

Chapter 9

The Goose Lake Area, Central Iowa

GOOSE LAKE is a privately owned marsh of about 100 acres. It is situated less than a mile east of Jewell, Hamilton County, Iowa, and three miles north of the Little Wall Lake area of Chapter 8 (Figure 8.1). I received cooperation there from many people, including Dr. H. H. Knight of Ames (manager of a club that leases hunting rights over most of the marsh), Dr. C. E. Anderson and Mrs. Anderson of Madrid (principal owners), Dr. Cecil Anderson and his daughter, Donna, Clark Voss, and Roy A. Bonner of Jewell (owners of the smaller tracts usually occupied by muskrats), former Conservation Officer Kay Setchell, and the trappers, Verl Black, R. E. Kautzky, Walter Sampson, John R. Reese, and Harry Hudspeth.

BACKGROUND

Between 1932 and 1940, the years when I made only a few incidental observations on the area, water levels were known to have varied considerably. The bottom of the south half was exposed several times because of drought. The whole marsh went dry in 1934, but water returned in 1935. Hendrickson (1936) referred to three feet of water and 30 acres of bulrushes and cattails over 80 acres of marsh as of midsummer, 1935; Scott and Sooter (1937), to the fact that during the period of their observations, August 21 to November 8, 1936, not more than 20 acres were in open water, the rest being grown to bulrushes and cattails. Dr. Knight informed me that, from 1937 to 1940, the water came back slowly but rather steadily, despite the continued drying up of Little Wall Lake, three miles away; the emergent vegetation was not noted to have changed greatly in these years.

No data exist that may be considered wholly reliable with respect to muskrat fluctuations from 1932 to 1940 other than the general

evidence that the species was sometimes scarce and never excessively abundant. It is unlikely that the 1934 drought left many alive, and little recovery would be expected before the summer and fall of 1935. By the fall of 1936, the amount of marsh habitable for muskrats was still very restricted.

In the fall of 1941, when I first thoroughly worked the area, a dense stand of vegetation dominated by cattails covered the south half, except in two small tracts of deeper water. The north half consisted of a shallow lake having scanty emergent vegetation but extensive beds of yellow water lily, coontail, and pondweeds. Including muskrats living in dry habitats, the fall population — located chiefly in the cattails of the south half — was estimated at about 700 through comparing their field signs with that of known populations observed elsewhere. About 60 muskrats were said to have been legally trapped. There was an illegal catch of unknown magnitude, for set traps were seen before the trapping season opened. Mortality from mink predation was noticeable about the dry lodges as winter progressed. Probably the majority of the wintering muskrats survived, and a density of around 400 or 500 adults, probably nearer the latter, for spring and summer, 1942, should not be far wrong.

A HEAVY POPULATION IN A STRONG HABITAT, FALL THROUGH SPRING, 1942-43

A regular program of investigation was begun in the fall of 1942, as soon as it became apparent that the muskrat population of the cattails was remarkably high. The water lay several inches to three or four feet in depth over all of the marsh bottom that was grown up to cattails, which meant that practically the entire stand of emergent vegetation of the south half was splendid muskrat habitat. The north half was more lakelike than before; its shores also harbored many muskrats, some in lodges though most in burrows.

Numerical determinations of the muskrats wintering, 1942-43, could not be made directly, but the indirect evidence is indicative. Mr. Voss saw what appeared to him an equal abundance of muskrats at Goose Lake in the fall of 1928 (remembered as the last season of legal spearing in Iowa), when 1700 were said to have been pelted. Some animals could be expected to have escaped even severe spearing and trapping, so a total fall population of between 1,800 and 2,000 (about 1,900?) for 1928 would seem quite within reason.

A figure similar to the above applied to 1942 would give a fall population close to 35 per acre for the heavily populated cattail growths of the south half and nearly 20 per acre for the marsh as a whole. The 1942-43 trappers' catch of fewer than 600 (catch actually reported: 538) did not drastically reduce the population. Winter mortality from miscellaneous causes (including trap injuries, disease, intraspecific strife, and predation) almost certainly did not exceed 100. Perhaps 1,100 to 1,200 muskrats survived the winter. The 1942-

43 trapping catch was said to have included an unusual proportion of large and presumably old muskrats.

In late March, 1943, many muskrats left wintering quarters to travel along the shore and to sit out on the ice. Minks took advantage of some of these. Ten of 29 contemporaneously deposited mink scats contained muskrat remains, whereas no muskrat remains were found in 47 mink scats of late fall to early March — although the minks had done much fall and winter digging into muskrat habitations. Very likely, the early winter trapping served to remove a large proportion of the individual muskrats that were or would have been vulnerable to mink predation: the ill-situated and those having tendencies to come out on the ice during thaws or otherwise to engage in hazardous activities. Indeed, the trappers followed a practice of setting traps in the vicinity of superficial signs that would work to eliminate exactly those animals, the same ones that would ordinarily make up a large part of the winter mink victims (see Errington, 1943; 1954b). A single winter horned owl pellet consisted of remains of an adult muskrat.

As the spring dispersal and establishment of breeding territories progressed into April, 1943, the tensions once latent in the top-heavy population of late winter were manifested. Fighting occurred especially near shore, where residents and transients were most apt to come in contact. Dead muskrats — principally victims of intraspecific strife and of at least three shore-ranging dogs — were to be seen literally everywhere about the marsh. Reese said that over 25 were killed in one week by auto traffic on the main street of Jewell. Goose Lake, about a half-mile distant at the nearest point, was not the only possible source of these travelers but it was the likeliest. An equal number of dead was reported to be scattered over the Voss farm, which lies between the marsh and the town. In one day, alone, I examined 11 freshly and recently dead along less than a half mile of shoreline; between April 20 and June 22, a total of 31 dead adults along the same shore. The numbers dying on other farms in the vicinity of the marsh must have exceeded 100 if the evidence from the Voss farm is representative. The total participating in the overland movements from Goose Lake in the spring of 1943 must have been several hundred.

A HEAVY POPULATION IN A DECLINING HABITAT, 1943

The overland movements from and about Goose Lake in the spring of 1943 are not thought to have been excessive in relation to the densities involved and the condition of the south half of the marsh. For all of the wintering pressure of the muskrats, an abundance of food in the form of cattail rootstocks remained available through the main period of dispersal.

But, by summer, it became apparent that nearly all of the cattails were dead or dying, in consequence of a further rise in an already

high water level following the raising of the sluiceway of a dam. A few scattered cattail plants grew where the deep-water stands had been, including some that were simply sprouting rootstocks floating on the surface. A cattail strip remained alive along a railroad grade, and a series of small living patches remained near a shore having tile flows and seepage water. With the exception of the railroad strip, these remnants ultimately became well eaten away by the muskrats. Failure of such a supremely important food supply was followed by pronounced readjustments. Essentially entire muskrat populations of some marshy tracts visited shore and raided adjacent corn fields.

The breeding population was fairly settled by the last week of April. At least 10 transients (some showing strife wounds noticeable at a distance) were still living vulnerably about the marsh borders. A month later, it could be seen that, as the height of the breeding season left fewer places among the established territories where surplus animals were tolerated, more animals were being forced ashore. Some of the newcomers to the shore zone could be recognized individually at times when observations were made as often as four days a week, and four of the most interesting were shot for examination.

Of 19 more or less strife-torn transients collected about Goose Lake or found dead in good enough condition to examine from late March to the middle of June, 1943, four were females. Of these females, a badly battered one collected on May 19 was pregnant though a transient; another, with only inconspicuous wound scars by June 4, was neither pregnant nor lactating but had given birth to a litter early in the spring.

From the field evidence, few young were judged to have been born after the middle of June. Four of 168 young of the year (mainly trapped by Reese) examined from Goose Lake or adjacent waters in November and December were "kits," or August-born young. Two of the twenty-seven Goose Lake adult females of which the uteri were examined macroscopically after the 1943 breeding season had conceived four litters each during the spring and summer. The placental scars of one of these suggested a very late litter. Three others of the twenty-seven females had placental scars thought to have represented litters born at dates materially later than the field data would imply, and at least two of thirteen other adult females from adjacent waters had late-looking placental scars. This would make six of forty local females that could be designated as late breeders. The six latest litters comprised nearly 9 per cent of sixty-eight evidently conceived by the forty females, or about three times the percentage of the late-born in the aforementioned 168 young of the year.

The total of only 68 detected sets of placental scars in the uteri of forty adult females known to have passed through the 1943 breeding season may be construed as reflecting population tensions. Five of the adult females had not conceived; 14 had conceived single litters; 12, two litters each; 6, three litters; and 3, four litters. Sixty-two of the

sets of placental scars were counted with fair satisfaction, but their mean of nearly 8 scars per set hardly suggests an appreciable decrease in size because of the crowding. One uterus indicated an early litter followed after an interval of two or three months by another litter. A recently pregnant female found dead on June 23 showed a similar irregularity in breeding, the placental scars of her previous litter having been assigned with confidence to early spring. Judging from the relative freshness of their placental scars, at least 8 of the 14 one-litter females gave birth to their only young after the middle of May.

Lodges, improvised nests, and bank burrows representing known or very probable breeding territories were repeatedly counted and the results kept separate for given units of marsh. The total arrived at gave the equivalent of 293 muskrat pairs, as of the middle of June. By this time, the population was as nearly settled as it ever became during the breeding season, with the fewest transients and lone animals about the outskirts of established summer territories. If allowance be made for possible undetected adult mortality in such established territories and for overlooked bank territories in tracts having too much water and dead vegetation to permit easy observation, the equivalent of about 300 pairs should not be far from the true total for the marsh. Of 80 November and December carcasses of adults examined from Goose Lake and vicinity in 1943, 42 were of males. Applying the 42:38 ratio, we would get 332 adult males for 300 adult females, or a total June population of about 630 adults.

