapping and 6.3 young per adult in 110 specimens taken during the rest of the 15-day open season. Undoubtedly, there were still adults among the approximately 200 animals untrapped, but the ratio of young per adult must have been high among the survivors of the trapping season. According to the changes shown by the age-ratios in the trapped samples as the trapping progressed, the true age ratio for the whole population of about 450 animals should have been about 10 young per adult. This gives a total of about 45 adults, of which about two-thirds, or about 30, should have been females—essentially the same number as those maintaining territories at the time of the first good checkup in late May.

In all probability, the 26 maintained territories recorded for late June corresponded to actively breeding females—which would balance out about right, in view of the three non-breeders found in the 23 carcasses of adult females examined. If the breeding performances of the 20 adult females examined be prorated to the total of 26 adult breeders, the total number of young conceived would be about 630. Prorating the data from precociously breeding young females would give about 30 more young conceived. The total number of young conceived for the marsh in 1957 would therefore be about 660, of which some 400 or more could have been reared to bring the population up to the 450 level of late fall. Rearing of 400 out of 660 conceived would represent a plausible degree of reproductive efficiency for a comparatively well-situated population, and no im-

portant ingress of adjusting animals from neighboring streams need be postulated to account for any of the 1957 fall population of muskrats on the marsh.

There was one place—in the food-rich shallows of the northwest corner of Little Wall Lake—that may have been stocked by newcomers from outside, moving in during late fall. This place was in the usual line of travel of such animals as did move into the marsh in some falls from a drainage ditch that runs close by. The number of muskrats living by themselves in the northwest shallows seemed to have been about the equivalent of an ordinary family group, or possibly 10 to 15; but these were not animals that were by any means proven to be newcomers. They were situated in a tract of marsh that had been most difficult for a human observer to get into in the spring after the melting of the ice, and the muskrats found there in the fall may have been an earlier overlooked pair and their increase.

The specimen data from Little Wall Lake contributed further to our knowledge of the 1957 breeding fortunes of the local muskrats. The adult female that conceived the one litter had only a single young in the litter, having a birth date assigned to April; this mother was rather small and considered to have been born late in the breeding season of 1956. At the opposite extreme was a female conceiving 38 young in four litters. The breeding adult females averaged well over three litters, and a fair amount of late-season breeding took place. The seasonal span of birth dates of Little Wall Lake young (including the two litters born to precocious young) may be assigned on the basis of placental scars to the following months: 13 litters in April, 19 in May, 18 in June, 12 in July, four in August, and one in September. The occurrence of only 3 (or 1.9 per cent) “kits” in 157 young of the year in the posted sample suggests disproportionately heavy mortality of the litters born toward the end of the breeding season.

The approximately 200 muskrats surviving the 15-day trapping season in December, 1957, suffered undetermined though probably light losses in scattered places during January and February, 1958. Although the evidences of these losses were found almost exclusively in shallow-water zones, and the minimal daily temperatures got down to 19 and 22 degrees below zero in mid-February, the losses did not seem to have been associated with freeze-out crises. Rather, there was a remarkable association between the losses and places at which some mortality had occurred from the hemorrhagic disease, not only during the previous winter but also, in three places, to minor disease foci dating back for many years.

Four minks could be individually distinguished throughout January. During the first half of February, only two seemed to be regularly frequenting the marsh. But, on February 17, at the height of the cold snap, at least six minks were briefly present. The minks showed interest in certain of the muskrat lodges chiefly during Janu-

ary; and, when considered closely according to their sites of deposition in different parts of the marsh, of 41 mink scats examined from old sites of dying from the hemorrhagic disease, 34 contained muskrat remains, compared with 4 in 14 scats examined from elsewhere on the marsh. Nevertheless, muskrats successfully wintered in all of the shallow-zone tracts that had any muskrats at the close of the trapping season, and no sweeping epizootics got started, either in the winter or the spring. No dead muskrats were found on Little Wall Lake after the ice went out.

A breeding-season checkup in early May, 1958, gave a total of 102 maintained territories, representing, on the basis of a winter age ratio of 53.7 per cent males, about 220 adults. This figure may represent more muskrats than actually had wintered on the marsh, for signs suggesting a few newcomers appeared in April in the northwest corner, near the usual route of travel of muskrats moving into the marsh from the nearest ditch.