

Chapter 7

The Wall Lake Area, North Central Iowa

WALL LAKE (Figure 7.1) is a state-owned glacial marsh of nearly 1,000 acres in Wright County, north of Blairsburg and southeast of Clarion. It is a public shooting ground open to fur trapping in season, unless specifically closed, wholly or partly, by official administrative order.

It varies in aspect from dry expanses of cattails, rushes, reeds, grasses, farm weeds, and bare bottoms to extensive blocks of open water interspersed with emergent vegetation. Unevenness of the bottom is manifested at times by low islands (of which some are grown to brush and trees), by wet channels and projections of higher ground, by shallows grading off into adjacent pastures or ending abruptly with ice-ridges, by timbered shores or reedy jungles enclosing lakelike bays. Some parts have sandy beaches and protruding boulders; others, peat deposits or deep mud.

The diversity of the muskrat habitat presented in most years would require subdividing for purposes of detailed reference, but, for general treatment, a few broad statements may suffice. The deeper tracts are in the south and southeast parts and in a series of three sloughs and connecting channels extending mostly north and south along the east central side. The shallower tracts comprise the north half of the marsh, some pastured shallows lying to the northeast, and sizable acreages in the south center and the southwest corner.

Over the years of my studies at Wall Lake, I received special help from personnel of the State Conservation Commission, especially Harry E. Rector, H. E. Colby, Walter W. Trusell, James G. Sieh, W. E. Ayers, and Paul E. Leaverton. The following trappers include those giving special cooperation: Verl ("Jack") Black, R. E. Kautsky, O. R. Sands, Walter Sampson, Harold Kaster, Hobart Abbott, E. A. Johnson, Robert Mosiman, Torkell Hill, Garry Hunter, and Charles and LeRoy Inks.

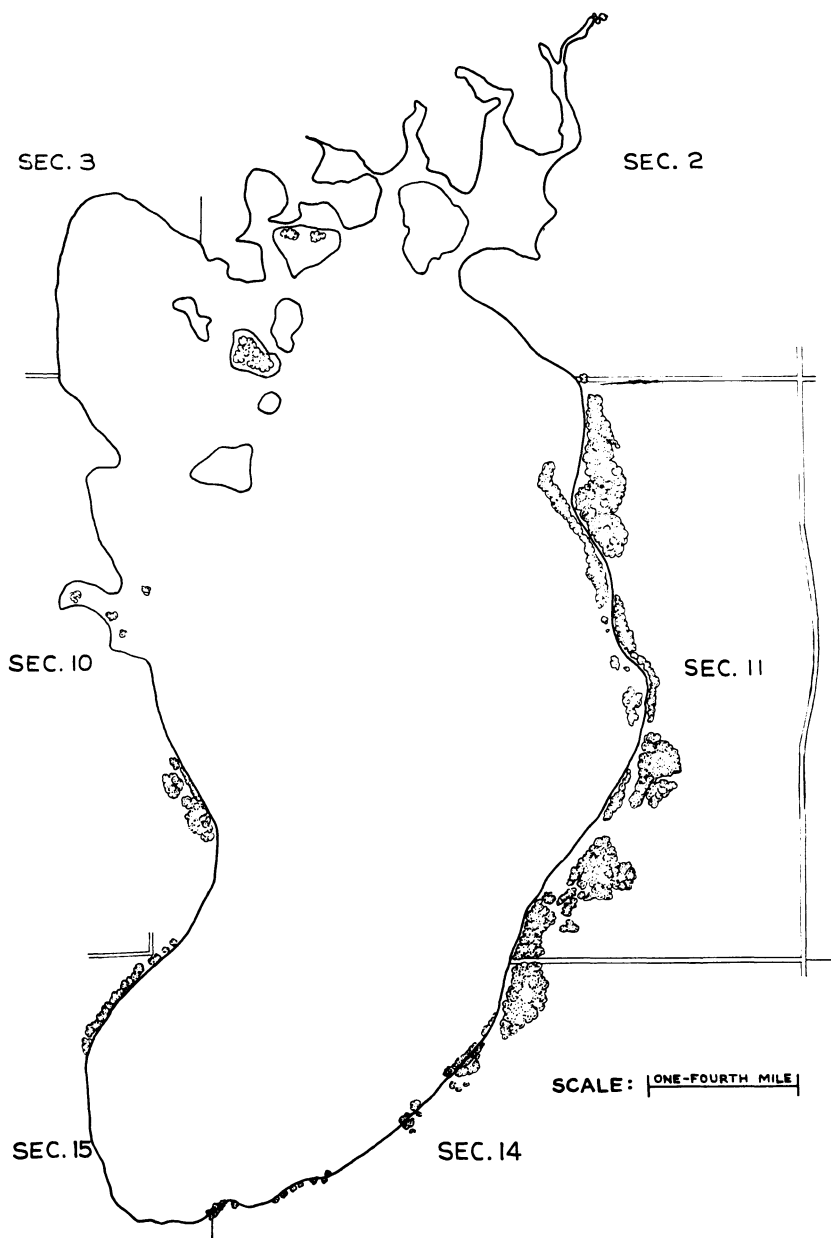


Fig. 7.1. Map of Wall Lake, north of Blairsburg, north central Iowa.

THE LOW WATER YEAR OF 1939

My first systematic inspection of Wall Lake was made in mid-May, 1939, at which time only the deeper parts of the marsh were covered with water — 24 acres in the southeast and a 10-acre strip along the east side. Presumably, the marsh was then in the early stages of recovery after the droughts of 1934, 1936, and 1937.

A census of breeding territories, made in early June, 1939, gave the equivalent of 11 pairs for the 24-acre tract and of two more pairs in three acres lying to the northeast. Later calculations gave 6 more pairs for the 7 acres of sloughs and channels extending northward to the end of the wet marsh. This adds up to the equivalent of 19 pairs or, using the previous winter's sex ratio of 51.0 per cent males shown by trapping catches, a breeding-season total of about 40 adults.

During the summer, the water of Wall Lake went down to about a foot and a half in the deepest places, but the vegetation here (especially broad-leaved cattails) became extremely heavy, and the localized muskrats thrived. By late October, the water was somewhat deeper over the wet tracts than in late summer. The late fall and early winter population was carefully estimated at about 280 on the basis of comparable known populations elsewhere. The wettest 15 acres of the 24-acre tract had about 12 per acre or a total of 210, including ingress animals such as those from two dried-out pasture sloughs to the south. For the 10 acres of east-side wet marsh, the fall population was estimated at between 65 and 70, probably nearer the latter figure.

Between the middle of the fall and early winter, the muskrats of the 10-acre series of sloughs and channels responded to the combination of dense vegetation and low water by building hundreds of lodges. These were of all sizes, with or without chambers, mud-plastered or not. After a hard freeze on the night of November 26, a very small proportion showed current use. There were in fact about five lodges to every muskrat of the 10 acres, with only certain lodges showing good to excellent signs.

By the middle of December, a crisis began to develop in the east-side shallows. The water had gone down so much in the preceding weeks that, even in the wetter parts, the lodges were surrounded by exposed frozen mud. By the end of the month, the muskrats of the drier parts were tracking about in the snow, and dogs from a farm yard as well as minks were interested in them. Bloody signs of intra-specific strife were sometimes conspicuous. Some muskrats living in mud lodges on open mud flats revealed their presence by muddy push-ups outlining subsurface channels but did not come out on top; it is now suspected that they had stores of duck potato. Five dead were found during the winter (of which at least 4 were fed upon by minks), and 14 of 46 mink scats contained muskrat remains. With the coming of spring, an estimated 18 to 20 muskrats were surviving here.

The population of the 24-acre tract of wet marsh wintered securely, though 9 acres of the shallower periphery were abandoned by residents withdrawing to the deeper 15 acres. All signs of external activity dur-

ing cold weather appeared to be that of wanderers (chiefly from depopulated parts of the east-side sloughs, a half mile or more distant), which characteristically frequented the abandoned lodges of the shallows. About 190 of 210 established residents evidently wintered, despite the presence of at least a half-dozen minks working the muskrat-occupied area. The minks dug into the lodges throughout the winter, but the muskrats maintained their best living quarters and as a rule left unrepaired only those of lesser importance. It was also apparent that even big minks (doubtless including some experienced in preying upon drought-vulnerable and wandering muskrats) were not inclined to enter certain of the lodges harboring large numbers of muskrats.

THE DROUGHT CRISES OF 1940 AND 1941

The parts and acreages of Wall Lake occupied by muskrats in the late spring of 1940 were the same as those occupied in 1939. In 1940, however, the breeding population was greater. Well after the spring dispersal, late-May checkups gave the equivalents of 11 pairs on the 10-acre east-side series of sloughs and of 30 to 35 on the wetter 24 acres. This would give a total of 41 to 46 pairs, probably nearer the latter, or a grand total of around 100 adults.

The muskrats of both deep marsh and shallows got along well through the first three weeks of June. Four of 30 mink scats for early May contained muskrat remains (probably all of the same animal), whereas no muskrat remains were found in 106 mink scats from late May and June. The maximum number of young muskrats present at any one time was estimated at between 500 and 700. Sixty-one young in 15 litters were marked, but only one was subsequently recovered as a subadult — that one in its natal locality.

By June 20, the bottom of about half of the 34 acres occupied by muskrats was exposed. Friction was observed among adult muskrats on one of the drier tracts, and the drought situation was becoming critical for many residents, although the species was not, as yet, suffering unusual mortality. Minks were frequenting mainly the deeper parts of the marsh, where they lived almost entirely upon coots. Red foxes, however, were displaying interest in two sets of shallow-water lodges — still limiting their explorations to areas of bottom sufficiently firm to prevent their feet from sinking more than an inch into the mud.

Despite a three-inch rain on the night of June 22, the drought emergency for the Wall Lake muskrats rapidly grew worse. Before the end of June, a calculated 30 to 50 muskrats (about three young to each adult) were foraging in the vegetation near drought-exposed lodges. During July, the habitats of between 50 and 200 muskrats dried out. By early August, the water level was so low that a muskrat population of possibly 250 (about two young to each adult) was exposed.

The responsiveness of the foxes (a family group) was spectacular (Errington, 1943; Errington and Scott, 1945; Scott, 1947). By the end

of July, the foxes had caught practically all the young muskrats on at least 20 acres of marsh. From late June to mid-August, 69 of 73 fox scats contained remains of young muskrats, mostly of animals between two and three months of age. No evidence was seen of foxes catching adult muskrats.

Track signs of the fox family indicated a definite system of maneuvers, with some foxes stationing themselves beside the trails between muskrat lodges and feeding grounds, while other foxes circled about. The effectiveness of the system may have resulted not so much from conscious teamwork as from the astuteness of old foxes in waiting near places where alarmed young muskrats would be likely to run. At one time, the foxes were working so close to the edge of the receding water that they sank two or three inches in the mud, but they did no digging into muskrat-occupied habitations.

Minks seemingly avoided the places that were intensively hunted by the foxes and were not known to kill muskrats in any place where water remained in lodge entrances. The minks did hunt in a dry part that was not exploited by the foxes, and four of eight mink scats from there contained remains of the same age classes of muskrats as the fox victims. Elsewhere on the marsh, seven of 27 mink scats for July contained muskrat remains, including three representations of adult muskrats.

Rains in early August reflooded the tract on which most of the living muskrats were concentrated, and the foxes discontinued their hunting on the marsh. There were still a few drought-evicted muskrats on surrounding land, and 3 of 17 fox scats and 6 of 31 mink scats from August and September contained muskrat remains. The bottom was fully exposed again by mid-October, but the foxes did not return.

The known catch during near-annihilative public trapping in November was 197. Of the sample of 105 trap carcasses that I examined, 14 were adult males, 22 adult females, 35 young males, and 34 young females. Seven of the 69 young were of "kit" sizes, and at least 3 and perhaps as many as 5 of the 22 females showed late-season sets of placental scars and thus evidence of some resumption of breeding with the temporary relief from the drought in early August. Early litters only were recorded for 6 of the 22 adult females. The mean number of 1940 placental scars per adult female was 19.2.

After the trapping ceased, a very few trap cripples wandered over the frozen bottom for a time, but there is no reason to think that any muskrats survived the winter of 1940-41 at Wall Lake. No muskrat remains were found in 145 fox scats deposited from October, 1940, to early March, 1941, nor in 4 winter mink scats.

Melting snow refilled the shallower parts of the marsh in the spring of 1941, and environmental conditions were much as they had been the year before. The marsh was naturally restocked with the equivalent of five pairs of muskrats and one unmated or nonbreeding female. During the period of muskrat movements over the countryside in March, an intact, freshly killed, maturing male muskrat was found

at a marsh-edge fox den, and one of 194 fox scats deposited from the middle of March through April contained remains of a second muskrat.

Wall Lake dried up again in August, 1941, but the muskrats were relieved by rains after three weeks of drought exposure. The foxes did not visit the dry part of the marsh where the muskrats lived, and no muskrat remains were found in 555 scats deposited from May through August. Two of 13 mink scats dated to the drought exposure contained remains of young muskrats.

After the late August rains, the Wall Lake population suffered no detected mortality until the public trapping in December, 1941. A sample of 15 carcasses consisted of 3 adult males, 3 adult females (one unbred in 1941, one having 19 placental scars in three sets, and one having 40 scars in four sets), 6 young males, and 3 young females. Thirty-two muskrats were trapped by the public, and the signs remaining after the trapping indicated that a couple of animals escaped, perhaps to winter successfully but more likely not to.

THE GENERAL POPULATION TRENDS AT WALL LAKE DURING THE RECOVERY YEARS, 1942-46

During the gasoline rationing of the war years, I visited Wall Lake only at long intervals or incidental to travel elsewhere. The data at hand covering the period of a pronounced population ascendancy are, accordingly, incomplete but they do illustrate trends.

The water level of late June, 1942, was high enough to cover 300 to 500 acres of bottom, and the whole marsh was densely grown to cattails, bulrushes, and reeds. Muskrats were all but confined to the 34-acres comprising the only habitable parts in 1940 and 1941. A rough estimate gave the equivalent of about a dozen pairs or about 25 adults. The fall population was estimated at about 175.

Wall Lake was closed to legal fur trapping for the fall and winter of 1942-43, but evidence was seen of violators on the marsh. No sign of external activity of muskrats was recorded in February and March, 1943. Of 24 winter mink scats deposited prior to a late February thaw, none contained muskrat remains, though minks diligently dug into the lodges. Sixteen of 49 scats deposited between late February and the middle of March did contain muskrat remains.

A checkup in late May, 1943, gave the equivalent of 16 pairs or about 35 adults — still localized (despite a higher water level than in 1942) in or near the deeper parts to which the muskrats had been restricted during the drought years of 1940 and 1941.

By winter, 1943-44, an area of about 192 acres was occupied by muskrats, and, on this, the wintering density was estimated at about 3 per acre, or a total of about 575. Many of the animals then present surely came in from the outside, as the general Iowa population in 1943 was the highest recorded during the entire research program, and much late summer and early fall adjustment was noted. Furthermore, Wall Lake was in splendid condition to attract newcomers after the

1943 breeding season. The marsh was still kept closed to trapping in 1943-44, and this protection seemed more effective than for 1942-43.

The 1944 breeding density, as of mid-June, was judged to have been the equivalent of about a pair per acre for the above 192 acres, or about 425 adults. The summer was extremely wet, and, by early August, Wall Lake was habitable and in excellent condition for muskrats over nearly its entire area, except for the deeper parts of the south end where cattail stands died. The biggest of several open spaces was about 10 acres in area, but the ecological losses resulting from the dying of cattails were far outweighed by the flooding of hundreds of acres of heavily vegetated shallows with a foot and a half to two feet of water.

A fall estimate of about 5 per acre or a total of 450 was made for a 90-acre fur-refuge tract set up by the Conservation Commission in the deeper and less vegetated south end of Wall Lake for the 1944-45 trapping season. The total trappers' catch for the rest of the marsh amounted to about 8,000. From the information available, the 1944 fall population should have been about 9,000.