Despite a great amount of friction between adults about the periphery of the marsh, some remarkable concentrations were tolerated in certain marshy tracts. An early June population of seven and one-half pairs per acre on six acres was arrived at on the basis of adults in sight at practically the same time. Including the above, the adults on the most heavily populated twenty acres of marsh averaged close to the equivalent of six pairs per acre, and these were primarily lodge dwellers, distinct from the equivalent of nineteen pairs that lived primarily in the burrows of two small islands in the midst of the twenty acres. The food situation here was described as very critical in my field notes as early as June 11, except for a surface covering of duckweed and a variable growth of submerged vegetation. Still, the adults were not seen to be unusually antagonistic toward each other, and four were once watched peaceably using together one of the lodges near shore.

On the other hand, the reproductive fortunes of the crowded area were poor. Young were to be seen about lodges, some in company with adults but many quite evidently living harrassed and furtively where they were able to live. Of five young victims killed by adults, all were between five and eight weeks of age. Doubtless other killings of young, including unweaned, took place out of sight, for, to avoid disturbing the muskrats of a privately owned marsh, I opened only two lodges at Goose Lake during the 1943 investigations. The vulner-

able young also were subject to substantial predation. During sixteen days in late June and early July, eight recognized victims of predators (two of dogs, six of minks) of between four and six weeks of age were found on land surrounding the six-acre tract having the heaviest population. Sixteen of 97 mink scats examined in late June from a den on one of the islands consisted of remains of young muskrats. The mink pressure on the young continued to some extent during July and August, nine of 161 scats containing remains of the young. In contrast, no muskrat remains were found in 31 scats of a big mink deposited from late April to early June, before the season's young muskrats began circulating hazardingly.

In early August, a careful effort was made, with the advantage of exceptionally favorable visibility, to obtain age ratios from two characteristic types of muskrat-crowded marshy habitat. In one type, where psychological or physical barriers discouraged dispersal of young, 16 adults and 18 young (7 to perhaps 12 weeks old) were counted. In the other type, from which good avenues of travel permitted easy movement—especially of young—to a shore zone near an increasingly raided corn field, the sample count was 32 adults to 26 young.

About 70 of the deep-marsh territories recorded as of the middle of June (including those of the islands) were those of a rather self-contained population. Application here of the appropriate sex and age ratios would give a total of about 147 adults and 165 young, or an early August population of about 312. Twenty-six other territories were believed to have been sufficiently unaffected by summer movements that they, too, might be regarded as similarly self-contained. The only age ratio (3 adults to 13 young of the year) available for the latter group is from animals trapped for fur in November. Considering the fact that the majority of these 26 territories showed scarcely any evidence of mortality in late summer and fall, the postbreeding figure of about 293 indicated by the 3:13 age ratio, combined with the general sex ratio of adults, should be as close to the truth as the data permit. A postbreeding total of 605 would seem quite within reason for the more or less self-contained territories.

Roughly, the 204 other territories (using the 300-territory basis instead of the 293 counted) may be apportioned among the following three groups: (A) about 110 affected by movements toward a corn field southeast of the marsh, (B) about 40, by movements toward another corn field and a field of soybeans on the west side, and (C) about 54, by movements toward the outlet leading to a ditch to the west and thus away from Goose Lake.

By early August, only about 7 of 33 former lodge territories in group C were being maintained—by about 24 muskrats in all. The shore territories seemed to have experienced little change as a result of the shoreward drift of deep-marsh animals, except as young produced in the shore territories may have migrated off to the southwest

along with the newcomers from the deep marsh. Several people working in the neighborhood of the outlet flow observed small companies of animals leaving the marsh. Fifty-eight carcasses of muskrats trapped in November from the ditch to the west of Goose Lake (where there is reason to believe that the migrants did much settling) consisted of 13 adults and 45 young of the year, which, for lack of anything better, may be considered a sample of the animals leaving Goose Lake. The ratio in November carcasses from the vicinity of the outlet and the south shore was 14 adults to 17 young. No significant changes in age ratios were known to have occurred here between August and the trapping, so, from the ratios at hand, it might be calculated that a total of about 245 left the marsh and about 97 remained in the south shore zone, as of early August. The 97 added to the 24 remaining in deep marsh would give a figure of about 120 still resident in group C.

In the A group, 88 of the original territories were in lodges, and the adults of about 40 territories, together with some young, appeared to be maintaining residence in late summer. A deep-marsh total of about 150 muskrats may be calculated here from sex and age ratios. The equivalent of about 70 adult females and associated males either lived in the bank burrows from spring to fall or there established themselves after the breeding season, upon coming to shore to forage. Application of a November ratio of 19 adults to 28 young would give a figure of about 365 for the shore-dwelling population, or a total population of about 515 for A, as of early August. One clear and calm September evening, between 45 and 50 muskrats were simultaneously in sight along a 100-yard stretch of shore that was visible in the dusk.

Only 15 of 40 territories assigned to the B group were centered about lodges, and, by August, practically all the occupants of these were coming to shore to feed on corn and soybeans. A nine-acre field of soybeans had nearly 100 well-beaten trails leading into it. The cultivated fields undoubtedly drew many of the young muskrats of other groups in the course of the postbreeding adjustments, which probably explains the high ratio of 30 young to 8 adults in November carcasses trapped mainly along the shore at this place. The early August population of B figures out at about 400.

Allowing for a calculated 245 (55 adults and 190 young) leaving the marsh via the outlet corner, the total of about 1,640 (about 575 adults plus 1,065 young) obtainable through adding up the figures from the different territorial groupings would be too high. Even if the age ratios arrived at were wholly representative for the groupings and their subdivisions, a recorded mortality of 21 adults for June and July was borne mainly by individuals that either were, or could have been, associated with territories. The data are not such as to permit accurate assignment of these losses to specific groupings. If the 21 be accepted as near the total midsummer loss of resident adults, it could

be subtracted from 575 to give a new base of about 555 adults. The new base, used with the over-all age ratio of 35.1 per cent of adults originally calculated for the marsh, would allow a grand total of about 1,580, which might still be suspected of being somewhat high. Scaling the 1,580 down a little more, we could get a revised grand total of about 1,550 in rounder numbers as the early August muskrat population of Goose Lake.

Later in August, more population adjustments occurred, but these were not of sorts to influence perceptibly the numerical status of the muskrats in the territorial groupings. Many of the muskrats took increasing advantage of the growths of yellow water lily in the north part, the animals of one stretch of shore abandoning the bean field to do so. Some were watched converging toward the north center from all sides, swimming distances up to 300 yards. The raiding of the corn field southeast of the marsh diminished (although the corn field to the west continued to show heavy use all fall), and the muskrats of the southeast part centered their feeding on natural shore growths and upon the rather sparse stands of hardstem bulrushes appearing during the summer. These bulrushes suffered very severe exploitation, as did the chief remnant stand of cattails. Hundreds of shallow muskrat burrows could be distinguished along the southeast shore.

Not much general change of feeding occurred in September and October, except that, as fall came on, the southeast corn field and the soybeans were again more heavily raided. Just before the trapping season opened on November 10, most of the shore trails remaining in use were those leading into the corn fields.

THE COLLAPSE OF A HIGH DENSITY POPULATION, CHIEFLY THROUGH AN EPIZOOTIC, 1943

What did bring a change in the late summer and fall status of the muskrats was the onset of a deadly epizootic of the hemorrhagic disease, apparently the first ever to be studied in detail.

Fortunately, for purposes of analysis in a situation already complex because of major variables, the disease losses for the first few months of the epizootic were almost entirely confined to the vicinity of the islands, or to the muskrats of some of the more self-contained territorial groupings. Before the bank dwellers of the islands were known to have become infected, about three animals were judged to have died per day during October and early November, which would suggest a loss rate from disease of about 100 per month; earlier in the fall, the average of muskrats dying per day evidently had been lower. The total disease mortality, from its first observed occurrence in August to freeze-up in November, was estimated at about 200.

Other types of mortality elsewhere on the marsh for the above period were fairly low in terms of muskrats present. Hostile displays — especially between big animals — were frequently seen in September

and October. Two of five dead adults found on shore during October showed typical wounds of intraspecific strife, the others being victims of a mink, of a dog, and of probable old age. On November 12, dozens of muskrats could be seen traveling across the new ice, and these behaved like transients or highly insecure individuals; three of four freshly dead ones examined had severe strife wounds. Increasing frictions of late fall were reflected by the contents of mink scats. Of 127 scats from the first half of October, only 6 contained muskrat remains, compared with 15 in 136 scats for the second half. Then, after trapping on shore had rather well eliminated the land-active muskrats, only one of 41 mink scats of mid-November contained muskrat remains.

In the course of about three weeks, late November to the middle of December, the disease spread to all muskrat-occupied parts of the marsh and brought to pass a most spectacular collapse of the population. The mid-November spurt of surface activity on top of the ice may be suspected of having accelerated this spread. As many as nine dead were found in a day, and these surely represented but a trifling fraction of the numbers dying out of sight, under cover of the ice, and inside lodges and burrows. For years afterward, bones of adult-sized muskrats continued to be exposed by dogs and woodchucks breaking into or digging out datable burrows that could hardly have been used by muskrats at any times except in the latter half of 1943, contemporaneously with the big die-off. For example, on February 15, 1946, and January 6, 1948, totals of 15 skulls of practically certain epizootic victims were counted amid the debris excavated by woodchucks renovating for their own use the upper parts of the 1943 muskrat burrows on an island having a high water (or 1943) circumference of 144 paces or perhaps 130 yards — a number of victims three times as great as the number (five) found on the island's surface and periphery during the epizootic.

Minks, after their nearly muskratless diet of November, soon discovered the new abundance of food in the form of dead or sick muskrats in the lodges and burrows. Altogether, 53 of 113 mink scats from the first half of December contained muskrat remains.

Conceivably 50 muskrats were alive on the marsh as of December 13 when the clearness of the ice permitted easy "reading of sign"; these were nearly all in places well removed from the islands. By spring, the mortality seemed to have been complete, as the first unmistakable sign of a living muskrat was found March 18, by which time an ingress of muskrats, via the outlet, was beginning. Muskrat remains were found in 22 of 43 mink scats for the second half of December; then in 43 of 85 up to the middle of March, but in only two of 36 for the second half of March and early April. While the sudden lowering of the water level by about 15 inches after breaking of a dam across the outlet in mid-December might have meant greater vulnerability of muskrats still present, the evidence suggested that

the occasional visiting minks were largely scavenging upon the muskrats that had died in the fore part of the winter. Remains or intact bodies of 13 muskrats were discovered during the main winter months, but nearly all of these had the aspects of having died in November and December, when the epizootic had been so conspicuously lethal. There seemed to be a further connection between incidence of muskrat in mink diet and periods of mild weather, when the softening of lodges and burrows allowed the minks easier access to dead muskrats within.

The population was practically wiped out by the end of 1943, and wholly so by the end of the winter. Of the 1943 postbreeding population of 1,550 muskrats computed on bases given in preceding paragraphs, fewer than 200 were accounted for as taken by trappers. After making as generous allowances as seem within reason for possible errors in computations, for unreported trap catches, and for all agencies of decline other than the epizootic, the latter would seem to have been the agency of mortality of between 1,000 and 1,300 of the muskrats.

1944 AND 1945, THE FIRST TWO YEARS AFTER THE GREAT COLLAPSE

The new population at Goose Lake quite literally began with the immigrants of late March, 1944. The principal avenue of ingress was the ditch leading to the outlet. Natural restocking progressed slowly, probably in consequence both of limited numbers of animals coming in (the surrounding habitats, except Little Wall Lake, had been severely trapped) and of the dying of newcomers soon after arrival. Nine fresh disease victims were examined in April and May, and eight of these were found on the shore within a few hundred yards of the outlet. On May 20, four freshly dead were seen, compared with but a single live one. The equivalent of two pairs became established (plus a shifting population of two to four judged to have been extra males), and young were produced in both territories by early July. The two breeding territories were in the southeast part of the marsh, centered in burrows about 80 yards apart. Four more animals (including three adults) were known to have died before the end of July, but no victims were found in August and September, and the disease was thought to have run its course. Largely through ingress, a population of perhaps sixty to eighty (probably nearer the larger number) was built up by October. The age ratio of eighteen trapped specimens was five adults to thirteen young of the year. In October, the disease with relative suddenness all but depopulated approximately the north half of the marsh — without, however, killing muskrats in the south half.

Judging from the chronology of the dead found, the new epizootic broke out almost simultaneously about the middle of October west of the islands and a couple of hundred yards to the north; and, in the space of three weeks, twelve were known to have died here in

places where they could be seen. Another dead was found on the east central shore, but the disease did not seem to get a start at this place. There was a fine set of burrows in a rocky road grade adjacent to a north stretch of the east central shore, and here eight victims were found, with dates of death estimated at between October 25 and November 4. The first known victim at the road grade died in the channel of the main burrow just where the others would repeatedly swim past it. The several muskrats that were alive in the north half on November 15 were regarded as newcomers attracted by vacant burrows. Two that came to the rocky grade were found freshly dead in a nest on November 21. A third muskrat, believed to have taken up quarters in the rocky grade about November 21, was obtained alive and uninjured on November 25 and was dead of the disease in its laboratory cage by November 27.

Clear ice in late November permitted a good checkup on the Goose Lake muskrats, and a current sign was found at only one place in the whole north half. By early December, the tracks of two or three evidently transient animals were to be seen on the snow-covered marsh, and, past the middle of the month, freshly dead remains (of one of the transients?) were found in the northwest corner. Two mink-eaten carcasses, fresh-appearing as of early March, 1945, were found about 200 yards from the one place where a sign had been noted in the north half in late November. It is not definitely known that the latter muskrats were diseased, but they well could have died from this cause at any time from December to March. Their freshness in early March may have meant simply that the mink then gained access to them after weeks or months of frozen preservation. All of six mink scats from the vicinity of these two dead consisted of muskrat remains.

Of 288 other winter mink scats, three contained muskrat remains — all of the three muskrat-containing scats picked up fresh on March 8 from one mink-opened lodge near the south shore. At least two minks were resident for most of the winter, but the above three scats constituted all of the detected evidence of minks feeding upon muskrats in the south half.

In addition to the infected live specimen from the rocky grade of the north half, 18 muskrats were reported trapped from the south half, and a survival of about 15 was calculated from animals seen and signs, as of March 21. This and the recorded mortality would account for about 60 of the animals present in the fall. Unquestionably, others died concealed in some of the north-half burrows, particularly in the rocky grade.

In late April and early May, 1945, two animals were found dead, neither of which was positively identified as a disease victim, but they probably were victims. An adult population the equivalent of six pairs was ascertained, as of June 16, with territories distributed at rather uniform intervals along the shore. No muskrat remains were found in 22 mink scats examined from April to July.

The status of the Goose Lake muskrats was favorable from late spring to early fall, although the water level became so low that the marsh bottom was barely covered in the thick bulrush fringes then making up the most attractive muskrat habitat. There must have been close to 100 muskrats (including late summer immigrants as well as resident adults and locally reared young) on the marsh by the first of October.

In early October, what had the aspects of a typical epizootic started in three parts in or near the center of Goose Lake. Practically all of the muskrats living adjacent to these three foci of infection, or in the central one-fifth of the marsh, were eliminated by October 19. By this time, twenty-two dead had been counted, eight about a single lodge. In late October, a freshly dead one was picked up in the southwest corner, but this did not prove to be the forerunner of a new die-off.

The epizootic subsided for several weeks between late October and late November. During mid-October, the lodges in the central area were dug apart with a spade and left with the debris in flattened heaps. This procedure was believed to have diluted the sources of infection for the muskrats remaining alive in or at the borders of the infected zone and for those newcomers that later established themselves in places where the previous occupants had died. After the advent of freezing weather, the experimental leveling of the lodges was discontinued. By early December, most of the newly restocked places of the disease-swept center and some adjoining them were again muskrat-vacant. Since no more dead were actually seen here, it cannot be demonstrated that the occupants died of disease. The chances are, however, that they died underground. By the last of November, the fresh body of a disease victim had worked up through the thin ice out from the south central shore, and the lodges near by showed an untenanted appearance, suggesting that an entire population group had died.

Favorable opportunities for "reading sign" under the ice permitted population estimates totaling about 60 muskrats alive, as of the middle of December, before the ice clouded enough to interfere with observations.

The 1945-46 winter survival was low — judged to have been only about 13 individuals, as of the middle of March. The known appearance of the disease in a previously unaffected part of the marsh at the time of the last good under-ice observations would be logical grounds for expecting it to have continued its spread. That the disease was the dominant agency of death is strongly indicated, but wintering conditions were sufficiently adverse to have brought about some mortality from causes other than the disease.

The water level was still low at freeze-up. As the frost line sank into the mud and peat of the muskrat-occupied, food-rich shallows, the animals built new feed houses on the ice over the deeper parts

and finally lived in burrows having little or no unfrozen water. With the exception of three distinctly ill-situated individuals that engaged in much surface activity, and either bore wounds of intraspecific strife or had extremities frozen through exposure, the muskrats nevertheless appeared to live securely through December. Of 43 mink scats for late November and December, two contained muskrat remains, and these almost certainly were from the body of one of the October disease victims.

Then, in early January, 1946, a three-day rain and thaw put about 5 inches of water over the ice and forced the muskrats living underneath to return to long-unused lodges that were out of repair. For a time they were highly vulnerable to mink predation. Seven muskrat bodies upon which the minks fed were dated to this emergency, including one (with a frozen tail) that had been traveling overland to a corn field before the rain. The crisis was of brief duration, lasting not longer than a day or two, after which the muskrats lived with noticeable security in their renovated quarters until late January. Only one of 32 mink scats for early January before and during the rain contained muskrat remains, but remains were found in 20 of 21 scats deposited immediately after the rain and coincident with the known feeding upon the 7 dead muskrats. After this, the incidence of representation of muskrat remains fell to 1 in 7 mink scats.

Following their apparently secure period in the middle of January, Goose Lake muskrats again attained prominence in mink diets. Forty of 50 scats for late January through the middle of February and 12 of 25 scats for late February and early March contained muskrat remains. Three dead muskrats of late winter were too fragmentary to reveal anything as to possible disease lesions, but 2 of these were found in the habitat adjoining that in which the population group evidently had died in late November. The third was found in the northwest corner, where residents were due to be wiped out by disease in April and May. The available data suggest a general spread of the disease under cover of the ice. On the other hand, muskrats did survive the winter in scattered places, among which was one of the disease foci of the October epizootic.