In late January, 1945, after the trapping, the principal evidence of living muskrats was confined to the refuge tract, which was appraised as too small for optimum effectiveness. Minks were active in expected places, but I had to work hard to find 17 winter scats, none of which contained muskrat remains. A single dead muskrat (an apparent transient on shore, cleaned up by a probable mink) was found on a visit the last of March.

A breeding census of late June, 1945, gave the equivalent of 10 pairs on 128 acres of the more open south end of Wall Lake; and, for about 800 acres of once-shallow marsh lying to the north, the density seemed to be the equivalent of about a pair per two acres. Application of the sex ratio of 59.6 per cent males in central Iowa trappers' catches for 1944-45 (data from the population crisis at Little Wall Lake excluded) to the 410-pair total at Wall Lake would give about 1,000 adults.

The long, dry Indian summer of 1945, marked by widespread adjustments on the part of stream-dwelling muskrats in particular, doubtless resulted in Wall Lake attracting some animals from outside. In mid-October, there were about one and a half large lodges per acre for the marsh, open waters and dense vegetation averaged together.

For the 1945-46 trapping season, the Conservation Commission set up another fur refuge, this one of about 200 acres and located in east central Wall Lake. The 1945-46 catch was about 7,000. Judging from a 1946 spring population, the equivalent of about 700 pairs, the 1945 fall population should have been about the same as that of 1944, or about 9,000.

Decided changes took place in the ecology of parts of the marsh in 1946. A cattail stand of about 40 acres in the north part of the fur refuge died out from an unknown cause. The popular opinion was

that this was a muskrat "eat-out," but close inspection showed that substantial tracts — indeed, acres — of dead stalks hardly had a tooth-mark on them, and the dead barrenness of the affected parts was almost unrelieved by green plants escaping. From the standpoint of muskrat ecology, the cattail die-off was offset by a newly-thriving growth of bulrushes in the deeper south end, which had lost most of its cattails as the water reached its maximum depth in 1944.

The spring dispersal was quite general by April 2, 1946, but with the heaviest populations still living in or near the refuge tract. Of 45 fresh and recent mink scats examined, one contained muskrat remains. The single dead muskrat found was an adult male dying from intra-specific strife. Several transients were seen sitting in shore nests, mostly at the edge of parts of the marsh that had been trapped during the winter. The population density averaged slightly less than the equivalent of a pair per two acres for the north part of Wall Lake and about a pair per acre for the south part, or about 700 pairs. Application of the 1945-46 central Iowa winter ratio of 54.7 per cent males should give about 1,550 adults as the 1946 spring population of the entire marsh.

I saw dead adults in scattered places in late October and early November, 1946, but none fresh enough to examine showed lesions of the hemorrhagic disease. Early in the trapping season (beginning November 10), Kaster saw as many as four dead floating about a lodge that later proved to be in a disease focus.

The trappers' catch was about 6,000. On December 20, 1946, after the trapping was over, decided differences could be seen in the external sign visible on the trapped marsh and the current fur refuge (which was the same as that of the previous year). The muskrats were by no means cleaned out of the trapped marsh, but there were few push-ups (wads of vegetation pushed up from below by the muskrats) or lodges having about them open water or thin ice due to muskrat activities. On the other hand, there were push-ups by the hundreds on the refuge away from the boundary, and nearly all of the big lodges were surrounded either by open water or thin ice. Considerable numbers of muskrats also were sitting on the ice about the protected lodges well after the general freeze-up. The trapping eliminated animals from about 50 acres of the refuge tract, which left about 150 acres as effective refuge. On the choicer parts of the refuge, the wintering population was estimated at 20 to 25 per acre, or a total of something less than 3,000 for the whole refuge. This would give a grand total of about 9,000 for the marsh, as of late fall, or a figure similar to the fall populations for 1944 and 1945.

Winter checkups during 1946-47 afforded insight into the functioning of the fur refuge. The west central edge of the refuge was bounded by thick and more or less continuous growths of reeds, which seemed to serve as enough of an impediment to under-ice movements to prevent the muskrats within the refuge from being exploited by traps set at the boundary. Where the refuge edges were characterized

by open water, or by interspersions of open water and clumps of sparse growths of emergent vegetation, the muskrats were eliminated for distances up to 200 to 300 yards within the refuge.

Trappers reported many wandering and dead muskrats, especially on or near the refuge. Three dead found and examined personally in late January, 1947, were aged, strife-torn individuals, showing no disease lesions. Two of these three were females, the other being of undetermined sex. Plainly, the refuge was the site of some unrest, but the majority of the animals wintering there got along with apparent comfort.

THE INTENSIVE STUDIES OF 1947, A YEAR OF TENSIONS AND COMPLICATIONS AT WALL LAKE

The 1947 breeding population was the equivalent of about 1,070 pairs, as of April 25. The 1946-47 central Iowa ratio of 52.9 per cent males shown by trap carcasses would give a total adult population of about 2,275. As late as April 11, this rather top-heavy population was still localized in the fur-refuge tract where it had wintered. Some evidence of muskrats was appearing west of the refuge, but the entire marsh southwest of the refuge was practically muskrat-vacant, even up to the refuge boundary. There were already, however, numerous transient muskrats along the south shore.

Then, an almost explosive dispersal took place in mid-April and, by April 25, the muskrat population of Wall Lake was essentially equalized over trapped and untrapped areas, alike. Only in one place — a tract of about eight acres next to the reedy barrier on the west side of the fur refuge — were the muskrats perceptibly more abundant than elsewhere on the marsh, and here the density was the equivalent of about five pairs per acre. About 145 pairs remained in the 200 acres of refuge; about 525 pairs were in 350 acres of heavy vegetation lying west and northwest of the refuge; southwest of the refuge, about 300 pairs were in 150 acres of marsh, which had been muskrat free two weeks before; and about 100 more pairs were in the south shore zone and associated deeper waters.

The above equalization of muskrat densities over Wall Lake was interpreted as a manifestation of acute unrest. Population adjustments continued: by May 7, the south shore zone and its deeper waters had the equivalent of only 25 pairs, a quarter of the 100 counted there on April 25; and the population of the 150 acres lying southwest of the refuge was reduced from the equivalent of approximately 300 pairs to very close to 150. Coinciding with this decline in the south part of the marsh was a northward shifting into the central and north parts. The food-rich shallows of the northwest and north edges and the pasture sloughs to the northeast gradually improved in attractiveness and habitability during a wet spring and early summer, and these drew a great many muskrats from the deeper parts.

In about 300 acres of centrally located habitat, including heavy stands of emergent vegetation in the north center, the adult popu-

lation present by late April changed little throughout May and early June. Two mink victims found on shore were likely transients of late April; no muskrat remains were found in four mink scats of early May. Of 2 adults known to die in late May, one died from undetermined cause — but probably hemorrhagic disease — beside a lodge near the place where Kaster saw the floating dead ones in the preceding November. The other was an adult female with the new breeding season's placental scars, dying in the same locality from severe intra-specific wounds.

A medium-sized male raccoon, collected for examination from the inside of a muskrat lodge in late afternoon of May 19, had teeth of a young muskrat of about three weeks amid the crayfish and avian remains in its alimentary tract. At this time, only one muskrat (of about 14 days) could be found in the neighboring lodges of a 200-yard stretch of shore zone in which at least four litters from one to four days of age had been seen on May 7. This stretch was another place that later proved to be in an infection focus of the hemorrhagic disease. The muskrat-eating raccoon had liver lesions that Dr. E. A. Benbrook, of the Department of Veterinary Pathology at Iowa State, regarded as similar to those with which he had become familiar in his examination of diseased muskrats.

The main breeding season of muskrats came on at Wall Lake in 1947 with the comparative suddenness of the spring dispersal. Seven of the 65 litters for which we have dates of birth were born in the second half of April, chiefly in the last few days of the month; 35 in May; 11 in June; 4 in July; and 8 in August.

By late June, a great reduction in numbers of centrally located lodges had become apparent. Seven dead young of between five and six weeks of age were found about a sample of ten lodges. The cause of mortality was not determined, but it could have been hemorrhagic disease, for it was most conspicuous near one of the deadliest of infection foci of later years.

On July 8, maintained lodges were scarce in south central tracts where dozens of litters of young had been kept earlier, and only three litters of young were found, all members of which were dead or dying from unknown disease or diseases. One of the dying litters consisted of eleven very small young having bodies covered by rashlike pustules. Four of six of another litter of small young were dead, and the other two young were barely alive, but none had recognized skin lesions. Two of three in the third litter, of about six days, were dead (one was freshly dead but healthy in appearance and the other had died soon after birth); the young that was still alive was thrashing as if in misery, its body shrunken and skin generally inflamed. A putrid young of about five weeks floated near the lodge containing the last-mentioned litter.

Most of the muskrats observed in the central vegetation during July were adults living in open nests rather than in typical lodges. These adults were fairly numerous, thus suggesting that the central

decline may have been due in large part to failure in propagation. By early August, it was seen that the losses of young in the affected area were continuing. Two dying litters of shrunk small young were found. On August 27, two of three litters of small young were found to be diseased, and five of the victims were brought in to the Veterinary Diagnostic Laboratory of Iowa State University, where they were examined by Dr. Paul C. Bennett. He reported (memoranda of September 9 and November 21, 1947) that gross lesions were confined to a very slight pneumonic condition and that a hemolytic streptococcus recovered from cultures proved to be nonpathogenic when inoculated into laboratory mice.

There were changes in the ecology of the marsh in 1947, some of which did not reach their culmination before the next year—for example, the dying of most of the river bulrushes from what looked like a virus disease. The reeds suffered from such a massive infestation of aphids that their vitality was probably lowered thereby, which may have been responsible for some of the observed dying of that plant. Many central stands of broad-leafed cattails died during the period of high water, and those remaining alive by midsummer were chiefly either in floating mats or anchored in the shallows. By fall, the open water tracts were generally larger than in 1946, the north shallows had less water and correspondingly wider margins of exposed mud, and the choice muskrat habitat was restricted to perhaps two-fifths of the marsh area.

By mid-September, a dead subadult and a young of about five weeks lay 50 yards apart near a burrow of the east side, probably hemorrhagic victims; another muskrat in decayed condition was found about 200 yards distant on October 30; and, on November 4, a mink-eaten adult female was found, together with muskrat remains in one of 10 fresh and recent mink scats. In early October, 19 fresh to fairly recent mink scats were examined along the southwest shore, of which one (a scat deposited about three weeks previously) contained remains of a young muskrat of about five weeks. Two of six summer and fall raccoon scats contained remains of very young muskrats.

Considerable midautumn mortality of "kits," or even of recently weaned young, was noted in the north half of the marsh. This was attributable in part to unusually large numbers of late young being present and in part to disease. Remains of a very young muskrat in a single mink scat dated back to early fall. Several decayed "kits" were seen floating in the north end before freeze-up. Specimens retrieved here after the ice went out in the spring of 1948, but datable to early or midfall, 1947, included two subadults and two young of five or six weeks.

The shallow northwest corner was subject to some illegal trapping in early November or possibly late October, 1947. On November 14, I found a trap with a dead muskrat in it—obviously missed by the trapper—and there were suspiciously few living muskrats in its vicinity. Except for this place, the shallows of the northwest corner

showed from the middle of November through December the most activity of muskrats on frozen mud and thin ice over shallow water that I ever saw. Hundreds of muskrats were traveling, feeding, digging, pushing up mud plugs, and building feed houses over about 80 acres of the northwest corner. The north central and northeast shallows were sites of similar activity, though on a less extensive scale. Occasional transients or poorly situated individuals frequented the entire shore line, and there were a few out on top of the ice in deep water habitats. In the main, however, the residents of the deeper tracts did not engage in outside activities, and their signs indicated comfortable living.

Of 44 mink scats of late fall and early winter, 1947–48, from the northwest corner, two contained remains of muskrats, and these were of young animals. Bloody trails about the exposed burrows and wet holes in the frozen mud denoted intraspecific strife. The single dead muskrat found here in December was an undersized adult male with a very bad cut across the anus.

Wintering losses in the shallows of the northwest corner were not excessive, considering the circumstances and the large number of muskrats present. The fragmentary remains of eight dead were found there in January and February, 1948, and most of these had been eaten upon by minks. No muskrat remains were found in eight mink scats for late January, but eighteen of thirty-three fresh to fairly recent scats found and examined in late February did contain this item. Five more dead muskrats — all mink-eaten — were found in March, and these included a big adult, a “kit,” and two small sub-adults. Eight mink scats dated to late winter contained no muskrat remains; but three of twenty-four scats for mid-March and ten of fifteen for late March did.

In many places where the water was only a couple of inches deep at freeze-up, the lodges were still well maintained by muskrats in early spring. Large tracts of the river bulrushes of the exposed bottom had snowdrifts over them at least during part of the winter, and the bulrush stands were often so thick that they furnished good cover as such, as well as a favored and abundant food. The readiness with which the muskrats were able to find soft mud and other material for plugging their passage holes over burrows or in the sides of lodges was also a big advantage to them. Some lodges on the mud flats were so tremendous that the central parts of their bases were unusually well protected from freezing.

Four late-winter dead found in the center and south half were two subadults and two emaciated old ones. This part of the marsh was infrequently visited by the scarce (possibly no more than two) Wall Lake minks, and the minks consequently did not find a deadly focus of the hemorrhagic disease. From the condition of the gonads of victims examined in the spring, the time of dying in this focus was dated to about January, 1948, if not somewhat earlier. The initial dying was confined to about an acre of mixed cattails and

reeds in the north center of the marsh. After the evidently quick killing off of the muskrat population of the acre tract, the epizootic appeared to subside until spring. Nineteen of the dead specifically examined and recorded in the field notes were assigned to this original focus, and at least a half-dozen others found there were too putrid for examination.

Wall Lake, for reasons of administrative convenience, was left closed to muskrat trapping for the 1947-48 season in conformity with a closed season over most of Iowa, where muskrat populations were generally low. As a result, a locally congested population entered the winter with little known reduction from human exploitation except in those parts that had been illegally trapped in late October or early November.

Sex and age data from the victims of the epizootic of the winter and spring of 1947-48 should give the nearest equivalent of ratios from trappers' catches. Of the 117 dead muskrats eligible for comparison (excluding the dead "kits," the aged, and the otherwise handicapped that were dying from time to time), 21 males and nine females clearly had been born prior to 1947, and 57 males and 29 females were judged to have been born in 1947. One other was a 1947 young of undetermined sex, making a total of 21 adult males, 9 adult females and 87 young of the year for what should be about the same as a late fall sample for 1947.

Of the five adults of known sex found dead at Wall Lake and recorded in the field notes for 1947, four were females. The abandonment of half to three-fourths of the territories of the southern part of the marsh between the last week of April and the first week of May is not fully appraisable in terms of ultimate losses. Inasmuch as it was accompanied by a heavy pioneering drift into the fringing shallows of the north end, it probably meant increased hazards for adult females in particular, as the water receded in late summer and fall. Then, too, the lay of the land to the northeast of the marsh is such as to promote a certain amount of emigration on the part of muskrats massing there. This is the principal avenue of travel away from Wall Lake during droughts, and it might also be during highwater stages. (A big adult was seen flattened on the highway to the east on June 26, when the water level of the marsh was at or near maximum.) In other words, it is likely (though not demonstrated) that many of the animals moving northward in the course of the late April and early May adjustment, including females establishing territories, did not permanently settle within the mapped boundaries of Wall Lake. The big disparity in the sex ratio of the adult victims of a nonselective epizootic (21 males to 9 females) is, despite statistical inadequacies, further indication of heavy losses of females somewhere along the line — particularly in view of the usual preponderance of females among wintering adults.