THE DRAMATIC VICISSITUDES OF 1946-50

The equivalent of 7 pairs became established as the 1946 breeding population of Goose Lake. All were in the south half, mostly in what had become the best-vegetated tract of about 20 acres in the southeast quarter. Here, in fairly extensive growths of hardstem bulrush, the territories were concentrated, yet still with their centers 100 yards or farther apart. The muskrats of the south half escaped the disease and lived securely through spring and early summer, although the animals attempting to live in the northwest corner continued dying. Four of 143 mink scats for the middle of March to early May contained muskrat remains.

In the northwest corner, three disease victims were found in April and early May, and no evidence of any other muskrats was seen there during the breeding season.

Between late May and August, an epizootic of surpassing deadliness apparently killed the entire muskrat population remaining on Goose Lake. A current sign was seen in but a single place during a checkup in the first week of August, and the maker of even that sign afterward disappeared. Later, an ingress of an estimated 80 to 100 muskrats restocked the more attractive parts of the marsh by late September. The newcomers displayed a tendency to take over and rehabilitate the previously used lodges and burrow systems, but nothing that could be called a real epizootic occurred during the fall months except in the vicinity of the islands.

The first probable disease victim found in the fall of 1946 died in late September or early October. In the last week of October and the first week of November, eight were known to have died: two in the southwest corner of the marsh and six either about the islands or on the nearest shore (within 150 yards) to the northwest. All of the 10 muskrat-containing mink scats in 32 examined for October were found together on the above shore northwest of the islands. Four dead were found that were assignable to the middle of November: one near the east central shore and three at one small lodge west of the islands.

At the latter lodge, the first disease victim was found freshly dead on November 11. The second was partly eaten by a mink about November 14. Later, mink-eaten remains of the third occupant of the lodge appeared. Six of 10 mink scats deposited near the above lodge contained muskrat remains, compared with only one of 53 other scats from the rest of the marsh in November.

Careful calculations gave a population figure of about 60 muskrats alive on Goose Lake as of late November, 1946.

Of three dying in December and in the first half of January, 1947, one was found near the islands, one (intact enough to be a clearly recognizable disease victim) was dragged by a mink from a lodge in the south center, and one was found in the southwest corner. Muskrat remains were found in six of 255 mink scats for this period, and five of the six scats with muskrat remains were deposited either on the islands or in the southwest corner — the two places where most of the muskrats had died of disease. Next, in the course of the winter, losses became severe more or less simultaneously in the southwest corner and in the whole south shore zone. During February, the remaining muskrats adjacent to and to the north of the southwest corner were wiped out, as were the hitherto secure muskrats of the southeast corner. The last places with living muskrats in the southeast part were at least close to the place where the mink had dragged the disease victim from a lodge in the south center, and the epizootic also could have been introduced through healthy muskrats visiting the

disease-swept lodges to the south. Ultimately, some fine burrows along the east central shore took on a dead appearance. Data on the sexual state of well preserved disease victims dug out of thawing lodges in early April confirmed the sequences of the winter epizootic, as these previously had been worked out through the regular field observations.

By March 20, evidences of living muskrats were detected in but two places, both isolated from the main occupied tracts. One of these isolated places had had a lodge with a solitary muskrat since fall. (This muskrat had been a recognizable individual, several times observed under favorable conditions.) The other place, in the northwest part, had a fall population judged at about eight; and, while there may have been winter mortality here, the March signs were sufficiently pronounced to leave an impression that several animals had succeeded in wintering. A survival of perhaps half a dozen, or about 10 per cent of the Goose Lake population beginning the winter, would seem fairly close to the truth.

For the period between the middle of January and late March, when the ice softened and began to break up, 213 of 249 scats from 4 distinguishable minks contained muskrat remains. From late March, through the first half of April, the incidence of muskrat-containing scats dropped to 3 in a total of 95.

On April 16, 1947, a tentative estimate of 5 breeding territories, or the equivalent of pairs, was made; by April 23, there was evidence of 10; by May 2, another had appeared; by May 14, so had another; and the same figure of 12 territories was verified on May 16. Two additional territories were later established, bringing the total up to 14, representing 30 or more adults. As muskrat habitat, the marsh had decidedly improved since 1943, the high-water year. The muskrats by now had their choice of good territorial sites in the bulrush and cattail stands of the south half and also in a tract in the northwest quarter.

Three dead adults were seen in the first half of May, and of these, the only one fresh enough for satisfactory examination was a disease victim. The latter lay beside the burrow in the northwest corner where the annihilative disease mortality had occurred in the spring of 1946. No muskrat remains were found in fifty-four scats deposited from the middle of April to the middle of May, 1947. Mortality of an adult (remains were found in a mink scat) and the loss of one territory about the first of June had an evident connection, but only this one scat of seventy-nine deposited in late May and June contained muskrat remains. The only other mortality of Goose Lake muskrats detected from the second half of May to late July was from cannibalism; on June 19, a lodge was opened for examination just in time to surprise a young of about five weeks as it was eating a freshly killed member of a litter of about three days. The cannibal was doubtless a member of a litter born to the same mother about

May 12. Members of both litters were still found in their natal lodge by July 24. On the latter date, two of the smaller size and five of the larger were simultaneously in sight.

Twenty-three litters were determined to have been born in the thirteen territories that remained functional, and at least five more litters were recognized, which (because of adjustments ultimately forced by drought) could not be assigned to any given territory. Of these twenty-eight litters, two were judged to have been born in the second half of April; six, first half of May; four, second half of May; two, first half of June; three, second half of June; three, first half of July; one, second half of July; six, first half of August; and one, second half of August. Some other young born in early July could have been members of a litter different from any listed above. A total of 29 litters for the thirteen territories would give a mean of 2.23 litters per adult female.

If 29 litters be accepted as the number born on Goose Lake during the breeding season, multiplication by the known mean size of 7.7 recorded for central Iowa litters of the 1947 season would give 223 young produced on the marsh. The peak population was reached about the middle of July, when a total of perhaps 180 (29 adults plus about 150 young) may be calculated. From this time on, the birth of late litters seemed more than offset by increasing mortality.

Many weeks of hot, dry weather followed heavy rains in June, and the Goose Lake muskrats were affected by drought as early as late July. By mid-August, considerable adjustment had taken place. The shallows of the northwest corner dried up first, and the muskrats abandoned two territories there. By late September, less than three inches of water remained over the mud of the north half, or the deeper part of the marsh, generally. One family group of muskrats of the southeast corner had moved nearly a quarter of a mile northwest to a set of lodges that had previously been abandoned by another group of muskrats moving into the north half. All muskrats of the southeast part (except a few stragglers) had either left the marsh (or died) or had moved into the north half. Meanwhile, the animals of the southwest corner had suffered heavy losses from emigration and mortality, with survivors largely establishing themselves in food-rich though dry stands of cattails and bulrushes. By mid-October, all marsh bottom of the south half was exposed, and only an estimated six or eight muskrats remained. At about this time, the last former territory at the northern extreme of Goose Lake was likewise abandoned, and the wet marsh population was about sixty (fifty-two counted in mainly open nests and eight more estimated for the burrows).

Rains in the last week of October restored the water level to about a foot over much of the north half, which had had little except wet mud on its bottom. Contemporaneously with the rains, the remnant of a family group in the southwest part moved about 150 yards to

the south edge of the water of the north half. In early November, water covered the deeper parts of the south half to a depth of a few inches to a foot, and the maximum depths of the north half were up to about 15 inches.

The field notes refer to a known mortality of 47 Goose Lake muskrats (5 of which had been tagged when young), from the onset of the drought through November. These included 20 victims of the hemorrhagic disease. Animals were found dying from the disease about September 7 in the southeast part of the wet north half, into which two family groups had moved from the drying south half. (Eight died in a triangle covering about 150 square feet.) Then, the contagion rapidly spread northward into the marsh where the muskrats were concentrated, but inexplicably subsided just when it seemed ready to sweep through the population. No certain or probable disease victims were found here after September 19. The disease also started up in one of the drought-exposed places near the south shore of Goose Lake, but this did not result in severe losses. Others of the dead found both before and after the time span of the recognized epizootic may have died from this cause, but rapidity of decay prevented accurate diagnosis in at least four possible cases.

Five of the drought-exposed dead were known to have been fed upon (and probably killed) by minks; and 6 of 71 mink scats deposited from late July through September contained muskrat remains. Six of 22 similarly dated horned owl pellets contained remains of 6 young muskrats — 5 of about four to six weeks of age and one subadult. Three muskrats were found killed by farm dogs, one probably died from a pathological condition of a jaw similar to the actinomycosis reported by Dozier (1943), one was struck by motor traffic as it emigrated southward from the drying marsh, and a tagged one died of the hemorrhagic disease on the southeast shore of Little Wall Lake, 3 miles to the south.

No muskrat remains were found in 81 mink scats for October and November, which may be said to reflect the passing of the period of greatest drought vulnerability. As of December 1, there were about 60 muskrats left in the wet marsh of the north half, plus possibly four in the shallows of the south half. The latter got along all right until the middle of December, when the shallows froze to the bottom, and the animals started coming out on top of the ice and to forage in the shore growths. There also was occasional land activity on the part of apparently two muskrats living in dry holes west of the wetter north half.