From the collective evidence, it should not be far wrong to assume a loss of a good half of the 1947 adult females, which would

leave a total of around 500 from which pro rata calculations might be made. Application of the available sex and age data would give a late fall or early winter population of around 6,500, a not improbable figure.

To try another approach: All of three main sources of quantitative data — predispersal enumerations after the melting of the ice in the spring, totals of dead picked up from disease-swept tracts, and counts of animals sitting around after eviction from lodges leveled during disease-control experiments — show densities of about 20 muskrats per acre wintering in superior habitat at Wall Lake, 1947–48. It would seem that similar densities entered the fall on a little over 300 acres, which would give about 6,000, plus about 800 estimated to be living in less attractive places. This, too, would give a figure not much in excess of 6,500 as the approximate population for the marsh, as of late fall and early winter.

On the basis of an average reduction from about 20 per acre to the vicinity of 15 per acre for 80 acres in the northwest corner and minor (call it about one per acre) losses on another 135 acres of shallows, the 1947–48 wintering loss in the north half of Wall Lake may be calculated at about 535. Possibly the figure would be around 600 for the entire marsh. If this were subtracted from 6,500 about 5,900 would be the number surviving the winter.

THE INTENSIVE STUDIES OF 1948: A YEAR OF SPECTACULAR LOSSES FROM THE HEMORRHAGIC DISEASE

The first 1948 spring highway victim east of Wall Lake was noted on March 21. On this date, an inspection brought out decided contrasts in the behavior of the muskrats living in different parts of the marsh. The muskrats of the north shallows were engaging in a great amount of activity on shore. In the south shore zone with its deeper water, the resident muskrats were leaving many signs about the lodges but hardly traveling on the land at all. Quite evidently, the more comfortably situated muskrats were less disposed to move from their wintering quarters than those that had been feeling an ecological pinch for some months.

The ice melted and broke up at Wall Lake during the last few days of March, 1948. On April 9, a good checkup of the best and most heavily populated muskrat habitat of the center revealed that the animals were undispersed. At the time of the visit, they were sitting around on rush rafts and the edges of the lodges. Little change in local status of the centrally located muskrats due to dispersal was noted during seven subsequent visits up to May 3, but variable numbers of transients worked the shores. During this period, nine dead transients were found near or on shore, of which seven apparently died of intraspecific strife wounds and one of hemorrhagic disease. None of 50 mink scats for April contained muskrat remains.

Somewhere about May 5, the main dispersal of the central muskrats began. A week later, the population remaining on Wall Lake

was well settled, except for the battered animals haunting the shores. A mid-May breeding census gave the equivalent of 529 pairs, or probably around 1,175 adults.

Wall Lake lost much emergent vegetation, particularly river bulrush stands, from the summer of 1947 to that of 1948. Three muskrat-vacant tracts of largely open water totaled over 500 acres, and there were other tracts similar in appearance except for their smaller sizes. To a considerable extent, the best muskrat habitats of the marsh in 1948 were irregular in outline and variable in size, occurring mostly in the shallower parts. The deep-water habitat consisted of bulrush and floating cattail clumps near the south end and some cattail and reed growths bordering deeper waters elsewhere. One of the most heavily populated tracts was a series of shallow muddy sloughs in the northeast corner, the vegetation of which was dominated by duck potatoes. River bulrushes remained abundant chiefly in the north half.

Fourteen dead muskrats were found near the east central shore in mid-April, of which the freshest 11 specimens were victims of the hemorrhagic disease. It could be seen that the 11 probably drifted to shore across a stretch of open water lying to the west. The source of the drifting dead was soon located: a 5-acre tract of bulrushes. It had floating bodies of at least 28 muskrats lying in sight on the water at the time of the first visit. The final count of 112 dying in this 5-acre tract within a space of weeks — over 100 within a single week — illustrates not only the infectiousness and virulence of the disease but also the densities of muskrats existing in limited and locally favorable habitat.

Post-mortem examinations of muskrats dying from the above epizootic and its extensions revealed a syndrome of lesions of a less common type but still one generally observed in central Iowa from late summer, 1946, through the first half of the spring of 1947. In this syndrome, the necrotic foci in the liver tended to be fewer (or entirely absent), whereas the intestinal hemorrhages tended to be more conspicuous than in the Iowa specimens studied from 1943 to the middle of 1946. In late April, the site of a different epizootic was discovered in the shallow sloughs at the northeast corner of Wall Lake. The disease syndrome of the victims here was characterized by lung hemorrhages, which left large portions of the lungs with the appearance of being almost solid clots, and by absence of apparent liver and intestinal lesions. The courses of both epizootics became complex as they progressed, as field experiments were conducted, and as muskrats entered the infected zones from the outside in connection with normal spring dispersal and establishment of breeding territories.

Through ex post facto "reading of sign," the April, 1948, die-off in the 5-acre tract was traced to the disease focus of about an acre mentioned in the discussion of 1947-48 winter mortality. This focus lay about 175 yards west of the above 5 acres. Evidence was also seen that one of the first to die in the 5 acres of river bulrushes had drifted

across an irregular channel of open water to the edge of another tract of river bulrushes — this of 8 acres — lying to the northeast.

This second tract of bulrushes had a per-acre density of muskrats similar to or even higher than the one of 5 acres. Two freshly dead victims were found on April 14 in the vicinity of the dead one judged to have drifted over about a week before. By April 20, 14 more dead were found, and the epizootic had depopulated about half an acre of the bulrushes radiating away from the vicinity of the animal that had drifted across the channel. The saving of the rest of the population of the 8 acres of bulrushes from the epizootic may be credited to experimental control measures, i.e., designed to remove or dilute sources of infection.

About a dozen animals could be seen alive in the 5-acre tract just before the lodges were experimentally leveled on April 21. Dying continued on a much reduced scale, and the rebuilt lodges were leveled. Thereafter, the epizootic appeared to subside, and lodges rebuilt by newcomers or survivors were left undisturbed. By May 24, about three weeks after the last freshly dead muskrat was found, the equivalents of 9 breeding pairs were established.

A southward spread of the epizootic from the site of the early-winter disease focus was manifested by animals beginning to die about April 10 in a half-mile, north-south strip of reeds surrounded by open water. Also an easterly extension of the south end of this reed strip was catching bodies drifting across a wide expanse of open water from the five acres of river bulrushes. Many of the reed-dwellers died here, April 13 to 16. At a little island of cattails, likewise in the line of drift from the nearly depopulated five acres of river bulrushes — which lay across open water about 600 yards to the northwest — at least 11 muskrats died on April 17 and 18.

Leveling of lodges in the latter sites was carried on, April 20–21, and this, with removal of the dead, seemed to suffice as a control measure — though, as a matter of fact, there had been for some weeks hardly enough muskrats left to do any dying. By late May, there were the equivalent of only five breeding pairs on about 25 acres in the reeds. At least 53 were known to die here, and, of these, 48 were found inside the lodges.

The most heavily populated part of Wall Lake was a series of river bulrush islands totaling about 35 acres (exclusive of open water) and having a pre-dispersal spring density of around 20 muskrats per acre. The north end lay a little over 200 yards south of the above-mentioned reed strip and separated from it by open water and a small patch of reeds lying between. The small reed patch was depopulated of muskrats toward the last of April, but, before then, the contagion reached the 35 acres of bulrush islands and their hundreds of muskrats. Foci of infections were found at the north edge on April 22 (three freshly dead and one in dying condition at a single lodge) and on May 3 (four freshly dead close together about 150 yards from those dying April 22); but measures were promptly taken

to prevent further spread of the disease in both cases. Whatever else happened, the massed population of the 35 acres escaped the sort of die-off suffered in the reeds, bulrushes, and cattails to the north, where the epizootic had largely run its course prior to human intervention.

West of the early-winter focus of infection, the epizootic started a mid-April advance on a new front, but chronology and the observed drift of infected bodies implicated the five acres of river bulrushes rather than, directly, the earlier focus. On this new front, the epizootic killed relatively few known muskrats and finally subsided. None of fifty late-April mink scats from a lodge contained muskrat remains. Some control work was tried here but not really enough to count. The explanation for the subsidence of the epizootic probably lies both in a scarcity of muskrats remaining alive locally (the habitat being neither very good nor heavily populated) and in warm weather lessening the infectiousness of the dead through putrefaction.

The pneumonic syndrome of the hemorrhagic epizootic got a fairly late start in the spring of 1948. The first recognized victim had died about April 17, a half mile north of the northernmost limits mapped for the spring and early summer spread of the commoner or hepatic-enteritic syndromes. I suspect that the infection was introduced by a transient, as the new die-off was first noticed along a marsh edge used as a highway by considerable numbers of foot-loose individuals.

In the course of the next six weeks, at least 28 muskrats were recorded as dying from the pneumonic epizootic, and the deaths of many more were believed to have taken place out of sight and out of reach in bank burrows. Indeed, it was estimated that upwards of 100 died here up to early summer, mostly along a quarter-mile stretch of shore near the extreme northeast boundary of the marsh. Control experiments were neither attempted nor considered feasible. A certain amount of dying continued for much of the summer, and an area of several acres remained depopulated until fall.

As the weather turned warm, dead muskrats experimentally left floating on the water in easily recognizable places disappeared in a relatively few days, and it is quite to be expected that increasing proportions of the late spring victims did likewise. Moreover, the technical problems of covering the nearly half of a square mile of marsh affected by the epizootics were so substantial that some missing of dead should be taken for granted, even if they had continued to be visible indefinitely.

Nevertheless, the dying occurred principally while the weather was moderately cool, and the heaviest mortality was restricted to tracts small enough to permit fairly thorough and repeated coverage. Also, systematic digging out of lodges in connection with control experiments surely did not leave any great numbers of the dead to disintegrate out of sight in lodges. I should question that more than one victim of the hepatic-enteritic epizootic was overlooked for every

two found and recorded, which, on the basis of a recorded total of 267, would give a total of about 400. The addition of the approximately 100 pneumonic victims to the other 400 would give a grand total of perhaps 500 for both epizootics at Wall Lake in the first half of 1948.

The control experiments were conducted cooperatively with the State Conservation Commission, with State Trapper Walter W. Trussell and Conservation Officer H. E. Colby being the principal representatives of the Commission during the experiments. Colby also patrolled the marsh at intervals throughout the summer searching for evidence of new outbreaks. This work may be appraised as having protected several hundred muskrats from death from the disease.

The population significance of the north central die-off, on the other hand, is not to be judged merely in terms of numbers of animals dying or not dying. There was such a state of overpopulation at Wall Lake in the spring of 1948 that considerable biological wastage was entirely to be expected under the best of conditions. In short, the epizootic in this part of the marsh had the apparent effect of eliminating a surplus that stood a good chance of being lost anyway, through one agency or another.

The extent that territorial adjustments of the muskrats took up the slack left by the heaviest die-off is illustrated by the distribution and densities of the breeding population, as of late May, when the final spring census was taken over the marsh as a whole. On comparable disease-free and disease-swept parts of the attractive habitat of north central and northeastern Wall Lake, the late May breeding densities stabilized quite uniformly at the equivalent of 1.8 pairs per acre on 94 acres. A total of about 135 acres of shallows to the north, including the shallows swept by the pneumonic epizootic, had the equivalent of 1.2 pairs per acre, whereas a larger (160-acre) tract of disease-free, though ecologically similar shallows adjoining to the southwest, had the equivalent of 1.0 pair per acre. These were the only local situations permitting valid comparisons.

At the site of the pneumonic epizootic, severe local mortality in relation to the muskrat densities continued into the summer. An area of several acres remained depopulated until a late-summer and early-fall drought induced substantial numbers of muskrats to move in from still shallower outlying parts of Wall Lake. A big movement here attained its greatest observed momentum in the first week of October. (On October 1, alone, four muskrats were seen freshly killed by traffic on U.S. highway 69 a half mile east of the edge of the drought-exposed shallows.) Many of the newcomers established themselves shortly before October 8 in the old burrows and lodges left vacant by the pneumonic epizootic. By mid-October, animals were again dying from disease at this place, although evidently nowhere else on the marsh. In this instance, however, the common hepatic-enteritic syndromes dominated, with just enough specimens revealing pneumonic or intergrading syndromes to indicate that all of the observed syndromes represented the same disease entity.

Through working over the marsh, part by part, and obtaining local population indices by forcing muskrats out of shallow-water lodges for counting, I arrived at a late October, 1948, figure of about 4,200. The major exodus because of drought-eviction, *per se*, had terminated by this time.

When the epizootic started again in the northeast focus of infection, the water surface there covered about five acres. A population of about 20 muskrats per acre or a total of about 100 was quite accurately determined. By October 23, a half acre or so was nearly depopulated, and, between then and December 1, the area depopulated was enlarged to about four acres, leaving an undiminished population on a little over an acre in the southwest end of the slough. Four disease victims were found to have died in mid-October, seven from October 20 to 23, fifteen about the first week in November, and six in mid-November. On the opening day of the trapping season, December 1, two freshly dead, evidently diseased, muskrats were seen in the southwest end, but trapping eliminated the rest of the residents before more could die. Trappers reported taking about twenty five from this southwest end, compared with four muskrats from the entire four-acre tract that had been disease-swept.

Partly connected with the slough having the northeast focus of infection, and similar to it in ecology and per-acre density of muskrats, a six-acre slough lying to the west escaped sweeping disease mortality up to the December trapping, though it did have minor and localized dying in November. The reported catch of about 50 for these six acres is patently incomplete. Post-trapping inspections showed evidence of muskrats being alive at but a single lodge.

The northeast focus of infection may be reconsidered. A freshly dead victim of intraspecific strife was seen on shore, October 23. On the same day, another unpopular one was watched as it withdrew under attack to the side of the slough. Soon thereafter, a pronounced egress was known to take place. Subtraction of the 35 recorded disease victims and the trappers' catch of about 29 from the mid-October census figure of about 100 would leave a difference of nearly 40 animals. In view of the absence of signs of muskrats surviving the trapping and the unlikeliness of much mortality being unaccounted for at this particular slough, an estimate of upwards of 30 muskrats abandoning the place after once being in established residence should be well in keeping with the facts.

The chronology of this late-October egress agreed with a detected movement of animals, including diseased ones, along the east central margin of Wall Lake. The first known disease victim — having the appearance of a transient — died along this travel route about October 23, at the water's edge. Two more battered transients died on land within the next few days. Shortly before the first of November, eight more were known to have died, and a sick one was seen on November 2, all within a 125-yard strip of shore and fringing growths of bulrushes lying a mile S.S.E. of the fall focus of infection from which egress had been noted.

On November 2, a freshly dead one was found a third of a mile farther south in the above shore zone. In the following two weeks, eight more were known to have died in this new place, including at least two strife-torn diseased ones dying on shore. By December 3, dead muskrats were found about a quarter mile still farther southwest along the shore, thus extending the known infected strip to nearly three-quarters of a mile. Thirteen more dying between late November and early December, 1948, were found during the 1949 spring check-up. This proved to be as far as the epizootic progressed down the southeast shore zone, although immediately to the southwest lay a narrow, 380-yard bulrush fringe having an area of about two and one-half acres in which possibly fifty, or even more, muskrats successfully wintered, trappers and disease notwithstanding.

Three muskrats dying in October were found in south central Wall Lake, but one of these had been shot by a hunter, another appeared to have died of old age, and the third was too decayed to show cause of death.

In early November, a die-off was observed to be starting at the edge of a moderately populated (around 10 muskrats per acre) 30-acre tract of river bulrushes of the south center, of which the east edge was separated from the epizootic zone of the southeast shore by 150 to 250 yards of open water. The first death from the hemorrhagic disease may be traced back to about October 25, and this victim apparently touched off the partial collapse of fall and winter here to be described. Insofar as its death antedated the dying of the occupants of the shore zone lying on the opposite side of the open water and agrees more nearly in chronology with the deaths of the first-observed diseased transients along shore several hundreds of yards to the northeast, this muskrat, too, may be suspected of having been one of those leaving the fall focus of infection more than a mile to the north. It and at least a few other of the dead later found bore the strife wounds of wanderers or otherwise unpopular individuals.