In contrast with the as yet comfortably situated regular residents of the wetter north half, the approximately six land-active muskrats were eliminated by predators in rather short order. Deaths of five were accounted for from about mid-December, 1947, to early January, 1948, including four mink victims and one fox victim. Of seventeen mink scats assigned to the first three weeks of December, none

contained muskrat remains; then, representations of this prey were found in twenty-three of ninety-four mink scats for late December through the first week of February. The feeding on muskrats by minks during this period was nearly all traced to muskrats that were either transients or individuals frozen out of the south shallows.

Until late January, the population of the wetter north half was visibly secure. It was not known to have suffered any losses whatever since fall, despite intrusions into lodges by probably three minks. The minks fed chiefly on fishes congregated in the muskrat channels beneath the lodges, on remains of dead ducks and coots, and to some extent on mice and rabbits of the surrounding land.

But, early in February, the wet marsh of the north half was freezing to the bottom. Muskrats were traveling in increasing numbers on top of the ice from one lodge to another in search of better quarters. Mortality began with a single mink victim about the first of the month. On February 6, an animal, blind and with flesh of tail frozen and chewed away, died from cold on the ice. Four muskrats (including one marked by toe-clipping) were known to have abandoned the marsh as the crisis became worse, and others doubtless did also.

The night of February 8 (the second of two cold nights during which temperatures fell to about 15 degrees below zero Fahrenheit) virtually completed the transition from tolerable to intolerable living conditions for the remaining muskrats of Goose Lake, although a few of the better lodges retained some degree of habitability for another week or longer. In less than three weeks, Goose Lake was devoid of living muskrats, very spectacularly as a result of their increasing vulnerability and through the agency of minks.

Not all of the February mink killings could be figured out from signs, but a relatively complete record of the exploitation by the minks was obtained from visits to the marsh on 15 of 18 days during the period of greatest mortality and from occasional visits thereafter. It is believed that the fates of very nearly all of the muskrats dying at Goose Lake after February 8 were accounted for — 20 in all.

Prior to the latter date, most of the muskrat activity on top of the ice had been in the southwest and southeast corners of the wetter north half where restless animals had explored unoccupied lodges and the burrows and vegetation of the shore. On the night of February 8, minks were known to have killed a muskrat in a land hole southwest of the north half and another one on or near the shore of the southeast corner. The final places of deposition of the carcasses could not be ascertained because of poor tracking conditions. Little could be learned of the circumstances of death of a third victim except that it occurred. On February 9, a mink killed three muskrats in the southeast corner of the wetter north half — apparently all there were — and left them piled uneaten inside of a lodge.

In late afternoon of February 11, five muskrats left the main lodge in the southwest corner for a smaller unoccupied lodge 45

yards away, where two of them remained. The other three continued to another unoccupied lodge 80 yards farther on. In the evening or night, a mink made three round-trip visits from shore to the latter lodge, dragging away two muskrats (to cache them in different holes in the upper chambers of abandoned muskrat burrows 55 to 75 yards away) and returning unsuccessful from the third visit. The third muskrat here was alive the next day, but the mink returned in the evening (February 12) to kill it and drag it 265 yards across the snow to another land hole. The mink later visited the first-mentioned lodge having the two muskrats, killed one and dragged it 190 yards to the same land hole in which it had deposited its first kill of the night. It returned for the last muskrat of the original five that had journeyed forth from the main lodge in the southwest corner, injured it but did not kill it. This muskrat returned to the main lodge, staggering in the snow and leaving blood as it rested; an animal corresponding to it died in the lodge, to be eaten by its fellow muskrats.

No sign of mink was seen for the night of February 13 in the southwest corner of the north half of Goose Lake. More muskrats left the main lodge to station themselves in the smaller lodge 45 yards away. During the night of February 14, the mink came back and killed three muskrats in and about the smaller lodge. It left two carcasses cached where killed and dragged the third to another small lodge near by.

During the night of February 15, one of the two dead muskrats cached as above was carried away by a mink, and a mink visited a place in the east central part of the north half where hitherto secure muskrats were coming out on the ice. Here, the mink killed two and left them uneaten (except for a few bites taken out of the neck of one) in a feed house. One of the victims had liver lesions of the hemorrhagic disease. The next night, the mink returned to kill and eat a third muskrat.

By February 16, only one place on the marsh was known to have living muskrats, and one muskrat was killed and largely eaten by a mink during the night. A second was killed and left uneaten on the night of February 20. A third — evidently the very last one — was killed on February 27. On March 1 and 5, checkups were made under favorable field conditions without finding any sign of muskrats remaining alive, in lodges, land holes, or anywhere else about Goose Lake.

Of 40 mink scats deposited from February 6 to February 26, 38 consisted of muskrat remains. After annihilation of the local muskrats, the minks (still about 3 individuals distinguishable on the basis of tracks) fed upon muskrat carcasses cached in various land holes and lodges for perhaps another week and even continued visiting the fragments of some carcasses past the middle of March. Only 2 of 9 mink scats found for this period contained muskrat remains, never-

theless, and it could be seen that this source of food soon became exhausted. Apart from 3 carcasses cached in the bottom of a lodge that filled with water during a thaw and froze over, nearly all of the muskrats killed by the minks in February were sooner or later eaten by minks, though often some days or weeks after the actual killing.

Altogether, mortality of 74 muskrats was detected at Goose Lake from the beginning to the end (late March) of the 1947-48 drought emergency.

Compared with other winter drought crises observed, the one at Goose Lake in February, 1948, was singularly severe in view of the depth of the water over the muskrat-occupied parts at freeze-up. In the winter of 1945-46, muskrats had, in fact, lived with considerable security in the rush-grown south half of the marsh after freezing of the shallow surface water and much of the mud underneath; but they still had had access to rootstocks and other rich sources of foods imbedded deep in unfrozen mud. In 1947-48, except for the vegetation making up the lodges, the entire food supply of the muskrats of the north half became encased in ice as cold weather continued — the coontail and pondweed growths, the rootstocks of yellow water lily, and the fishes that found their last refuge in the muskrat channels — and the muskrats simply could not gnaw it out in satisfactory quantities. For a time, certain individuals seemed to specialize on frozen fishes, and there was feeding by muskrats on remains of some of the muskrats killed by minks; yet, as the water of different parts of the north half froze to the bottom, the muskrats broke out of their lodges virtually in groups, to search diligently about the vicinity for more livable quarters. As a rule, the muskrats were in fair to good flesh and uninjured by cold at the times of their death, but their alimentary tracts tended to be rather empty or filled with harsh material. It was apparent that they suddenly had become hungry and desperate.

Another distinction having a bearing on this winter crisis should be pointed out. Instead of the large, insulating lodges of cattail and bulrush marshes, the lodges of the north half of Goose Lake were small shells of ice-lined coontail and algal masses, heaped around holes or cracks in the ice. Even the largest were eaten-out shells, having disproportionately large basins within, and very limited ramifications of burrows and channels underneath. Inferior for protection during cold snaps, caving in during thaws, requiring frequent repairs whatever the weather, these flimsy structures doubtless did not impose the handicap on their occupants as did the sealing of the food supply by the ice, but they surely were not much of an asset when the crisis came. Indeed, Iowa muskrats may sometimes remain alive for weeks in midwinter in drought-exposed marshes — the necessity for outside foraging and the presence of minks notwithstanding — if only they can withdraw into the better types of lodges.

On the whole, the February situation exemplified a combination

of adverse factors beyond muskrat limits of toleration. The mink predation followed standard patterns and was appraised as being symptomatic of vulnerability rather than a true cause of population decline of the muskrats. Except possibly for a group of three muskrats living partly in a land burrow and partly in adjacent lodges, few of the animals killed by minks would have stood, under the existing circumstances, much chance of survival even in the absence of the minks.

Although the winter-killing of the entire Goose Lake population in February, 1948, had not been due to disease, muskrats coming in from outside during the spring dispersal started dying soon after their arrival. Only 2 diseased dead were actually found, these dying about April 5 and April 18, but, at the time of death of the second disease victim, mink-eaten remains of 2 other muskrats were found in the vicinity. Muskrat remains were found in 2 of 23 mink scats deposited in late March and the first week of April and in 6 of 59 scats for the middle two weeks of April.

By early May, three evident territories had been established, and, on May 21, a settled breeding population the equivalent of eight pairs, or perhaps twenty adults, was determined. Five of the territories were in the increasingly heavy vegetation of the south half of the marsh. The other three were along the northwest shore of the north half, in a thick and attractive fringe of cattails and bulrushes less than 200 yards long. Of the latter three territories, one — this near the site of most of the known mid-April mortality — seemed to be depopulated in late May or June.

In response to summer drought exposure of the south half, occupants of three territories in the vicinity of the islands converged in August at the north end of the largest island where it adjoined the wetter north half of Goose Lake. Here were four sets of well used burrows close together in what had all the aspects of common ground. The occupants of the two remaining northwest territories also reestablished themselves near deeper water in response to the drought.

In the southeast quarter, the movements of two family groups of muskrats were traced. One of these two groups moved in gradual stages northward from the south center of Goose Lake and finally arrived at the south edge of the deeper water of the north half in early October. The other group also worked northward but nearer the east shore, arriving at and renovating in late August the exact set of burrows where the late summer epizootic of 1947 had started. Here they died in 1948, also — six demonstrably in the first week of September and four more in the next six weeks.

Five more had died by mid-October at or near a lodge about 180 yards west northwest of the lethal burrow system, but thirteen muskrats living at this and a neighboring lodge escaped death temporarily. On October 21, one died at an isolated small lodge hundreds of yards

from either of the two infection foci. All three of seventeen contemporaneous mink scats that contained muskrat remains were from a set of dry burrows previously known to have been occupied by a muskrat in the south half of the marsh. This appeared to reflect simple drought vulnerability rather than availability of a disease victim to minks.

The new fall epizootic, following some three months of apparent quiescence, operated with notable irregularity in a low population mainly restricted by drought to the north half of Goose Lake. A very satisfactory census on October 21 gave 39 live muskrats, with 17 dead having been accounted for since early September, or a known early fall population of 56—about 60, allowing for some overlooked mortality. Sex and age ratios of 18 specimens were 2 adult males, 1 adult female (with 22 placental scars of 3 litters assigned to early May, early June, and early July), 12 young males, and 3 young females.

After the October 21 census, 2 more died of disease at widely separated places, including one dying on the east shore about 200 yards north of the burrow system where the 10 had died in September and the first half of October. No more mortality was detected from any cause until 4 died in the second half of November, at a small lodge not far from the site of death of the disease victim found lying on the shore. Of a maximum of 33 muskrats remaining alive by the opening of the trapping season, December 1, authorized trapping accounted for 14. (A few others probably were taken by unauthorized persons, as signs thereof were noted near the main island.) By January 7, 1949, after closing of the trapping season, muskrats were still alive in three lodges, a total estimated at between 12 and 15; and there appeared to have been disease loss in a set of burrows that had been dug late in the fall. By the middle of February, the marsh had no recognized sign of living muskrats, but later data suggest that a lone animal may have survived in one of the island burrows. Remains of a muskrat in one of two midwinter fox scats were probably from a victim that had been active on top of the ice.

The contents of the 1948–49 winter mink scats lined up well with known events at Goose Lake. Of fourteen scats examined for December, seven contained muskrat remains from two determined sources: two trapped muskrats partly eaten in the traps and two of the late November disease victims that I removed from the water and threw up on the lake bank, later to be consumed by the minks. Muskrat remains were found in but one of fourteen January scats, this one from the new burrow in which it is believed that the muskrat occupants had died; for February, remains were found in thirteen of sixty-five scats. Forty-eight scats for March and early April revealed no feeding upon muskrats.

Goose Lake had no resident muskrats whatever during most of the spring of 1949. Between April 3 and 7, a sign of either a lone winter survivor or of a newcomer was recorded. This individual later

disappeared, and the marsh remained barren of detected muskrat signs until May 24, when fresh droppings were again found. At some time later, probably in June, the equivalent of three breeding pairs became established. Two of the new territorial sites were within 200 yards of the dry outlet, about 200 yards apart, and in some of the most attractive habitat of the marsh. The third territory was near the north end of the larger island, about 150 and 175 yards from the other territories. What seemed to be a single animal lived in another place.

The water reached without exceeding the overflow level in early May, and the marsh was in splendid condition for muskrats most of the summer. Then drought restricted the surface water to the north half and to the two deepest parts of the south half. By early September, one of the family groups had moved about 250 yards in gradual stages, finally to construct an elaborate system of burrows and small lodges close to the site of the lethal burrows of the preceding two summers. September was a month of considerable local adjustment on Goose Lake, much of which seemed to be on the part of locally reared subadults, but the signs appearing at the extreme north end suggested the behavior of outsiders. The lone adult mentioned for the south half stayed in its accustomed home range despite drought exposure until killed by a mink about freeze-up.

A highly satisfactory census of 29 muskrats was made by direct enumeration in the north tip and northeast corner in late fall, 1949. Fair estimates of populations in other parts were about 17 for a territory in the south half, where the muskrats appeared to remain as a self-contained unit in a food-rich place having some surface water; the lone muskrat later killed by the mink; about 23 in or near the island burrows; and about 11 remaining along the east central shore after moving as a family group from the drying south half.

Of the total of about 80 arrived at, the first known to die was one that looked as if it might have succumbed either to disease or old age in late October or early November. The year 1949 was the first since the collapse of 1943 in which the marsh did not have at least one epizootic. None of 115 mink scats deposited from September through November contained muskrat remains. Water levels were much as they had been during the two previous winters.

One of seven mink scats from early December contained muskrat remains, but that scat was from the lodge in the south half that had been occupied by the lone adult. Up to the end of December, no general crisis was brought about at Goose Lake by the sinking of the frost line into the mud, though few of the muskrats could have had access to much unfrozen water except in their deepened channels. One of 18 mink scats for the middle to the end of December contained muskrat remains.

By mid-January, 1950, the water in the deepened channels had frozen, and the mud above had buckled from the pressure. The musk-

rats of the north half had withdrawn to their bank burrows by the first of the year, and their small lodges out from shore and their larger mud-plastered shore lodges both remained unrepaired after intrusions of minks. In contrast, the bigger rush lodges of the food-rich shallows of the south half had mink holes promptly repaired, and push-ups continued to appear on the ice. By early February, the rush lodges of the south half, too, showed no evidence of living muskrats, and any muskrats yet alive at Goose Lake were either in bank burrows or living under the ice away from externally visible habitations. In this period, proof of death of only six distinct victims was found, but 27 of 66 scats examined from probably three resident minks contained muskrat remains. At the time, this winter mortality was attributed to predation by minks upon muskrats vulnerable because of a freeze-out crisis, but, by the following year, it became evident that sites of the 1949-50 wintering mortality included some serious foci of the hemorrhagic disease.

An early March thaw put up to ten inches of water over the old ice and brought the marsh up to within about three inches of its overflow level at the dam. This water flooded many of the mink caches of dead muskrats. Fourteen of twenty-four scats dated from mid-February up to the flooding contained muskrat remains, whereas this item was found in none of seven scats deposited March 6-8 in the vicinity of some of the best caches. But four of six scats that were fresh on March 14 contained muskrat remains.

I opened, on March 6, all lodges and parts of some of the most accessible burrows, without finding any sign of living muskrats, nor was any found a week later, when the melt water froze over the old ice. Visits were made in the latter part of March as the ice receded from the shores, and the marsh continued to be devoid of current muskrat signs. No muskrat remains were found in 21 mink scats deposited in the first half of April.

The first evidence of a newcomer to the marsh following the annihilative winter losses appeared about April 5. What was probably the same animal was seen in the same vicinity — the heavy bulrushes of the east center, quite apart from any of the 1949-50 wintering retreats of muskrats — on April 14. It was a big animal, battered in appearance, and depending for shelter on temporary nests in heavy rushy growths.

THE RECOVERY YEARS, 1950-52

From spring throughout the rest of 1950, environmental conditions were the best for muskrats at Goose Lake since before the pronounced deterioration of marsh vegetation in 1943. Not only did the south part grow up heavily to bulrushes and cattails but much of the north part was thickly fringed with marshy emergents. Water conditions remained favorable, although practically no overflow into the outlet occurred until fall.

In late April or early May, a lone, pregnant female moved in and built a small lodge; she raised a single litter born about May 13. On May 4, a pair of muskrats, distinct from the pregnant female, was watched mating out from the entrance of the same burrow system where the late summer epizootics of 1947 and 1948 had been observed to start. This pair seemed to disappear permanently soon thereafter, almost certainly dying from hemorrhagic disease at one of the deadliest foci of infection on the marsh.

Prior to about the first of October, the only muskrats detected were those of the one-litter family group living there since May. Then, as water overflowed the dam following locally heavy rains in late September and early October, immigrants trooped in via the flowing outlet. Most of this movement and resettling was over by the middle of October, but diminishing evidence of its continuation was seen in the second half of the month. Goose Lake was the sole central Iowa observational area to draw any substantial immigration in the course of drought-forced adjustments on the part of stream-dwelling populations, and that occurred only while water flowing in the outlet offered an inviting avenue of travel.

Estimates made from bubble signs under clear ice, November 11, 1950, gave a figure of around 150, which would mean an increase in the fall of 1950 of around 140 animals, datable largely to the month of October.

Indirect evidence of hemorrhagic disease was seen in the vicinity of the old focus of infection where the mated pair almost certainly had died in late spring. One of the lodges erected in October within easy cruising distance of the infected burrow system showed disuse by the time that the ice formed, and, on December 9, a small mink dragged a dead muskrat out of the neighboring lodge. Two of three mink scats deposited in this part of the marsh in early February, 1951, contained muskrat remains. Under such circumstances, this sort of sign is highly indicative of disease mortality.

Elsewhere on Goose Lake, the muskrats wintered well up to mid-February. No muskrat remains were found in 35 mink scats gathered from November, 1950, through January, 1951, away from the suspected disease focus. Unauthorized activities of a trapper were noted about the muskrat lodges on opening day (November 25) of the trapping season, but I am sure that few if any muskrats were actually trapped there.

Sinking frost lines in midwinter were accompanied by rather general abandonment of feed houses and the smaller lodges. Many of the larger lodges were dug into by minks but these were usually repaired rather promptly. In one instance, one half of a large lodge continued to be used by muskrats, while the other half was left with an unrepaired mink hole. Outside activity was noted on the part of a single muskrat in early February.

Of 191 mink scats examined from mid-February through April,

1951, 49 contained muskrat remains, and 26 of the muskrat-containing scats were deposited in the vicinity of the old disease focus of the east central shore zone. During this late winter and early spring period, mortality of at least five muskrats was detected, and a fair case could be made for the demise of at least eight more — mostly, but not exclusively, in the vicinity of the same old disease focus. Away from here, one muskrat that persisted in coming out on the ice during thaws was killed by a predator (probably a great horned owl); a rather minor amount of mortality took place in shallow water zones of the northwest corner and north end as the ice thickened; and perhaps two or three animals (judging from remains found in mink scats) died after the ice went out.