During the first half of November, 69 were known to have died in the river bulrushes of the south center, and another sick one was seen. For the second half of the month and early December, 24 more dead were found. Trappers reported seeing still others in early December, but they may have picked up some of these for pelting, for I could find only one dead in the designated places after the trapping ceased.

The front of the south central die-off took the month of November to advance westward about 700 yards, or the length of an east-west belt of vegetation less than 200 yards in width. Experimental control measures (removal and dilution of sources of infection, as tried out in the spring) quite evidently checked the dying in the first-infected eastern third of the belt; but shortage of man-power available to the Conservation Commission prevented us from doing the full amount of work we felt was needed in the middle and western thirds, and the contagion kept spreading westward until freeze-up. Following the control measures conducted on November 9 on 12 acres of the

eastern third having the severest mortality, the rate of dying fell off in a pronounced manner; but, during the last week of November, the epizootic was seen to be flaring again among the remnants of the population that earlier had escaped. The known late November mortality of 5 dead on the 12 acres may be compared with 59 known dead for the initial sweep.

Trappers working the bulrush belt of the south center soon discontinued their trapping of the disease-swept eastern third when they found how relatively scarce the animals were — about three per acre estimated on the basis of the bubble signs under new ice. As a result, more muskrats remained alive after the trapping in the part of the central bulrush belt that had been more nearly depopulated by the November epizootic than in parts where animals were only beginning to die as the trapping season opened. Following the trapping, the south central epizootic seemed to remain quiescent for a couple of months, finally killing the remnant muskrats early in February, 1949.

The chronology of the late-October, 1948, egress of diseased muskrats from the fall focus of infection in the northeast corner also agreed with hemorrhagic outbreaks in parts of Wall Lake other than those so far mentioned. About 1,100 yards S.S.W. of the fall focus, animals started dying in the last few days of October in the west center of the marsh. All of the muskrats of a 90-yard stretch of the outer edge of an extensive growth of reeds seemed to die (nine were found) by mid-November, but the epizootic was not known to have spread farther from this site by the beginning of the trapping, on December 1. The surrounding densities were moderately low, of perhaps five per acre.

The center of another die-off consisted of about two-thirds of an acre of wet, rushy shallows about a half mile northwest of the above and about 1,000 yards W.S.W. of the northeast focus of infection. It lay adjacent to a six-acre residual pocket of wet marsh in the generally drought-exposed northwest corner of Wall Lake. The per-acre density of muskrats for the combined six and two-thirds acres was estimated to be, as of mid-October, slightly in excess of the 20 per acre actually determined for the focus of infection of the northeast corner, or possibly 25 per acre.

Animals were first known to die in the tract of two-thirds of an acre toward the end of the first week of November, and this place appeared completely depopulated by the middle of the month. Only six dead were specifically recorded from here, but visibility in thick stands of river bulrush was so poor, and human travel on foot or by canoe so difficult, that many other dead could have been overlooked. Six additional muskrats dying about the same time were found within a 150-yard radius on exposed marsh bottom, but, of these, only one was fresh enough to be positively identified as a disease victim. An animal that may have been a diseased transient died in late October or early November a quarter mile to the south, but without precipitating any local die-off there.

As the trapping began, December 1, a single dead muskrat was

discovered in the six-acre tract, at the edge of the depopulated two-thirds of an acre, and another died there soon after. The epizootic looked as if it were on the way to bigger accomplishments when the trapping sharply reduced the population. Most of the few muskrats surviving the trapping appeared to die in early or midwinter. Three of eight early-winter mink scats contained muskrat remains. The tract did have a small group of muskrats — residents of a single big lodge — that successfully wintered.

Two more of what were probably disease victims died about the middle of November, some 250 yards apart, between 1,100 and 1,200 yards south of the northeast focus of infection. One died 100 yards or more from the nearest muskrat habitation; the other, in the midst of one of the heaviest muskrat populations on Wall Lake. No other deaths were noted here before the trapping season opened.

A trapper brought in and pelted two dead found in the center, north of the south central epizootic area and approximately a mile south of the northeast focus of infection. When these were posted, December 3, one was found to have hemorrhagic lesions. A third dead animal was found about a quarter mile to the west, but it was a very aged one having no lesions suggesting infectious disease. Twenty-six carcasses of locally trapped animals were also examined. These represented the trapper's total catch for this part of the marsh. With the melting of the ice in the spring, 16 more disease victims were picked up, all in early winter sexual condition, with times of death dated to between freeze-up and the beginning of the trapping in December, 1948.

Near the south central shore, almost two miles from the northeast focus of infection and a good half mile from the nearest known disease victims of the south center, a lone animal was found to have died about the first of January, 1949. The site of dying was in the disease focus first suggested by the activities of the muskrat-eating raccoon in 1947. The only other dead muskrat found so far south in Wall Lake during the 1948 dying was a trap cripple, which apparently had died of injuries.

The legal trapping catch in early winter 1948–49 figures out at around 3,000 animals. In late October, 1948, there had been indications of extremely early illegal exploitation of the muskrats of about 60 acres of river bulrush shallows in the northeast part. The toll from this was thought to have amounted to hundreds of muskrats, judging from the local distribution and densities of those remaining compared with the densities on adjoining tracts of marsh during November.

Of 298 trap carcasses and disease victims for which sex and age data were obtained for the fall of 1948, 24 were adult males, 28 adult females, 136 young males, and 110 young females. Counts of placental scars were obtained for 22 adult females, three of which had not conceived in 1948. One had conceived a single litter; 6, two litters each; 10, three litters each; and 2, four litters each. Fifty-one sets of pla-

cental scars shown by the 22 adult females were chronologically distributed as 23 early in the breeding season, 26 in the middle of the breeding season, and 2 late in the breeding season.

The 1948 field data indicate a negligible loss of adult females between midspring and midautumn except for about 94 trying to live on an aggregate of 96 acres of the drought-exposed north fringes. Subtraction of these from the May census figure of 529 would leave about 435 remaining alive on the marsh up to the time of the illegal trapping of the northeast corner in October. The fall and early winter sex and age data prorated would also give a remaining population of about 373 adult males and about 3,822 young of the year, or a grand total of about 4,630 muskrats. This, allowing for several hundred illegally trapped or otherwise disappearing from the bulrush shallows of the northeast corner, would agree with the late October figure of about 4,200.

For many weeks following the legal trapping in early December, 1948, little additional evidence of mortality was detected. Between early February and the middle of March, 1949, 15 of those surviving the fall die-off and the trapping in the south center were known to have succumbed to the hemorrhagic disease in an area having a diameter of about 130 yards. This all but completed the depopulation of the 30-acre tract of river bulrushes in the south center, bringing up to 110 the number of disease victims found there.

A big mink was attracted to the site of the February flare-up of the epizootic in the south center, and it subsisted to a considerable extent on the dead muskrats for at least five weeks. Of the locally gathered mink scats, only two of 42 deposited between freeze-up and midwinter contained muskrat remains, compared with seven of 9 for late February and early March, one of 11 for the middle of March, and none of 21 for April.

Contemporaneously with the February flare-up of the hemorrhagic disease in the south center, a similarly localized die-off started nearly a mile to the north, in the part of the marsh where the illegal trapping had been done in October and in which no disease losses had been recorded since the epizootic of the previous spring. The local density of muskrats escaping the trapping (legal or illegal) was estimated at two or three per acre. Four mink-eaten bodies were seen in an area about 100 yards in diameter. The uneaten body of a diseased wanderer lay on a lodge, and a sixth dead one was old and strife-torn but without recognized disease lesions. Muskrat remains were represented in the one mink scat examined.

In summary, the recorded number of muskrats demonstrably or presumably dying from the hemorrhagic disease on Wall Lake, late summer, 1948, through March, 1949, totaled 233, in contrast with 8 found dead chiefly from apparent old age and strife wounds. The field work was sufficiently intensive to preclude the likelihood of any large proportion of disease victims being overlooked. The overlooked victims might perhaps be estimated at about fifteen individuals for a

depopulated quarter acre of slough lying immediately west of the northeast focus of infection, about ten for the two-thirds of an acre of wet marsh in the northwest corner, perhaps three or four more dying nearby after the trapping, a dozen or so found but not reported by trappers in the south center and along the southeast shore, and about thirty more allowed for as dying but not found on or about the rest of the marsh.

This adds up to around 300 as disease toll for the fall and winter of 1948-49. The figure is not as high as the total arrived at for the spring losses from the hepatic-enteritic and pneumonic syndromes combined, but the fall and winter disease losses were, in this case, superimposed upon losses occurring incidental to normal population adjustments instead of merely substituting for other losses.

SPRING TO FALL, 1949, A PERIOD OF IMPORTANT CHANGES

The muskrats surviving the legal trapping on Wall Lake in early December, 1948, were mostly confined to a moderately trapped area of about 25 acres of excellent habitat in the northeast center, but there was a lesser group along the southeast shore. Other than at these two places, there were a few muskrats in the disease-swept south center, and a few distributed very locally in the west center, in the northwest corner, and in the northeast shallows.

The ice was partly out of Wall Lake by March 25, 1949, by which time the winter survivors among the muskrats could be observed swimming in the open water and sitting at the edges of their lodges. Some muskrats from the southeast shore moved north to dig into the upper parts of the infected burrows of the east central shore. After an interval of about a week, these newcomers, too, began dying. Here, five were found that died of the hemorrhagic disease in the first half of April. No evidence of muskrats re-establishing themselves along the east shore north of the wintering grounds was seen until after the breeding season was over.

Six more muskrats were known to die during April or early May in the south central tract that had been disease-swept in the preceding fall, early winter, and midwinter. The rate of dying slackened in May, though the equivalent of seven breeding pairs remained within a radius of about 150 yards. The disease mortality left a number of apparently unmated animals scattered through 30 acres of bulrushes, but the picture is confused by continued ingress from the southeast shore zone and from a small tract lying to the northwest in which some successful wintering occurred.

The spring dispersal also put the equivalent of four pairs in the previously depopulated center lying just north of the disease-swept south center. These appeared to move in from either the south center or from the southeast shore via the south center. At any rate, a drift-route could be made out from the south, whereas a wide (nearly a half-mile) muskrat-vacant space lying to the north separated the newly repopulated part of the center from the wintering grounds of

the northeast center. A single animal was found dead of hemorrhagic disease in the central tract on May 10. In mid-April, a freshly dead hemorrhagic victim was found in the well-populated northeast center, but it did not start any known die-off. Several hundreds of yards to the west, three dead muskrats were found close together, probably dying about late April, and a fourth died about the first week of May. Two mink-eaten carcasses of transients on shore—of which one died near the old focus of infection of the northeast shallows under circumstances indicating disease—were dated to about the first 10 days of April.

In addition to the total of 18 muskrats listed in the Wall Lake notes as certainly or probably dying from hemorrhagic disease in the spring of 1949, I would estimate that 20 to 30 more (exclusive of young of the season) died in and about the northeast focus of infection and on four small tracts in the central marsh. The dying from this cause subsided almost completely by early summer.

Breeding censuses, as of the middle of May, gave the equivalent of 94 pairs, or about 200 adults. The settled breeding populations clearly reflected wintering success in particular tracts of marsh. Fifteen of 21 territories or the equivalent of pairs of the south one-fifth of Wall Lake were localized in the southeast shore zone, in one of the two places where substantial numbers had wintered. To the north, in or near the disease-swept, trapped-out south center, 15 territories were established, with local sources being evident in some cases but with fair numbers of the muskrats coming across from the above south-east shore zone. In the northeast center, 43 of 54 territories were distributed within a quarter mile of the tract where wintering success had been greatest, and the occupants of the other 11 territories probably came from the same source. All of the four breeding territories listed for the northwest corner were found in the vicinity of the one known place where muskrats had wintered. Much excellent marsh away from wintering grounds had no resident muskrats up to the end of May, nor, likely, during any part of the 1949 breeding season.

Mating was inefficient among the animals of the scattered territories of the south center and adjacent parts. Of 9 adult females from here that were examined during a week of legal trapping starting December 1, 1949, 6 had not conceived young during the 1949 breeding season, and the other 3 conceived 5 litters (all early ones) among them. In addition to the 9 adult females, the late fall and early winter sample of 90 specimens from the south half of Wall Lake included 6 adult males, 39 young males, and 36 young females. The high proportion of young of the year in this sample was clearly due to a differential movement of young into the south and central tracts of marsh away from the northeast center in late summer through early fall. No August-born young were noted in the sample.

A sample of 40 carcasses was obtained from the northeast center: an adult male, 7 adult females, 14 young males, and 18 young females. The young of the year included 4 assigned to late July. Two of the

7 adult females of this lot conceived 3 litters each in 1949, and the other 5 conceived 4 litters each. Of the total of 26 litters represented by placental scars, 6 were assigned to the middle or the latter part of July, yet none to August. The northeast center females conceived a mean of 31.3 young.

The adults of the northeast center remained much in their breeding territories throughout the summer and fall despite the southward and southwestward drift of large numbers of their season's young. This drifting was an adjustment both to worsening drought conditions in the north half of the marsh and to the reappearance of splendid growths of river bulrush over wide expanses of the center in which this species had died out during the epiphytotic of 1947. As of mid-September, the rejuvenated central stands of river bulrushes were fairly well filled up with immigrant muskrats, but about 50 acres of cattail and hardstem bulrush islands lying south of the river bulrushes of the south center and separated from them by 50 to 100 yards of open water remained practically without muskrats. However, five weeks later, there were numerous muskrats among these islands, and, by the middle of November, almost every clump of cattails or hardstem bulrushes had its lodges.

By late fall, the wet and muskrat-occupied area of Wall Lake was constricted by drought to about 295 acres, of which about 160 acres had 6 inches or more of water over the bottom. After the passing of the late summer and early fall period of minimal friction, the muskrats of the more solid blocks of partly exposed shallows were reluctant to make further adjustments because of the excessive trespassing over established home ranges that such entailed. On the other hand, late fall adjustments from shallow to deeper water in well-vegetated parts of the marsh were general where they could be accomplished unimpeded.

A subadult died in late summer, 1949, along the east central shore, which had been depopulated during the 1948 fall die-off and in which transients continued to die in the spring of 1949. During November, 7 victims of hemorrhagic disease (all subadults) were found dead here. A 140-yard stretch was left depopulated (except for a single live muskrat) by the opening of the short legal trapping season on December 1.

Two diseased dead, dying in late October or early November, were found outside a lodge in the south center, a quarter mile southwest of the infected shore zone. On December 26, a freshly mink-bored lodge with the sign of a mink dragging a muskrat outside was seen about 110 yards from the lodge with the two dead ones. On the following day, this mink-bored lodge was dug out, and the hind-quarters of a mink-eaten muskrat retrieved, but not enough remained to show whether it was diseased.

A very putrid muskrat, with time of death dated to about mid-October, was found in late December near the exact center of the marsh. In early January, a mink dragged a muskrat outside a lodge

about 100 yards from the site of the above dead one. One other dead muskrat had been reported by a hunter in late October from the west central part of the marsh. Mink signs were moderately abundant; of 31 scats examined for late summer through December, one (deposited in late September) contained muskrat remains.

Harold Kaster's (letter, January 9, 1950) highest estimate of the total number of muskrats legally taken on Wall Lake in December, 1949, was about 700. The trapping much reduced the occupants of all parts that were readily accessible by boat, at the same time affecting relatively little the occupants of the muddy shallows.