Preliminary estimates of Goose Lake breeding territories were made in late April, 1951, and the total arrived at was 45, or, following the central Iowa sex ratio of 58 per cent males for the fall of 1950, a total of about 107 muskrats. This value checks fairly well with the estimates of the wintering population after allowing for mortality. No evidence of movement in or out of the marsh via the flowing outlet was found either in the spring and early summer or in the fall of 1951, so the breeding population and its increase may be considered self-contained for this particular year. Extensive territorial readjustments were noted by the middle and latter part of May, but these were practically restricted to the vicinities of the territories recorded a month earlier. Irrespective of changes in the exact locations of territories, the totals to be perceived in given tracts of the marsh tended to remain unchanged.

Second and third checks from mid-May to mid-June gave the same territorial totals as in late April, except that three territories were apparently lost early in the summer. One of the territories considered lost without compensating gain elsewhere was at the site of the familiar old disease focus of the east central shore. Enterprising dogs (individuals known as habitual muskrat hunters) seemed responsible for the uncompensated loss of two territories. (Actually, five systems of bank burrows representing muskrat territories were thoroughly dug out by the dogs, but, in three of these territories, the occupants evidently succeeded in avoiding capture and in adjusting to this molestation.) Approximately 100 adult muskrats should have been alive on the marsh by late June, with the prevailing food and water conditions being excellent and the hemorrhagic disease killing muskrats only in a very restricted area.

By fall, 1951, Goose Lake was still in excellent condition for muskrats. Its supporting capacity appeared to be nearly equal to that of 1942, when the marsh had offered the best habitat for muskrats during the entire period of study. But, although the total quantities of superior food were similar in both years, the composition and distribution of the food plants of 1951 differed greatly from that of 1942. In 1942, the main food supply was a dense stand of broad-leaved

cattails covering roughly the south half, whereas, in 1951, the emergents of the same area were largely bulrushes, with more open spaces. However, in 1951, there were far more bulrushes elsewhere on the marsh, besides thick growths of duck potato dominating the open water shallows, as well as considerable stands of cattails.

No evidence of summer and fall mortality from hemorrhagic disease was found on Goose Lake until early October, when muskrats proved to be dying in two places. One place was the site of most of the dying of the previous winter and spring, the notorious east central focus at which muskrats had died since 1947 (except in 1949 when they had not been present there). The other place, though muskrat-vacant in 1950, was the only site of suspected dying from the disease that had occurred on the marsh in 1949. Later in the fall, a few diseased dead were found in a third place, not so very far from the last-mentioned. All together, only eight dead muskrats were recorded in the Goose Lake notes for October and November, 1951. Four of 284 trapped carcasses examined in late November and early December had liver lesions, all well-advanced in healing.

Sex and age ratios of the trapped carcasses were 19 adult males, 17 adult females, 135 young males, 113 young females. Aside from 18 young of "kit" sizes (7.3 per cent of the young), most of the young were of decidedly large sizes by early winter. Five of the animals classed as young females of 1951 had conceived single late (early August to early September) litters—5 young each for 4 pregnancies and 4 young for the other. The 17 adult females had conceived 58 litters or a mean of 3.4 litters, with a mean size of 8.0 young per litter. Of the 17 adult females, 1 had conceived a single litter, this one assigned to May; 2, two litters each; 3, three litters each; and 11, four litters each. Eleven of the 17 adult females were judged to have given birth to their last litters in August or later.

About 40 adult females were left on the marsh before the trapping, as of mid-November. The fur trapping on the main part of the marsh was conducted in such a way as to leave about half of the population for breeding stock and to obtain the most representative carcasses for examination. The sex and age ratios for the carcasses, applied to a base of 40 adult females, gives a total fall population of about 670.

The above calculations ignore the young contributed by the precocious young females in 1951. According to the sample data, the adult females conceived about three and one-half times as many late-born young as did the precocious young females. Even if it be assumed that the young born of precocious young mothers had survival chances equal to the chances of the late-born of experienced adult mothers, only about nine young (fewer than 2 per cent) of the total of 584 young of the year arrived at from the calculations may thus be credited to the precocious females.

At least 300 muskrats survived the trapping, and most of these

wintered well, including the occupants of the shallower parts and also including most of the occupants of two strips of shallow shore zones that had not been subject to trapping. All detected mortality — at least 17 dead were accounted for — after the first of the year took place either at or near definite disease foci. Three regularly resident minks frequented these places. None of 54 mink scats deposited from late fall through January contained muskrat remains, compared with muskrat remains in 7 of 34 for February and in 31 of 88 for March.

Signs of spring dispersal from wintering quarters were noted as early as March 20, 1952, although the ice covering was still unbroken about all except the edges of the marsh. Only the very slightest evidence was found of animals leaving the marsh entirely. As of early May, 120 breeding territories were distinguished, which following the winter sex ratio of 54.2 per cent males, would give a remaining total population of about 260 adults. This would seem consistent with the other population data, allowing for the death of 40 to 50 muskrats at the disease foci between early January and break-up.

The disease foci continued to be sites of mortality. At least 19 territories were depopulated during May and the first half of June through the agency of the pneumonic syndrome of the hemorrhagic disease, thus cutting down the adult population to about 220.

Goose Lake had some remarkably high breeding concentrations in the late spring and early summer of 1952, all in places on which little or no effective trapping had been carried on during the preceding fall and winter. The most prominent was one of 15 territories in a rushy shore-zone strip having a total area a little less than one and three-quarters acres.

From late June on to fall, local population adjustments tended to refill the disease-swept places, but little further dying was known to have occurred prior to October. Such repopulation through post-breeding adjustments was generally rather incomplete, however, and most of the formerly disease-swept tracts (there was a single outstanding exception) had decidedly fewer muskrats by fall than the neighboring tracts that had been spared disease mortality.

The marsh remained in good condition for the muskrats up to mid-September. As a fall drought progressed, the occupants of some of the shallower tracts became relatively more exposed. The most pronounced adjustment occurred in the extreme northwest corner, which went dry in late summer. This corner had a mid-May population the equivalent of eight breeding pairs — five of them farther than 100 yards from deeper water — and these territories had been highly productive of young up to August. As of that time, the muskrat occupants of 21 large and medium-sized lodges had been concentrated in a strip of drying shallows about 150 yards in length and from 20 to 30 yards in width. By the last of October, signs of perhaps a dozen remaining muskrats could be made out in the northwest shallows, mainly occupants of the 3 territories situated nearest the

deeper water of the marsh proper. The others adjusted along the 150-yard strip, and then, after much explorative traveling back and forth over an 80-yard trail to the deeper water, took over the site of a food-rich old disease focus that had been all but muskrat-vacant since spring. By mid-November, only a single muskrat seemed to be left in the 8 former territorial sites of the northwest shallows.

The next-to-the-shallowest area of Goose Lake having considerable numbers of muskrats in residence in 1952 was near the west central side. The occupied lodges never had been completely drought exposed (in the sense of losing all surface water) during the summer and fall. Far greater restlessness was noted on the part of the equivalent of the 19 pairs and their season's young living here than on the part of the muskrats of the northwest corner. Beginning about mid-October, much evidence of fighting and abandonment of former home ranges was noted, with footloose wandering occurring particularly over the farm land to the west. To a lesser extent, similar observations were made about other shallow-water zones of the south half of the marsh. Many strife-battered animals reached the deep-water north half of Goose Lake, there to find temporarily endurable living conditions. One type of adjustment on the deep-water north half is illustrated by the erection of a large lodge near the center — outside the ordinary cruising radii of the shore-dwellers — in early October. Twenty muskrats were taken from this isolated lodge during a few days of trapping in mid-November, and the lodge was still being maintained after the trapping!

In comparing the peaceful adjustments of the muskrats of the northwest shallows and the far more troublous ones of the west central and south shallows, certain distinctions as to *chronology* of the events should be recognized. The actual drought exposure of the muskrats of the northwest shallows was incomparably more severe than were the exposures involving the other shallows, but the residents of the northwest shallows accomplished most of their adjusting before the end of September, weeks before any notable intraspecific tensions became apparent. The residents of the west central and south shallows, though living in superior habitats compared with the early-abandoned northwest shallows, were trying to adjust at a time of fighting and wandering on the part of increasing proportions of animals leaving familiar home ranges.

The ingress of the muskrats of the dry northwest shallows into the adjacent old disease focus precipitated the first detected mortality from the hemorrhagic disease since the pneumonic syndrome epizootics of late winter and spring had subsided in May and June. On about October 16, 1952, a large subadult died right in the middle of the disease focus. During the next three weeks, an epizootic spread from this place southwestward along the shore zone for 200 yards and northward for at least 55 yards. It was estimated, on the basis of newly dead lodges and other signs, that about three-fourths of the

population of this 255-yard stretch — including many of the former occupants of the northwest shallows — died during the last ten days of October. All together, remains of thirty-one dead were found in this disease-swept stretch up to mid-December, and many other dead were doubtless overlooked. The degree of depopulation in consequence of the epizootic is indicated by the fact that fewer than a dozen animals were taken from the stretch during the fur trapping — and here the trapping was done very intensively. The disease mortality amounted to the equivalent of about eighteen complete family groups.