On the afternoon of December 7, the last day of trapping, I worked over an 18-acre sample of partly exposed shallows in the northeast center and estimated a surviving population of around 8 to 10 per acre. Similar remaining populations were estimated from the signs visible in mid-December on about 75 acres of hard-to-trap shallows extending off to the south and southwest. An allowance of 8 survivors per acre for about 90 acres would give something over 700 shallows-dwelling muskrats entering the winter. I do not think that many more than 100 escaped the trapping on the rest of the marsh. The approximately 800 survivors added to about 700 legally trapped, and with an allowance of about 50 for mortality from trap crippling, a minor amount of illegal trapping, disease, and miscellaneous losses, would give a fall population of about 1,550.

Judging from the sample data, the females of the 54 breeding territories of the northeast center conceived closed to 1,700 young and the 40 females of the rest of the marsh conceived fewer than 200 young, which would give a total of about 1,875 young conceived on the marsh in 1949. Ingress of animals from drying streams in the vicinity may be considered immaterial in 1949, probably no more than would offset the numbers abandoning the marsh. Survival rates of the young were surely high, and the survival of about 1,375 of 1,875 conceived young that would be needed to give us a total fall population of about 1,550 muskrats seems not at all out of reason.

THE LATE-WINTER EMERGENCY OF 1949-50

With around 700 muskrats living in more or less exposed shallows of Wall Lake, and week following week of sinking frostlines and winter drought, a large-scale crisis was in prospect as midwinter approached. As early as late December, the muskrats of the central shallows were simply popping out of the lodges and passage holes in the marsh bottom during a thaw, but nearly all went back in and stayed in when the weather turned cold again. In early winter, there were three places in the center and one place in the northeast center where what seemed to be individual muskrats habitually came out daily to forage in the river bulrushes. The animal active on the ice of the northeast center was a trap cripple. A mink scat deposited here about the first of January contained remains of a muskrat hind foot—indicative of close scavenging on fragmentary remains—and no

further sign of the trap cripple was seen thereafter. On January 7, a mink got one of three foragers that regularly came out in the central shallows. By January 16, the other two muskrats were still coming out at the expected places in the central shallows irrespective of the cold weather; similar observations were made January 19.

Rather suddenly, about January 19, the under-ice retreats of some muskrats of the central and other food-rich shallows froze dry, and four animals started engaging in cold weather surface activities for the first time known thus far in the winter. One of the four, in fact, worked on top on January 18, and, in the afternoon of January 19, left its home range as a footloose wanderer. It was tracked down and looked at near shore, about 250 yards away. Another of the four newly active ones left its lodge about noon of January 19 and, after about 60 yards of surface foraging, had the misfortune to visit a "bored" lodge harboring a mink. The mink quickly overtook it on the ice, killed it, and dragged it into the "bored" lodge.

Only 2 of a sample of 50 mink scats deposited from the first of the year up to January 19 contained muskrat remains, and one of these two was the previously mentioned scat containing the remains of the muskrat foot from the northeast center. The chief items of mink diet were meadow mice living in the drier of the muskrat lodges, small bullheads congregated in the plunge holes of some of the wetter lodges (these bullheads were exploited by resident muskrats as well), and the dead coots shot by hunters in the fall. There were at least 3 big minks and a small one regularly working the central shallows in mid-January.

On January 19, three muskrat-occupied sites totaling about 4 acres of shallows were frozen to the bottom; by January 29, the affected area was about 45 acres; by February 4, about 60 acres. Up to this time, only the muskrats of the central shallows had been suffering greatly from the freeze-out. By February 7, about 2 acres of the northeast shallows and about 20 acres of the shallows bordering the wetter south part of the marsh were likewise frozen to the extent that their muskrats were coming out. Then, on February 8, nearly 6 inches of heavy wet snow covered Wall Lake, followed in the next week by storms that left two to three or more feet of snow drifted in the reeds and bulrushes. This snow decidedly lessened the wintering crisis for the shallows-dwelling muskrats, both by stopping the descent of the frost-line and by affording surface-active muskrats protection in their foraging for bulrush rootstocks on top of the ice.

During the period of most lethal exposure between January 20 and February 7, 19 mink victims were specifically recorded, and 13 of 21 mink scats contained muskrat remains. All of the above scats that did not contain muskrat remains were gathered from the northeast center where the muskrats continued to live securely. Later, from mid-February to early March, muskrat remains were found in 7 of 17 scats.

Mink predation upon exposed muskrats was often spectacular.

One mink killed and cached four muskrats in one night and day, and signs were seen in several places of minks overtaking and killing muskrats on light snow.

The fates of two of the muskrats that ended up wandering about the deeper south part were determined. An old male died sitting in a small rush clump. Another animal with a frozen tail was killed by a mink.

The thaw of early March removed all but the larger drifts, but the melted snow restored living conditions for muskrats of the shallows to about what they had been in late December. Some muskrats continued to work about on the surface, but most remained under the ice and in the lodges. It was quite apparent during early and mid-March visits that the surviving muskrats of the central shallows were generally getting along well.

As nearly as I can figure, the total wintering losses through February among about 800 muskrats amounted to about 200, confined almost entirely to a total of about 60 acres of shallows.

There was evidence that the hemorrhagic disease killed muskrats now and then in the vicinity of the lodge in the south center where two were known to have died in the fall. A muskrat was active in the snow about 55 yards from this lodge on February 6, and the next day 2 fresh mink scats containing muskrat remains were found near by. The lodge also had on March 13 another fresh muskrat-containing mink scat and, on March 15, 3 more. The minks must have had access to at least 2 dead muskrats in here. The previously mentioned old male found dead sitting in a rush clump died 60 yards away, and the mink-eaten wanderer with the frozen tail was within 200 yards; but I doubt that they were diseased.

Between December 7 (when the one-week trapping season closed) and late winter, two big deep-water lodges were frequented by most of the surviving muskrats within a radius of about 125 yards. Mink-eaten remains outside of a hole in one of the big lodges on March 10 caused me to watch this tract closely. On March 13, remains of two others (including a nearly intact one fed upon by a mink in a neighboring feed house) were found, as well as another muskrat that came out of one of the big lodges to be overtaken on the ice by a mink, killed, and cached in a snowdrift about 50 yards away. Both of the two intact or nearly intact dead muskrats — including the one actually killed on the ice by the mink — showed typical hemorrhagic lesions. On March 15, the two big lodges and fourteen lesser habitations in their vicinity were chopped apart. Five more dead were found, four in one of the big lodges and one in the other. Three dead were intact, dying from hemorrhagic disease while huddling together in one corner of a lodge chamber. This made a total of nine recorded as dying in or about the two lodges. As of mid-March, the nearest muskrats known to have been alive were in a lodge about 140 yards away. These lodges were within 225 yards of two other sites of fall and winter disease mortality.

Elsewhere on the marsh, some imperfectly appraisable mortality took place after the crisis from freezing out had passed. Mink-eaten remains of two muskrats found near the northeast shallows were believed to have been of wanderers, but the question may be asked as to why they had been wandering. An epizootic, only suspected in mid-March, was discovered to have depopulated about four acres in this part of the northeast shallows and to have killed unknown numbers in adjacent parts. On March 10, two fresh mink victims were found in the central shallows (an intact one was emaciated but had no recognized disease lesions), and two other muskrats were engaging in outside activities. On March 13, remains corresponding to the two surface-active animals were found. Remains of three more were found on March 20. Thirteen of nineteen mink scats deposited here during the first half of March contained muskrat remains, compared with seven of sixteen scats for the south center where the minks were known to have been feeding upon disease victims.

Another possibility is one of sexual tensions forcing the beginning of the spring dispersal before the ice went out. A traffic victim was seen on U.S. highway 69 southeast of Wall Lake, March 15, and three of four males dying on the marsh itself from March 9 to 13 were in full breeding condition. In late March, a surface-active animal was collected from the northeast center, but it proved to be a fat and apparently healthy adult female. Also at the very last of the month, a pronounced but still localized dispersal took place in gradual stages from the northeast center, days before the actual break-up of the ice.

Minks were still responding to the availability of surface-active muskrats, whether the latter were vulnerable because of disease or not. Twenty-one of 42 mink scats deposited in the second half of March contained muskrat remains, including 3 of 14 scats passed after the softening of the ice and the appearance of much open water.

Slightly over 400 were judged to have survived on Wall Lake until the ice went out in 1950. This survival was all but confined to four main blocks.

One of these blocks comprised about 18 acres of muskrat-occupied shallows dominated by river bulrushes in the northeast part. It was not very successfully trapped during the short fur season. After the trapping, it had a carefully estimated population of between 145 and 180, more nearly the latter, or about 170. This block included the site of the deadly epizootic of early spring, and it is thought that about 15 muskrats per acre died on 4 clean-swept acres, plus maybe 20 or more on another 4 acres lying adjacent but less severely affected. There were some possible disease losses from 200 to several hundred yards away in other parts of the block, besides miscellaneous losses as from mink predation on ill-situated animals, winter wandering, and the like, and these may have totaled another 30 or 40. The best evidence indicates that about 60 survived the winter on the 18 acres.

The block having the most muskrats after the trapping — estimated at between 600 and 750, more nearly the former figure, or perhaps

about 630 — was about 75 acres of the central shallows. Losses from mortality and departure were locally severe during the winter. It had minor foci of disease between the fall of 1949 and the spring of 1950, but sweeping epizootics did not get started. Most detected mortality occurred through the agency of the mink predation upon frost-evicted muskrats already described. The greatest wintering losses were confined to a tract of about 25 acres of shallows located almost in the exact center of the marsh, which tract was all but depopulated, with an estimated mortality of about 150. The winter and early spring losses on the other 50 acres of the central shallows amounted to about 150 muskrats more, from disease, frost-eviction, and mink predation, combined, thus bringing up the total post-trapping, pre-dispersal losses to about 300. If the early winter post-trapping estimates are nearly correct, the survival might be something over 300 for the 75 acres, but this figure is a little higher than the number actually believed to have survived. Possibly it should be about 275.

Approximately 100 animals were considered alive elsewhere on the marsh after the trapping in December, 1949 — these being almost entirely localized in two wintering blocks in the south center. One block of about 22 acres was dominated by river bulrush (with minor growths of hardstem bulrush), but it had considerably more water than either the central or the northeast shallows. The muskrats of this block, though well-situated with respect to ordinary environmental features, were practically eliminated by hemorrhagic disease by spring. It is doubtful if more than a half dozen survived there out of a post-trapping population of perhaps 25 or 30.

The other block consisted of a zone of about 60 acres of mainly river bulrush shallows adjacent to the deeper waters and the cattails and hardstem bulrushes of the southwest tip of Wall Lake. For the 70 or 75 muskrats present in mid-December, 1949, the winter survival was high. No post-trapping losses of consequence were detected, and it may be judged that perhaps 70 survived.

SPRING TO FALL, 1950, AN EXCEPTIONALLY INFORMATIVE PERIOD

With the rains of spring and early summer, the water level was restored almost to within a foot of the high water mark of the mid-forties. Large tracts of formerly dry marsh thereby became habitable and attractive for muskrats. Yet only the wintering area of the central shallows had any pronounced emigration, and to this source may be ascribed most of the Wall Lake muskrats moving more than a few hundred yards during the spring dispersal, including those leaving the marsh to wander cross-country. The main route of travel of the central muskrats, from late March through most of May, was in a southeasterly direction. Apart from the wandering (which took place early and was essentially over soon after the ice covering disappeared), the movements most closely studied were those of an orderly extension of home ranges or breeding territories into previously vacant but attractive bulrush stands — especially into a disease-swept tract and

into what was formerly a drought-exposed stand of bulrushes immediately to the south of the central shallows. Most of the restocking traceable to the central shallows took place within a 500-yard radius. There was practically no movement northward into the splendid habitat awaiting recolonization by muskrats in about the northern two-fifths of the marsh.

A few animals left the northeast shallows before the surface ice melted, to go to shore, but even these did not work along the shore line like real transients. Establishment of breeding territories could be quite satisfactorily traced within a radius of a quarter mile or less from known wintering quarters. From here, too, the animals worked westward, southward, and eastward but not northward. I do not know the origin of a single 1950 territory in the northwest corner of Wall Lake, 1,000 yards from the nearest place where muskrats got through the winter.

As of mid-May, 1950, the breeding population of Wall Lake was quite accurately determined as the occupants of about 131 territories, or the equivalent of at least an equal number of females plus associated males. Following the sex ratio of 46 per cent males in 139 fall and winter specimens, we would have about 243 adults. The occupied areas totaled 292 acres.

The relative shortage of males in combination with the scattered distribution of many of the territories cut down the efficiency of mating in certain territorial groups. Moreover, the dying of disproportionate numbers of adult males from hemorrhagic disease in late spring (seven of eight dead adults in sufficiently good condition to sex when found during the second half of May were males) did not remedy this unbalance. By early summer, there may not have been more than two males per three females in the adult population of muskrats on the marsh.

Except in the northeast shallows, little or no dying from hemorrhagic disease occurred between late March and late April. Then, about the time in late April when newcomers were establishing breeding territories in old foci of infection, the dying was resumed. No sweeping epizootics took place until later, but muskrats were found dead in May and early June at or near all recent disease foci. By late June, a severe die-off all but depopulated one of the best muskrat areas in the south part of the marsh. We can charge to hemorrhagic disease the loss of at least 28 and possibly as many as 35 of the 131 territories, as of early July.

Meadow mice (*Microtus pennsylvanicus*) proved to be an unexpectedly adverse factor from the standpoint of early productivity of muskrats at Wall Lake in 1950. This species of mouse occupied large acreages of dry or nearly dry marsh in the fall and winter of 1949-50, living in the muskrat lodges and feeding chiefly on the rootstocks of river bulrush incorporated therein. Despite conspicuous predation by minks, short-eared owls, and marsh hawks, substantial numbers remained to become real marsh dwellers as the waters rose in the spring.

The mice of tracts having much lodged or floating vegetation — such as the northeast and the central shallows — could, by alternately running over the debris and swimming, travel about where they wished away from their retreats in the muskrat lodges. The mouse occupants of lodges situated in deep or more open water were marooned there and searched the lodges for food with a desperate intensity. In either case, the mice were for many weeks (until the marsh grew up to lush vegetation in June) dependent upon the bulrush rootstocks and what little variety of other foods they could find in a flooded habitat.

After it was noticed that the mice were thoroughly working the interiors of lodges for food, a study of possible predation by the mice upon young muskrats of helpless sizes was undertaken. Accordingly, 12 mouse-infested lodges that were kept in continued repair by adult muskrats as territorial headquarters were marked and later re-examined at appropriate intervals. Of these 12 territorial lodges having mouse occupants, all were in river bulrushes except one, which was in reeds.

It happened that half of the territorial lodges having mice were in rather open or deep water and the others were in shallows partly covered with emergent or floating vegetation. The fortunes of muskrats in rearing young in lodges containing mice were decidedly better where the lodges were in well-vegetated shallows rather than surrounded by open water. In the latter lodges, the mice usually appeared to clean out the accessible young muskrats within a few days after birth. Little or no successful rearing of muskrats occurred in the early part of the breeding season in five of the mouse-infested lodges. Some reduction in size of muskrat litters through depredations of mice is indicated by the field data from seven productive territories. Five of what were regarded as mouse-reduced litters averaged only 3.1 young at about one week of age.

A possible connection between the hemorrhagic disease and miscellaneous mortality of young muskrats may be mentioned. Apart from such obvious events as a suckling litter being left to starve after the death of the mother — resulting in the loss of one of the 61 litters handled on the marsh in 1950 — all of the intraspecific attacks known to be suffered by small young occurred in disease areas. One newborn litter was almost completely eaten by an adult muskrat that behaved in a way characteristic of a sick animal. Another litter in a disease area was lost under conditions suggesting intraspecific predation. In a third instance, a newly weaned young was bitten to death with extraordinary ferocity by a sick adult in a neighboring territory; the victim's intestines and part of its liver protruded from one side of its abdomen, more intestines from the other side, and a hind leg was bitten through and broken.

Most of the 1950 trapping at Wall Lake was done by skilled and cooperative trappers. Of the approximately 1,000 animals trapped, the carcasses of 952 were examined. Seven of 164 back-tags that had

been placed upon young muskrats were recovered as a result of the trapping. The most interesting tagged animal was a precociously breeding female trapped at the age of 213 days practically where it had been tagged at the age of 16 days; its placental scars indicated the birth of a litter of 5 young in August, or a conception at around 3 months of age.

The ratio of 45 adult males to 79 adult females (36.3 per cent males) in the trapped sample of 952 carcasses illustrated the unbalance in favor of the females known to have existed on the marsh early in the 1950 breeding season. The over-all sex ratio was 51.2 per cent males. The sample of 828 young of the year (442 males, 386 females) contained 53.4 per cent males, compared with the 55.9 per cent males in 202 young examined soon after birth and 56.8 per cent males in 111 "kits" examined in the trappers' catches.

Of the 79 bona fide adult females (i.e., those born prior to 1950), 17 had not conceived during 1950, and 15 of the 17 were found in carcass lots totaling 447 specimens taken largely from parts of the marsh that were underpopulated in spring and early summer. On the other hand, only two of the nonbreeding adult females were found in the balance of the 505 specimens taken largely from tracts sufficiently well populated to permit efficient mating.

Other contrasts are afforded by the numbers of litters conceived by the breeding adult females living in underpopulated and well-populated tracts. Of 27 adult females that managed to breed despite a relative shortage or unavailability of males in the places where they lived, 5 (18.5 per cent) conceived a single litter each in 1950; 10 (37.0 per cent), two litters each; 4 (14.8 per cent), three litters each; and 8 (29.6 per cent), four litters each. Of 35 adult females that bred in a better populated marsh, only one (2.9 per cent) conceived a single litter in 1950; 8 (22.9 per cent), two litters each; 8 more, three litters each; and 18 (51.4 per cent), four litters each.

Considered in terms of litter production, the 1950 means for the underpopulated tracts were 1.64 litters for all adult females and 2.56 litters for those actually breeding; in the well-populated tracts, the means were 3.05 litters for all adult females and 3.23 litters for those breeding. Over the whole marsh, the means were 2.30 litters for all adult females and 2.94 litters for those breeding.

Of 69 litters conceived in 1950 by the sample of adult females living in the underpopulated tracts, 17 (24.6 per cent) were judged from the appearance of placental scars to have been born in April; 20 (29.0 per cent), in May; 15 (21.7 per cent), in June; 13 (18.8 per cent), in July; and 4 (5.8 per cent), in August. Of 113 litters conceived by the adult females of the well-populated tracts, the births of 17 (15.0 per cent) were thus dated to April; 24 (21.2 per cent), to May; 26 (23.0 per cent), to June; 29 (25.7 per cent), to July; 15 (13.3 per cent), to August; and 2 (1.8 per cent), to September.

For the marsh as a whole, the seasonal distribution of 182 litters conceived by adult females of the trapped sample in 1950 lined up as

34 (18.7 per cent), in April; 44 (24.2 per cent), in May; 41 (22.5 per cent), in June; 42 (23.1 per cent), in July; 19 (10.4 per cent), in August; and 2 (1.1 per cent), in September. To get a true cross section of the season's breeding, we must add to these the single litters conceived by 22 females that were themselves born during the 1950 breeding season: five litters assigned to late July, nine to August, and eight to September. This would give a total of 204 litters conceived by the population sample examined — 34 (16.7 per cent), in April; 44 (21.6 per cent), in May; 41 (20.1 per cent), in June; 47 (23.0 per cent), in July; 28 (13.2 per cent), in August; and 10 (4.9 per cent), in September.

The precocious breeders in the underpopulated tracts conceived more young apiece than did those of the well-populated tracts (a mean of 5.7 as against 4.9), but the mean size of the litters conceived by bona fide adults in the underpopulated tracts was smaller (7.4 as against 8.3). For the entire marsh, the mean of placental scars counted in the uteri of fully adult females was 8.1 per litter; in the precocious young females, 5.3 per litter. At Wall Lake in 1950, the over-all mean was 7.7 for the 204 litters counted from placental scars and from 14 complete very young litters previously examined in the nests. The 14 complete young litters examined in the nests averaged 7.1 young in each, and 80 sets of placental scars of adult females trapped in approximately the same parts of the marsh where the litters had been handled during the field studies averaged 7.4 scars per set (or litter). If allowance be made for a minor amount of resorption of embryos in the uteri and for young born dead, the means from placental scars and from nest studies are in good agreement.

On the basis of field and specimen data (see Appendix C for details), the 1950 fall population was calculated at about 1,600.

THE 1950 CHANGE IN STATUS OF THE HEMORRHAGIC DISEASE AT WALL LAKE

Following the scattered dying of late spring and early summer and the deadly local epizootic of June, 1950, no evidence of mortality was personally seen on the marsh up to freeze-up, nor by skilled trappers who looked over their prospective trapping grounds in advance of the opening date. During the trapping, only two dead animals were reported as found by trappers under circumstances suggesting disease (one had died from lung and kidney hemorrhages and the other from acute intestinal hemorrhages), yet 30 or 6.7 per cent of a series of 446 trap carcasses examined for disease lesions had characteristic necrotic foci on the livers. This was a high incidence of infection for such a series of active animals taken at large, and the disease was surely of nearly general distribution over the marsh.

It is of interest that most (not all) of the animals showing conspicuous liver lesions were very young ones, in contrast with the previously noted inability of the very young to live long enough, at times of big die-offs, even to develop liver lesions.

Post-trapping checkups through December revealed no evidence

of important losses at Wall Lake. One animal suspected of being diseased wandered about in the snow for at least a half mile and died sitting on the side of a lodge. Perhaps a week later, its frozen body was discovered by a mink, wrenched loose, and dragged away. In late December, the site of the late-spring die-off in the northeast part had two lodges lying close together that were taken over by a mink. A once disease-swept tract in the south center had three neighboring lodges also with unrepaired mink holes and showing continued mink use. This indicated the possibility of mortality of muskrats from hemorrhagic disease. Elsewhere on Wall Lake, the muskrats surviving the trapping had all appearances of getting along satisfactorily up to the end of the year.

THE "GOOD YEARS" OF 1951, 1952, AND 1953 AT WALL LAKE

By midwinter, 1950-51, nine local sites of mortality were distinguishable, of which two were sites of light losses considered incidental to deep freezing of shallows. The other seven were foci of the hemorrhagic disease, and only two of them were at sites not found during the previous year — and, at both of the latter, the losses also were light and did not continue into the summer. At one of the five old foci of infection, losses were known to have involved a few wintering animals, then to have ceased by spring. Four of the foci not only had animals dying from time to time during cold weather, but there the disease also continued to kill locally until about the middle of May, 1951. By early June, all of Wall Lake's local epizootics seemed to stop, after partially depopulating a total of about 30 acres, including about 22 acres previously known to have been disease-swept one or more times in recent years. Some further mortality probably due to disease was noted at a lodge situated within 100 yards of one of the foci: a mink was known to have eaten a newly-weaned young, and the body of another young was found floating in the water on a midsummer inspection.

Not counting young of the 1951 season, 22 dead muskrats were specifically recorded at Wall Lake between early spring and mid-May, and half of these were intact enough to examine for disease lesions. Two of the latter 11 had died from undetermined cause (old age would be as good a guess as any), and the other 9 showed diagnostic lesions. Of the 9 disease victims, 7 had the appearance of having *almost* beaten the disease, having livers that were heavily spotted with necrotic foci in all stages of healing. In one case, about a fourth of the volume of the liver was necrotic. In another, nearly all of the liver lesions were healing or healed except for an active lesion 4 mm. in diameter, or about twice the diameter of the larger that are ordinarily seen. Intestinal hemorrhages were recognized in only 2 specimens, and, in one such case, the hemorrhaging was slight. One of the 2 individuals that died without building up extensive liver lesions had severe lung hemorrhages.

Comparative post-mortems on 2 adult females and their suckling litters made on the afternoon of May 18 were especially interesting.

One female died probably in the morning of the day of the posting, but she had not been caring for her litter of 11-day (age estimated) young for some days. Five starved-looking live and one dead young were scattered about the bed of the lodge. The dead young had several liver lesions, and one of the 5 living had at least a single lesion starting to form. These young were the remnants of 11 conceived of the litter. The female had a new pregnancy of 8 embryos about 5 mm. in diameter, and it may be conjectured that the onset of her sickness may have cut down both the size and rate of development of her second pregnancy.

The second adult female died about 18 hours before the posting, a victim of the pneumonic syndrome (though she had a few liver lesions). She did not conceive again after the birth of the litter she was suckling. She had 11 placental scars corresponding to her suckling litter, of which 7 young were found in three different places within the lodge chamber, having died an estimated 8 to 30 hours previously. The age of the one living the longest was estimated at about 10 days. While these died from hunger and neglect, 2 of the dead young had liver lesions, including one young with a heavy spotting.

Minks and other flesh-eaters responded most decidedly to the availability of muskrat flesh at three of the four foci of infection at which disease mortality continued into the summer. Three minks that were distinguishable as individuals stayed out in the center of the marsh far into the summer, subsisting for many weeks upon a diet of water birds and the diseased muskrats to be found at two of the foci. A family of raccoons similarly occupied itself about another disease focus, this one being 200 yards from shore. The fourth focus of the early summer was not discovered by mammalian flesh-eaters in time for exploitation.

Twelve of 15 muskrat carcasses found at mink retreats of the center after the ice went out were unsuitable for diagnoses; but 2 intact fresh carcasses (without a toothmark of a mink on them) and one other (of which the mink had eaten the head only) showed characteristic lesions. Two carcasses eaten upon by minks had sufficient growths of algae and water mold on tails and feet to indicate that they had been dragged to higher places after periods of floating in the water. Thirty-six of 43 mink scats deposited about the central retreats during the first half of May — the period of greatest mortality about the mink-frequented disease foci — contained muskrat remains, compared with nine of 90 deposited earlier in the year and one of 30 deposited from mid-May to mid-June. When the muskrats of the center stopped dying from disease in early summer, the minks stopped eating muskrats, though the minks remained at those places, and there were many muskrats (including young) still alive there. Moreover, when minks later moved away from the disease foci to work other central parts, they managed to continue eating water birds but had little if any luck with the muskrats — even when taking over muskrat-maintained lodges for temporary living quarters.

The details of what the family of raccoons did are not so clear. The

raccoons leveled the lodges in an area of about six acres. It is conceivable that this family group learned to raid the nests for helpless young muskrats, but I doubt if this would have yielded them enough meat to encourage them to make a specialty of it had it not been for numerous large dead muskrats lying around. I found two dead adult muskrats that they had overlooked.

As of early May, 1951, 243 certain or highly probable breeding territories were enumerated on Wall Lake, or, following the overall early winter sex ratio of 51.2 per cent males, a total of about 500 adults. This is in good agreement with the figure of about 600 calculated to have survived the early winter trapping. After the trapping, a winter and early spring mortality of about 100 should have been quite within reason.

The spring and early summer die-off resulted in the loss of about 35 territories, including those established prior to the breeding season census of early May. An estimated 65 adults died during the period of notable mortality from late April to mid-May. Allowing for some scattered mortality from miscellaneous causes, this should have left about 425 adults on the marsh as potential breeding stock.

From midspring through the summer of 1951, Wall Lake was in a most attractive condition for muskrats — approximating its condition for the years immediately preceding 1947 — with water covering nearly all of the bottom. Seventeen of the territories for 1951 were established in the north half of the marsh, at varying distances (up to a half mile) from places occupied by muskrats during the past few years. Eight other territories were distributed along about a mile and a quarter of shore zone that had no muskrats in the winter of 1950–51, and about a half mile of this same stretch served as a refuge area for transients. About seven lone animals, thought to have been surplus males, gravitated to this place and maintained solitary nests from late April to at least the middle of May. Otherwise, the tracts having the breeding territories were the ones wintering the muskrats, though local dispersals within a 200-yard radius of wintering quarters were commonly traceable.

Territorial sites were distributed at densities of one or two per acre over the greater part of the regularly occupied marsh, with occasional aggregates of up to five territories per acre. Local growths of broad-leaved cattails were the outstanding inducements for such territorial massing.

Three of the examined lodges containing litters of young muskrats were also occupied by meadow mice, and, in one of these, the young muskrats probably were preyed upon by the mice. Only two of this muskrat litter were left at the age of about four days. One of the other two muskrat litters was reared up to weaning without detected loss from the mice, and the other still had nine young at the age of about ten days despite the presence of a mouse family.

In late summer and early fall, very localized dying occurred in two places on Wall Lake. One of these places was the earlier "bach-

elor quarters" of the southeast shore zone. More muskrats moved in here after midsummer, and some rehabilitated a number of old burrow systems at the site of the shore-zone epizootics of the falls of 1948 and 1949. A hunter saw two sick-acting muskrats here about the middle of October, 1951; one was hardly able to move, and the other tried to attack him on shore when he went near it. One of five mink scats found here and assigned to this date contained muskrat remains, as did two of nineteen examined between late July and late August.

The second place was an area including part of one of the central disease foci of the spring and early summer. This place (of about three acres) was nearly muskrat-vacant by mid-September and had been for some weeks. Later in the fall, the vacancies filled up again, and no more evidence of dying was found until late December, when the first wintering mortality on the marsh was detected.

Extremely few dead muskrats were reported by hunters and trappers during October and November, 1951. One hunter saw three dead in the water about a lodge in one of the cattail islands of the south part. The trappers, who covered the marsh very thoroughly in connection with a week of legal trapping in late November, reported finding only four dead animals, of which the single one examined was a disease victim typical of those almost but not quite recovering. But the disease was obviously widespread; 45 or 10 per cent of 450 trap carcasses that were examined for disease lesions had necrotic areas (mostly in various stages of healing) in their livers — an astonishingly high incidence and one suggesting that most of the animals were contracting the disease in sublethal cases. The most conspicuous lesions were usually to be seen in the youngest animals, yet it was clear that these young were showing pronounced resistance, in contrast with their dying without visible lesions during the deadlier epizootics.

The trappers took, in a special trapping season applying to Wall Lake in 1951, approximately 1,850 or, at the outside, perhaps 1,900. The 1,047 carcasses examined consisted of 58 adult males, 68 adult females, 527 young males, and 392 young females. One hundred and twenty-four or 13.5 per cent of the 921 young of the year in the sample were of "kit" sizes. Of the 394 classed as young females, 13 or 3.3 per cent were precocious breeders, each giving birth to a single litter (averaging 5.5 young or a total of 71) assigned to August or later. Of 67 adult females in the sample for which placental scars could be counted and aged, 8 had not conceived in 1951; 3 conceived single litters each; 8, two litters each; 20, three litters each; 27, four litters each; and 1, five litters. The seasonal distribution of the 192 litters born to the 67 adult females may be judged from placental scars to have been 19 in April, 47 in May, 50 in June, 48 in July, 26 in August, and 2 in September.

The "Allee effect" of inefficient mating in sparsely populated areas is well-illustrated by the data in hand. Of 7 adult females taken by the trappers from isolated rush clumps, 6 did not conceive at all in 1951, whereas but 2 of 61 taken from the more populous parts failed

to conceive. That the muskrats lived sedentary lives on this marsh during the year is demonstrated by the tagging as well as by the observational data. A female born and tagged in 1950 and 4 tagged young of the year that were recovered in the 1951 trapping were all trapped in the vicinities of where tagged. The 1951 muskrat population of Wall Lake also was isolated, out of the lines of travel of adjusting stream populations, and quite clearly self-contained.

The central parts of the marsh were the sites of remarkably high rates of survival of the young despite the continued summer residence of the minks there and early mortality in two major disease foci. A sample of 450 carcasses taken from a strip about a quarter-mile wide and a mile in length and running right through the middle in a north-south line consisted of 26 adult males, 27 adult females, 236 young males, and 161 young females. The 20 productive adult females in this lot conceived a mean of 3.15 litters and 23.8 young, or a total of 475 young. Two precocious young females each conceived a single litter of 5, bringing up the total conceived by the sample's breeders to 485. The 397 young of the year in the trappers' catches corresponding to the 485 conceived by the sample reflect a reproductive success of 82 per cent.

Outside of the above strip, 40 productive adult females conceived a mean of 3.15 litters and 26.8 young or a total of 1,099 young. Eleven precocious females of this other sample conceived a total of 61 young in single, late litters, thus bringing up the total conceived to 1,160, compared with only 524 young, or 45.2 per cent, reared. For the combined sample represented by the trap carcasses, the rearing of 921 of 1,655 conceived amounts to a reproductive success of 56 per cent.

Of the 425 adults judged to have been left on the marsh after the late spring and early summer disease losses, about 230 should have been females, following the 46.0 per cent ratio of males in the sample of 126 adults taken by trappers. The sex and age data applied to an adult female population of 230 surviving the 1951 breeding season would give a calculated total fall population of about 3,530, including about 3,100 young of the year. About 203 of the 230 adult females should have been productive, averaging 3.15 litters and 25.8 young, which would give about 5,237 young conceived or born in about 639 litters, plus about 230 young in 44 litters from precocious young breeders, or a total of about 5,467 young.

The survival rate of late-born young was unusually high at Wall Lake in 1951. For the animals of the trapped samples, 28 or 14.6 per cent of the litters conceived by adult females and all of 13 litters conceived by precocious young females were assigned to August or later. This figures out at 295 or 17.8 per cent of the total of 1,655 conceived by the trapped sample during the breeding season. The rearing of 124 "kits," or 13.5 per cent of the 921 young of the year in the trapped sample, demonstrates that the late-born had nearly as good a chance in 1951 as did the early-born — quite different from what often is the case.

The week of trapping removed only a few of the many minks frequenting Wall Lake in the fall and winter of 1951-52, and, when snow came, it was obvious that the marsh had an exceptionally heavy population of minks — perhaps the largest number in decades. One small tract studied intensively in early January had at least 3 minks that were distinguishable on the basis of tracks (including an enormous one that left, while running in firm, wet snow, an imprint of a hind foot measuring 51 mm. in width, at maximum spread); and almost all other parts of the marsh, visited then and thereafter until spring, likewise had mink signs. My guess is that there may have been up to 20 minks, mostly large ones, wintering on or about the marsh. They gave the muskrat-occupied parts a thorough working during the entire time that an ice covering existed, and their relations to the wintering muskrats were carefully studied.

Even early in the winter, the minks were repeatedly smelling the lodges (this could be deduced from the trails running past or over the lodges) but, except for certain places, were not digging into them. Most of the mink holes then being made in the dwelling lodges were promptly repaired by the muskrat occupants. But, in late December, a centrally located tract about 150 yards by 200 yards in size (the site of the probable late summer or fall epizootic previously referred to) began showing many unrepaired mink holes, and, for about the next six weeks, minks were obviously interested in this place. The minks were similarly interested in a smaller tract about 300 yards away (also the site of an old disease focus) from about January 10 to the end of the month. Mink-eaten remains of seven muskrats were found in these two suspected foci during the above period, as were muskrat remains in seventeen of thirty-one contemporaneous mink scats. Three other victims were later found, including one with typical lesions. Away from these foci, muskrat remains occurred in one of nine mink scats deposited in the south half of Wall Lake from freeze-up to mid-February.

In early January, the minks became interested in a number of lodges in and near the old disease focus that had been so thoroughly worked over by the family of raccoons in the spring of 1951. Remains of 3 dead muskrats were found here during the next three weeks, and 4 of 17 contemporaneous mink scats contained muskrat remains. A fox also scavenged on a dead muskrat that probably died of old age; and 1 of 2 fox scats from here contained muskrat remains, compared with their absence in 34 other fox scats examined on the marsh during the winter. Two muskrats dying in the winter were found in the northeast shallows, at the site of the pneumonic epizootic of the spring of 1948. These were too putrid to show possible disease lesions when examined, but one had suffered loss of part of its tail from freezing before it died.

The sparsely populated, food-rich, but shallow northwest corner was the site of some mortality that at first seemed to reflect restlessness of individual muskrats with the approach of the breeding season, but some dying from disease was found here later. Four different

places were seen in mid-February where muskrats were coming out on the ice, though only the shallower of the waters froze to the bottom. A muskrat was found freshly killed and eaten upon by a mink at one of these places, and remains of a second victim were found in the same general area. Mortality of at least two more was detected in March, and dying from disease was known to have continued into May. No muskrat remains were found in 70 mink scats deposited here from late fall through January, but 10 of 14 February scats and one of 15 March scats had representations of this item.

An imperfectly dated epizootic was detected in the south center, at the site of a rather sweeping June die-off in 1950. A mink dragged a probable muskrat in the snow on January 10, 1952. On March 10, mink-eaten remains of nine muskrats were found here, and all 16 fresh and recent mink scats contained muskrat remains, as did all 5 fresh scats from the shore zone. The evidence suggests that these muskrats were dead long before the minks got to them. The mink holes were almost restricted to the sun-softened southwest sides of the lodges, and the most nearly complete carcass found on the visit of March 10 smelled strongly of decay, though the mink had freshly dug it out of a chamber regularly used by living muskrats. Of two animals known to have died in early winter, one was of a young trap cripple probably dying of its wound, and the other at least had no liver lesions. This tract (about 15 acres) included the site of a deadly epizootic after the ice went out in 1952.

Only two places were found in 1952 where spring or early summer disease mortality at Wall Lake had no evident connection with winter foci, and at neither of these two places were the losses extensive up to mid-June. Only one of the winter disease foci failed to have some spring dying as well, and this exception related to a tract having no known victims of the pneumonic syndrome of the disease.

Elsewhere on the marsh, in the spring and early summer of 1952, the pneumonic syndrome occurred to the practical exclusion of the other syndromes, to which the muskrats were currently showing a high degree of resistance. One pneumonic victim did have an enormously enlarged and necrotic spleen, and others occasionally had a few liver lesions or slight enteritis, but, on the whole, the only gross lesions to be seen in the pneumonic victims were localized in the thorax. At the site of the deadliest epizootic, the last victim showing substantial liver lesions died about April 8; of 22 victims later recorded from here, 11 were too decayed for diagnosis, but the other 11 showed the expected pneumonic lesions. Of 32 victims recorded from the other sites of continuing spring and early summer mortality, 7 were found sufficiently fresh for posting, and these all had the pneumonic lesions.

In all three cases where locally sweeping epizootics got started at Wall Lake in the spring of 1952, the dying began at sites of heavy mortality of past years, including two foci notorious for their disease losses since 1948. After these localized epizootics gained momentum, they spread about wherever contiguous muskrat populations re-

mained to take the infection, with resulting mortality in the affected tracts of close to 90 per cent whenever the dominant syndromes switched from the hepatic-enteric to the pneumonic.

Some evidence of spring dispersal away from Wall Lake was noted in 1952, but, while the marsh population then did not appear to be *quite* as self-contained as during 1949, 1950, and 1951, it is doubtful that any really important movements out of — or into — this observational area took place in 1952. Many of the muskrats of the south center were evicted by violent storms washing away the less sheltered lodges; otherwise, the muskrats seemed to stay to breed in parts of their familiar home ranges of the past winter. Only the food-rich northwest corner drew any great number of animals during the spring dispersal, and the evident source of these was the north center, lying within 600 yards of the outermost places reached and settled by muskrats of the north half. The storm-evicted occupants of the south center first concentrated in the nearest heavy vegetation, then dispersed along routes that could not be traced with complete satisfaction, though many obviously moved into previously muskrat-vacant islands of cattails and bulrushes.

The field notes indicate a total of 455 breeding territories on Wall Lake, as of early May, 1952. On the basis of the sex ratio of 55.1 per cent males shown by the winter-trapped carcasses, the initial, more or less settled, breeding population figures out at about 1,035 adults, plus whatever number may have been living in or about territories overlooked in the censusing of heavily vegetated parts of the north half. Allowance for about 20 of such overlooked territories would give a total of about 475 territories, or about 1,075 adults. Few territorial concentrations exceeding two per acre were found; exceptions were four territories in a cattail clump of less than an acre, 11 in four acres, 10 in two acres, and 5 in one tract of about one-half acre. The latter had a lodge containing young of two different females.

During May, 33 territories were recorded as lost through the agency of the hemorrhagic disease. Eight more were recorded as lost in the first half of June. Thus, about 100 adults were eliminated from the 1952 breeding population, which would then leave a mid-June population of perhaps 975 adults remaining in well over 400 functional territories.

The responsiveness of minks to the disease foci at Wall Lake was, if anything, more notable in the spring and early summer of 1952 than in 1951. In 1952, no spring focus of any consequence failed to draw the attentions of minks, even when located near the center of the marsh — in fact, the evidence is that the minks stayed over from winter at these places. Whereas none of 165 mink scats gathered in May and June away from the foci contained muskrat remains, 32 of 198 scats from the foci did contain muskrat remains. For the main focus, 32 of 102 scats gathered during April (the month of severest disease mortality) contained muskrat remains. As long as the muskrats kept dying, the local minks took advantage thereof, though overlook-

ing many dead muskrats, probably about two for every one they found after the ice went out.

After all but depopulating the 15-acre tract where the heavy dying of winter and spring occurred, the pneumonic-syndrome epizootic did about the same thing in early June in a neighboring tract of about four acres. Wide areas of muskrat-vacant marsh on three of four sides of both of these tracts seemed to prevent further spread. No evidence of dying was found after the third week of June until early fall, despite the fact that, by July, muskrats were moving into the disease-swept areas and establishing themselves there.

A breeding female that had apparently been living for many weeks in the main area of the pneumonic epizootic was taken for a specimen on June 30. She had no recognized liver or other lesions, but the small sizes of her two pregnancies of the season (6 and 5 young) might suggest earlier illness. The mean size of 17 complete litters handled up to this time in 1952 was a little less than 8.

A probable case of ringworm skin disease was seen, June 12, on a young muskrat of about 9 days in one of the bulrush islands of the southeast center. It had two large hairless patches reminiscent of the many victims of *Trichophyton* studied at Round Lake, 1935–38 (Chapter 5).

Of the young muskrats tagged on Wall Lake in May and June, 1952, five were turned in by trappers in the fall. Four of the five were caught close to, the fifth approximately 1,000 yards away from, sites of tagging. This was about the sort of pattern shown by the field data on movements. While it was clear that muskrats appeared in late summer and early fall in places several hundreds of yards from those having had breeding populations earlier in the year, it was just as clear that the majority of family groups tended to stay in the vicinities of their original territories of spring and early summer. Many fair-sized tracts of excellent marshy habitat remained unpopulated by fall for the obvious reason that insufficient movement occurred away from adjacent territorial sites to put muskrats into them.

The one outstanding example of population adjustment that was studied occurred on the part of a local population living adjacent to a tract of about seven acres that had been depopulated in April and May by a pneumonic epizootic. By midsummer, the habitat of the local population that escaped the epizootic had deteriorated, and the living animals simply took over the depopulated tract in gradual stages. The end result was a mass shift over distances varying from 50 to almost 300 yards, leaving, by late summer, the deteriorated habitat virtually unpopulated and the formerly disease-swept tract well refilled with muskrats.

Along the southeast shore, a burrow system at which muskrats had died at intervals since the fall of 1948 — and one of the few places where dying had been noted in the fall of 1951 — was the only site of dying discovered at Wall Lake between late June and late fall, 1952. At least one animal died here about mid-September, right where

victims were usually found. Then, no further evidence of dying was found until November 7, when a freshly dead "kit" was found at another disease focus of limited area near the south central shore. This "kit" had lesions suggesting low resistance. From the latter focus, a very deadly epizootic was traced in the shore zone for about 130 yards to the west on November 9; the three other victims examined all had lesions suggesting low to moderate resistance. A third old disease focus, this one in the southwest center, was also known to be the site of substantial dying in early November; two dead were found here by trappers, and a large proportion of the diseased specimens caught in traps came from this general area.

Trappers' catches from Wall Lake during a 10-day open season in mid-November, 1952, amounted to more than 4,000 muskrats. The intensiveness of the fur trapping evidently prevented the late-starting fall epizootics from spreading over much of the marsh away from the disease foci.

A sample of 276 trapped carcasses believed to be representative was examined, and 10 or 3.6 per cent showed liver lesions. There were no small young among these carcasses, in contrast with the large proportions of young in the trapped carcasses showing healed or healing lesions in 1951. Moreover, the 1952 specimens of Wall Lake animals that were diseased yet still active enough to be caught in traps generally showed moderate to severe lesions, some healed-looking and some indicating that the victims were about to succumb.

It should not be assumed that the late-born young were not contracting the disease in the fall of 1952. Rather, the likelihood is that the late-born young were not staying alive long enough after contracting the disease to be caught in traps or to build up liver lesions.

Using a minimal basis of 400 productive territories and the sex and age ratios of fall (27 adult males, 19 adult females, 149 young males, and 81 young females), a pre-trapping population of 968 adults and 4,842 young, or a grand total of 5,810, may be calculated. Although this figure may be as accurate as any permitted by the data, my feeling is that the fall population actually was somewhat higher.

The sample of 19 adult females had a total of 498 placental scars in 63 litters, or a mean of 26.2 young conceived in a mean of 3.3 litters for the breeding season. One female conceived two litters in 1952; 11, three litters each; and 7, four litters each. Of the litters represented by the placental scars, the times of birth of 3 were assigned to April, 16 to May, 17 to June, 17 to July, 8 to August, and 2 to September.

No evidence was found of breeding by precocious young females at Wall Lake in 1952, though bona fide adults did plenty of late breeding. Two of the 17 "kits" found among 230 young of the year in the trapped sample were animals of about six weeks, or animals born in late September. A ratio of only 7.4 per cent "kits" among the young of the year is sufficiently in contrast with 15.9 per cent of the litters judged to have been born in corresponding months to indicate

a disproportionate mortality of the late-born young. Part of this disproportionate mortality is attributed to greater susceptibility of late-born young to disease.

Approximately 2,000 muskrats survived the fall trapping, of which an estimated 75 to 80 per cent entered the winter of 1952-53 in the shallower but food-rich central and north parts of the marsh. The south part was not only more accessible to trappers using boats, but it also lost sizable acreages of food resources through natural causes.

The muskrats of the trap-thinned south part suffered light wintering losses, and these losses were all but restricted to two major disease foci. The few minks wintering here centered their attentions about these foci. Remains of 10 mink-eaten muskrats were found, and 44 of 99 mink scats contained muskrat remains.

In the north shallows, the muskrat wintering losses were possibly 100, occurring through a combination of disease in minor foci, freezing of the shallower places to the bottom, and mink predation upon vulnerably situated animals. As the spring breeding season came on, the muskrats did a certain amount of fighting and shore-wandering, which also meant some more mink predation upon those muskrats trying to live at the greatest disadvantage. An extremely high concentration of minks — an estimated 12 to 15 — wintered here, to stay on into the spring and summer.

Of 715 mink scats deposited in the north shallows from early winter to midwinter, 203 contained muskrat remains, compared with 62 of 297 scats for late winter through the first of March and 57 of 455 scats for the second half of March. Of 23 mink-eaten muskrats noted for the north shallows for this period, only 3 were found in known disease foci, but neither is it certain that any of the other 20 were away from places where dying from hemorrhagic disease had occurred; and it may be judged that disease loss constituted about half the wintering loss of about 100. For April, 61 of 433 mink scats contained muskrat remains, but this item was not found in 167 scats for the first half of May, after both dying and shore-wandering of muskrats had largely ceased. The April exploitation was clearly linked with dying of muskrats at disease foci; of 8 dead adult muskrats examined in sufficiently fresh and intact condition to be diagnostic, 7 (including 2 partly eaten by the minks) were disease victims. The prompt letup in feeding by minks upon muskrats in late April is significant insofar as a settled muskrat population of about 1,000 adults was living securely in the north shallows, even in meadow-edge habitats that were thoroughly worked over by the numerous minks.

During late winter and early spring, 1953, raccoons dug open lodges in one of the principal disease foci of the south part of Wall Lake, and they continued visiting this tract until midspring. Two raccoons were seen asleep in the top of a lodge having a dug-out nest of young muskrats, and other nests in the vicinity were raided. Of 60 raccoon scats deposited from late March to early May, 17 contained remains of young muskrats, and the muskrat-containing scats had bones of dozens of individual young muskrats aged up to several

weeks at time of death. Some scats were packed masses of tiny muskrat bones and teeth. This exploitation ceased in early May, and none of 23 raccoon scats deposited here from mid-May to early June contained muskrat remains. Most of the opening of muskrat lodges by raccoons in May and June occurred in a second disease focus, but none of 44 locally deposited raccoon scats contained muskrat remains.

The above raccoon-muskrat relationship appeared to be neither a simple matter of direct predation nor exploitation of disease victims. The centering of attentions of the raccoons in or about disease foci was striking — many shore-zone lodges and burrows adjoined both of the raccoon-worked foci, but the raccoons did not disturb them. Yet, much of what went on in the general areas of the disease foci did have aspects of direct predation, with the raccoons digging out nests having young muskrats; and the one thing that seemed to terminate the raccoon predation was the harrassed adult muskrats moving their territorial headquarters out into deeper water or into other places where the raccoons were unlikely to swim. Of course these territorial shifts also may have reduced the chances of family groups contracting the disease. The leg bone of a half-grown muskrat at one of the raccoon retreats suggested scavenging on a disease victim, for this size muskrat should normally be able easily to escape capture by raccoons. It may be that the raccoons learned that the foci were likely places in which to seek dead muskrats and that, while there, they got started hunting the perfectly normal but helpless smaller young muskrats in the nests.

A mid-May, 1953, total of 708 maintained territories represented about 1,900 adults. Over half of these muskrats were located in the shallower but food-rich northern third of the marsh, and, at the high water stage of spring, the shallower parts were not necessarily very shallow in terms of muskrat habitat. Two local concentrations the equivalent of 7 pairs of muskrats per acre were noted.

The shallows became drought-exposed in late summer and early fall, with extremely severe consequences to the occupants of 130 territories and less serious consequences to the occupants of another 300, or more, territories. By mid-October, fair remnants of the original populations (consisting for the most part of large animals) were still living in the dried-out territories. (One muskrat found freshly killed by a dog was an old male.)

Population remnants could be seen at sites of old disease foci as well as elsewhere. At one of the later foci, 7 of 11 mink scats from early October contained muskrat remains, compared with 2 of 30 scats deposited a short distance away. Mortality was recorded at another disease focus, but none of 8 scats for late September or early October contained muskrat remains. The occurrence of muskrat remains in 8 of 9 scats from a long-dry place probably reflected predation upon drought-exposed muskrats; elsewhere it was remarkable how little the drought-exposed muskrats were exploited by minks except at old disease foci.

Six of about 1,000 raccoon scats hastily looked over in the dry

tracts contained muskrat remains. All 6 were from the near vicinity of known foci, including one of the most consistently deadly on Wall Lake — the acre-sized focus in the north center, from which the main die-off, winter and spring of 1947–48, had started.

From spring through early fall, most of the old disease foci were left almost devoid of muskrats, as dying occurred about as fast as the foci were reoccupied by newcomers. The 1953 drought surely reduced the disease losses by leaving some of the worst foci so dry that they no longer held attractions for muskrats after late summer. Foci that were sites of late fall dying were those becoming refilled by readjusting animals during about the middle of the fall and were almost restricted to the south center. At these, some dead were reported by hunters and trappers as early as a month before the trapping season opened on November 10, but no epizootics really got started. With the opening of the trapping season, public trapping removed many of the dangerously situated newcomers just as they were beginning to die.

The catches of two groups of trappers included muskrats taken from the south central disease foci, and 839 carcasses of these catches (representing the first week of trapping) were examined. Of the 256 that were first caught, two animals, or fewer than 1 per cent, had a few small liver lesions. Of the 583 caught some days later, 16, or nearly 3 per cent, had liver lesions, and, of the 16 diseased livers, 8 had substantial to large numbers of lesions that were obviously getting a good start. The lesion changes would seem to indicate a build-up toward a potentially serious epizootic.

Totals of 916 carcasses of trapped muskrats were examined at Wall Lake in November, 1953: 72 adult males, 68 adult females, 468 young males, and 308 young females. Of 69 adult females examined in the fall, 8 had not conceived young in 1953; 6 had one litter each; 5, two litters each; 27, three litters each; and 23, four litters each. The mean number of litters for the 69 adult females was 2.71 and, for the 61 breeders, 3.07. Seasonal distribution of the litters of the above adults: 22 or 12 per cent of 187 litters were assigned to April; 45 or 24 per cent to May; 48 or 26 per cent to June; 44 or 24 per cent to July; 27 or 14 per cent to August; and a single one to September.

Twelve or 3.9 per cent of the young females in the trapped sample conceived a single small (averaging 5.4 young), late (born from late July through September) litter. All together, the birth dates of 39, or 20 per cent of the sample of 199 litters yielding quantitative data, were assigned to August and September. That these late-born young did not thrive as well as the young born earlier is indicated by the occurrence of only 90, or 12 per cent, late-born animals (assigned to birth dates after July) in the 776 specimens of young of the year in the trapped carcasses. Among the 90 late-born young in the mid-November carcasses, 16 were judged to have been born less than two months previously.

Many young animals in at least the better-situated of the drying

territories made successful adjustments after the breeding season. They were able to move into the more disease-free parts that had favorable water levels, fair to excellent food resources, and were still relatively underpopulated by muskrats. There was also considerable late breeding on the wetter two-thirds of the marsh, even in places where most of the marsh bottom was exposed except for the deepened channels about the muskrat lodges. Yet, in the latter places, the excellence of the food supply (mostly river bulrush) offset many of the disadvantages of the low water as long as plenty of surface water actually remained in the channels up to the onset of hard frosts.

Wall Lake, being outside the travel routes of muskrats adjusting to the drying of surrounding streams, had an essentially self-contained muskrat population in 1953 — that is, except for some muskrats leaving the dry north end and perhaps other shallows to wander. The calculated population of adult females still alive on the marsh by the beginning of the trapping in November was about 480. This base, used with the ratios shown by the trap carcasses, gives a pre-trapping population of 6,480, or, in rounder numbers, about 6,500.

The trapping pressure was excessive on Wall Lake during the 30-day open season beginning November 10, 1953. Except for the occupants of certain hard-to-get-at shallows, the muskrats were nearly cleaned out, and probably no more than 300 survived the trapping. The survivors of the trapping were further reduced by losses from disease and winter-killing. Almost annihilative mortality was noted during the winter at 4 well-known shallow-water disease foci, at which remains of 17 probable disease victims were found. There were muskrat remains in 113 of 134 scats deposited by perhaps 4 minks frequenting the disease foci, December through February. Elsewhere in the partly or completely exposed shallows — including suspected but not actually proven disease foci — 19 dead muskrats were found, of which the two intact specimens were disease victims. Fourteen of 28 mink scats deposited at scattered sites contained muskrat remains.

TWO YEARS OF UNDERPOPULATION, 1954 AND 1955

The Wall Lake breeding census of mid-May, 1954, gave the figure of 52 maintained territories, representing about 130 adults. The area received enough spring rain to become a generally excellent muskrat marsh again — but with only about a tenth of the breeding stock that it could easily have accommodated.

Signs of at least a fair amount of reproduction could be noted during the summer in those few tracts in which the low breeding population tended to be distributed in clumps of territories. Away from these clumped territories, there seemed to be little or no reproduction by animals living in isolated small cattail, reed, or bulrush islands. Later, the inefficiencies of breeding as a result of too-low population densities were verified by specimen material obtained from trappers in late November.

Of approximately 500 muskrats trapped by the public in 1954, the

carcasses of 266 were examined: 14 adult males, 24 adult females, 141 young males, and 87 young females. Nine of the 24 adult females had not conceived in 1954, but the samples were trapped from those parts of the marsh having had by far the largest numbers of isolated adult muskrats during the breeding months. Three of the 24 adult females gave birth to single litters dated to May — they probably had been pregnant when taking up residence in out-of-the-way places. Of the other 12 adult females, 6 conceived 2 litters each in 1954; 2, three litters each; and 4, four litters each. Assigned birth dates of the 37 litters: 2 litters to April, 10 to May, 11 to June, 11 to July, and 3 to August.

Seven of the 87 young females of the trapped sample were precocious breeders, and one of these gave birth to 2 litters — 5 in each litter and assigned to late July and late August. The birth dates of the other 6 litters of precocious young females were assigned to August.

The population of resident adult muskrats surviving until the fur trapping figured out at about 80, and the number of young reared on Wall Lake in 1954 at about 675. Of these young, about 600 were born before August, and, of the late-born young reared, about 45 were — on the basis of existing ratios — born to the precociously breeding young females. The actual fall population may have been somewhat higher than the total of about 755 muskrats calculated; after allowing for overlooked territories and possible small numbers of newcomers from the outside, an estimate of about 800 may be made.

About one square mile of marsh was habitable for muskrats by late November, 1954, and, following the trapping, this area had a population of about 300 entering the winter. Only a little dying was noted in fall and early winter, this all being confined to old disease foci. One of the 266 trapped carcasses that were examined had a liver lesion suggesting the hemorrhagic disease. Of a total of about 320 lodges, 31 were found opened by minks between freeze-up and mid-December, and 26 of these 31 mink-opened lodges were either in or adjacent to disease foci. Even so, remains of only three probably diseased muskrats were found in this period, and none of 101 early and mid-December mink scats contained muskrat remains. As the winter progressed, the diminishing evidence of living muskrats in the vicinities of major foci indicated that epizootics were spreading under the ice on a considerable scale. An abundance of minks — estimated at between 15 and 20, probably nearer the former — worked muskrat-occupied and muskrat-vacant parts alike, and these minks were most responsive to new sites of dying as the local epizootics spread away from the old foci of infection. Eighty-six of 329 winter mink scats deposited after mid-December contained muskrat remains. Only 3 specimens of 42 dead muskrats were in good enough condition to examine for lesions of the hemorrhagic disease; all three proved to be diseased, including one apparently killed by a mink while starting to hemorrhage. Probably at least twice as many muskrats died as were individually recorded in the course of the winter studies, so an esti-

mate of about 100 dying mainly from the hemorrhagic disease would seem reasonable.

The breeding season census, as of the first half of May, 1955, gave a total of 97 functional territories. Application of the sex ratio of 58.3 per cent males obtained at Wall Lake in the preceding late fall and early winter would give a total of about 233 adults for the settled late spring population. One territory had been lost shortly before the breeding season census — presumably from disease, in view of its location in a small focus of known deadliness — but only one specimen of an animal dying from disease was found in the course of the spring. The majority of the territories were maintained in parts of the marsh considered fairly safe on the basis of their disease histories. Nevertheless, a few territories were in time established in some of the deadliest foci and were almost certainly lost, in turn.

By late fall, only about 70 acres remained covered by water, and practically the entire muskrat population was concentrated in a tract established as a state fur-refuge area. A total of 256 medium-sized and larger lodges in the wetter parts of the marsh should signify a population of about 1,200.

Most of these muskrats got along well up to the end of December, though evidences of both disease loss and drought vulnerability were recorded. The shallow, thickly-vegetated central and north parts had a heavy population of minks — estimated at about 30 on the basis of signs — and these minks were exploiting muskrats in two places suspected of being sites of dying from hemorrhagic disease. Eleven of 29 mink scats from these two places contained muskrat remains, compared with no muskrat remains in 52 mink scats examined from other muskrat-occupied parts. At this time, there was some but not much activity of ill-situated muskrats on the surface of the ice.

THE COLLAPSE OF 1956

By late January, 1956, muskrats were active practically everywhere on the surface in the muskrat-occupied parts, to the accompaniment of much intraspecific fighting and mink predation. A freeze-out crisis reached acute stages, which continued unrelieved into March. Fifteen trails of minks dragging muskrats were noted during six inspection trips made over a six-week period. Muskrat remains were found in 92 of 100 mink scats, as well as in all 4 fox scats examined during the middle two weeks of February. (An unrecorded number of fox scats examined at random earlier in the winter had contained no muskrat remains.)

As many as five bodies of muskrats were recorded as cached in a single mink retreat in a muskrat lodge, and the source of these dead was a disease focus about 150 yards away. After the melting of the ice, three muskrat disease victims were examined at the focus itself. One of the three had recently died, and times of death of the other two were datable (on the basis of stage of sexual maturity) to the period when the minks had been active dragging muskrat bodies from this

place. Later in the winter, it became clear that very heavy mortality from disease was occurring under the ice in some of the places that had had the most muskrats at freeze-up.

As of mid-May, the muskrat-occupied parts had a total of about 80 maintained territories representing about 200 muskrats. Some movement away from the marsh was known to have occurred in late February and early March, but most of the fall-to-spring decline of approximately 1,000 muskrats must be assigned to mortality. No accurate means of dissociating this mortality exists. The best I can do is to estimate that about 800 died of disease during the winter and that the loss of the other 200 may be charged to departure from the area and to freezing, fighting among themselves, and mink and fox predation upon ill-situated animals that got into dangerous habits of foraging on top of ice and snow.

Four of 81 mink scats examined in May contained muskrat remains, and all 4 of the muskrat-containing scats came from a place where dying from disease was suspected of continuing.

The case history of the muskrat population became truly astonishing during the summer of 1956. It is true that the marsh went dry, but drought did not account for the wholesale abandonment of territories taking place in early summer. As early as mid-June, I was seeing evidence of abandonment of once-maintained territories while water remained sufficiently deep to permit me to reach some of them by canoe. Within the next two weeks, and before the last of the surface water disappeared from the majority of territories, abandonment progressed to the point where I could, with certainty, find only 2 of the original 80 territories still being maintained. I could not trace the movements of the vanishing muskrats, nor could I find signs of many living at large in thick food-rich vegetation of the dry marsh surrounding the abandoned territories.

The tract of marsh that still had water covering the bottom shrank from 70 acres as of mid-May to about 4 acres by early September. By then it was clear that mostly adult muskrats were congregating in food-rich retreats within a 300-yard radius of the last surface water. By mid-September, all surface water was gone, at which time the remaining muskrat population was estimated at about 45, including about 20 on a couple of acres having the most conspicuous density. The total muskrat-occupied area was then about 6 acres. By late September and well into the fall thereafter, this population was maintaining itself without evidence of further loss.

I cannot account for the almost total disappearance of the Wall Lake muskrats in November or early December, 1956. The only muskrat I could find there in mid-December was collected for a specimen at the place where what was thought to be this same animal had been living alone since early fall — at the last territory clearly being maintained on the marsh. The specimen was an adult female that had conceived four litters in 1956, for which birth months estimated from placental scars were April, May, June, and August. The latter line-up

of birth months was in excellent agreement with field data on sizes of young found in the original territory.

After a drought-exposed and muskratless spring, Wall Lake had some surface water restored — over perhaps 50 acres of bottom — by the May and June rains of 1957. A lone muskrat came into the marsh to establish itself about the second week of July, in habitat good enough to have accommodated hundreds. No further sign of this individual was traced past midsummer. Later signs indicated that a few more animals may have come in during late fall. As of late December, there was on the marsh one large lodge harboring a single muskrat. In another tract about a half mile distant were two close-together structures of feed-house type, freshly opened by a mink and having no current sign of living muskrats.

At the same time, the wetter parts of Wall Lake were frequented by five minks that could be individually recognized on the basis of track differences.