Elsewhere on the marsh a considerable amount of late fall and early winter dying was localized about old disease foci. From one to eight dead were found at or near seven of these, including some old foci at which no mortality had been observed for years. One that had been notoriously deadly between 1944 and 1946 had few if any muskrats in its vicinity until the fall of 1951. Apart from a single dead muskrat found near by in the spring of 1952, reoccupancy of this site had not been accompanied by renewed dying until November of 1952, but five were known to have died here up to mid-December. Another site of disease mortality in the falls of 1947 and 1948 had muskrats living at least near it in 1951, but it was not until the fall of 1952 that muskrats again were known to have died; from late October to mid-November, 1952, eight dead were found, and one of ten specimens systematically shot here for examination had severe lesions. The deaths of six were recorded from mid-November to late December, 1952, from a lodge at which at least three had died in winter and spring, 1951–52, but at or near which no mortality had been detected during the intervening summer and fall months. Twelve living muskrats showing lesions of varying severity, including some (in four cases) indicative of approaching death, were taken for specimens mostly in the latter vicinity in early December, 1952.

The most notorious of the disease foci — the site of most of the hemorrhagic mortality of recent years — showed evidence of only one death during the fall of 1952. Prior to the fur trapping in mid-November, this place did have fair numbers of muskrats (which had moved in during some local population adjustments of mid- and late summer). After the trapping, few muskrats remained in the infected tract.

The 1952 fur trapping was done in two periods of the open season. In mid-November, 282 muskrats were taken before freeze-up from the open water part of the marsh. In early December, 125 more were taken, but all except about 30 of these were from the partly dry shallows of the south part. The sex and age ratios in possession for a total of 399 fall specimens gave 13 adult males, 19 adult females, 188 young males, and 179 young females. But these ratios should not be applied directly to the approximately 100 territories that remained functional after the known dying had ceased in June, for the evidence

on local adjustments points to disproportionately more young in both major trapped samples than held true for the marsh population as a whole.

The single tagged young recovered during the 1952 fall trapping well illustrated the behavior that must be considered in applying sex and age ratios to shallow-zone territories during a dry year. The animal had been tagged in May in one of the territories of the north-west corner that almost went dry in late fall, and it was trapped in the open water at least 150 yards to the southeast. On the other hand, a few of this family group (which conspicuously included large, surely fully adult animals) remained in the original territorial lodge until the trapping was over and did not get near any place where traps could feasibly be set. This type of behavior could easily be traced through "reading of sign" between many shallow-zone territories and deeper adjacent waters.

Of the 282 muskrats caught in the open-water part before freeze-up, 259 were sexed and aged. They were 5 adult males, 11 adult females, 125 young males, and 118 young females. These represented a fair cross section of the occupants (all ages) of 16 territories, plus a large proportion of the adjusting young of 11 more territories of adjacent shallows. From the above ratios, the population of the marsh that was accessible by boat during the trapping figures out at about 375. The evidence from trapping partly abandoned territories of the shallows after freeze-up indicates that from 1 to 7 or more muskrats were left in each territory, averaging perhaps 4 in each. The figure of 4 per territory applied to the 11 partly abandoned territories of the shallows adjacent to the early-trapped area gives 44, which, added to the 375, would give a rather circumscribed population group totaling about 420 animals, as of early November, 1952. The figure of 420 also agrees with an estimate made on the basis of the trapping results: by the last day of open-water trapping, the catch rates had fallen off sufficiently to indicate that, with a catch of 282, about two-thirds of the population in and about the open water had been taken.

The population of the south part of the marsh, which was not trapped before freeze-up, is harder to calculate satisfactorily. Subtraction of about 30 taken from the open water part after freeze-up from the total of 125 then trapped on Goose Lake would leave about 95 taken from the south shallows and their remaining tracts of fairly deep water. These 95 represent an estimated three-fourths of the adults and young of 6 partly abandoned territories, plus most of the adjusting young from about 11 other territories. In addition, there were about 20 occupied territories at which no effective trapping could be done because of the shelter afforded the animals by immense snowdrifts. Well-maintained though more or less exposed territories had a mean of about 11 animals prior to the trapping, in contrast to the estimated 4 per partly abandoned territory. From the

population samples obtained during the trapping, a pre-trapping population of about 365 may be calculated for the south and southwest shallows and associated deeper waters.

The total fall population would then figure out at about 785 muskrats, as of early November. Allowing for a mean reduction of 7 muskrats each for the 19 territories of the west central side that had been partly depopulated through egress without known compensating gain elsewhere on the marsh would account for about 130 animals presumably engaging in cross-country movements in October. A total loss of the equivalent of 18 complete family groups from the epizootic of October and early November in the northwest corner — these groups averaging about 16 muskrats each, according to excellent sampling data from disease-free neighboring populations — would give a loss figure of about 290 for this part. For the rest of the marsh, the pre-trapping fall losses from disease, predation, fighting, and wandering probably did not exceed 50 animals. Adding a total fall loss figure of about 470 to the pre-trapping total of 785 would give a grand total of about 1,255 muskrats, as of mid-fall, 1952.

Concerning the 1952 breeding statistics: of 17 adult females carefully examined during the trapping, one had not conceived in 1952; one had conceived a single litter (assigned to June); 2 had conceived two litters each; 6, four litters each; and 1 had conceived five litters assigned to the calendar year. Four of 179 young females born in 1952 had themselves conceived single, small (averaging 5.5 young), late (August) litters. The 16 breeding adult females of the sample had conceived a total of 52 litters, or a mean of 3.3, with an assigned seasonal distribution of 6 in April, 11 in May, 16 in June, 15 in July, and 4 in August. The mean size of litters conceived per adult female was 8.2. Among the 367 young of the year examined in late fall and early winter, 24 or 6.5 per cent were judged to have been August-born, compared with 8 or 14.3 per cent August-born litters in the total of 56 (including those of the precocious young females) for which seasonal data were obtained.

MORE YEARS OF VICISSITUDES, 1953–55

It was apparent by mid-December, 1952, that the approximately 350 muskrats judged to have been alive after the fur trapping had prospects of severe wintering mortality ahead of them, and so it happened. At this time, most of the muskrats of the disease foci that had escaped traps and disease died with relative suddenness. The dying now occurred more or less simultaneously in widely-separated places and accounted for at least 100 animals. In late December, a period of conspicuous wintering crisis began for muskrats living in shallow-water zones. Between then and March 13, 1953 (the last day that the ice permitted walking), I spent 44 afternoons on the marsh studying the complicated wintering histories of local groups of muskrats and the responsiveness of mammalian flesh eaters thereto.

The dead and handicapped muskrats were exploited by a population of at least nine distinguishable minks — representing just about the maximum levels that the minks themselves would tolerate. In addition, Goose Lake was regularly worked over by red foxes and, occasionally, by farm dogs and a winter-active striped skunk and a raccoon. Up to late December, the feeding by flesh eaters upon muskrats had been chiefly scavenging, but, soon after, the minks and foxes ceased working the disease foci, to work systematically about the places where the muskrats of the shallows were confronted by a mounting freeze-out crisis.

Whole groups of the muskrats traveled regularly back and forth between exposed lodges and the snowdrifts covering certain of the better feeding grounds, and the more insecure naturally drew some predation. But, even in the shallows, considerable numbers of muskrats were able to survive in the protection afforded by the snowdrifts or a little unfrozen water or mud beneath the ice, and, even here, a large proportion of the muskrats eaten or carried off by the minks and foxes had clearly been dead when found. Some of the victims had self-amputated frozen tails signifying hardship if not death from freezing. The bodies of others had been wrenched by predators from frozen mud or from frozen lodges. Once, a mink obligingly revealed its source of food by eviscerating a freshly dead muskrat dragged from a lodge and leaving the intestines — distinctly hemorrhagic from disease — in the trail. Many fresh-appearing dead muskrats that I found in late winter and early spring were refrigerated victims having times of death traceable, from sexual condition or stage of pelt-priming, to the December die-off. Utilization of the local muskrats by the minks paralleled closely the changes in availability of this item as food. No muskrat remains were found in 27 late-summer and early-fall mink scats, and remains were found in only three of 113 scats deposited in early and mid-October, at the beginning of the dying from the hemorrhagic disease. For late October and early November, when the dying was all but restricted to the sweeping epizootic of the northwest shore, 10 of 66 mink scats contained muskrat remains. From mid-November through December, the period of most dying from hemorrhagic disease after freeze-up, 47 of 86 mink scats contained muskrat remains. Many victims of this dying were also found in frozen condition by the minks later in the winter, at the time that the lodges softened in the spring. Extremely high incidences of muskrat remains in mink scats for January (in 51 of 60), and for the first half of February (in 48 of 52), reflected not only continued availability of muskrats dying earlier but also the increasingly severe wintering crises confronting the muskrats trying to live in the less habitable shallows.

Mild temperatures during the second half of February relieved the wintering crises for many of the muskrats surviving up to then, and the incidence of muskrat remains in mink scats dropped to 31 of 43.

However, cold snaps that followed thaws imposed deadly hardship upon individual muskrats before they were able to adjust to the flooding of their subsurface retreats. In two instances, muskrats were known to have left their home ranges to station themselves in unfamiliar places elsewhere on the marsh, and to die later when caught by cold weather.

Thirty-five of 53 mink scats from the first half of March contained muskrat remains, at a time when essentially all of the muskrats that had successfully wintered at Goose Lake were living with security from predation, but this was also a time when minks had convenient access to disease victims in many softening lodges that they had not previously penetrated. None of the seven mink scats examined during the second half of March contained muskrat remains, though floating dead from early winter were appearing at old disease foci.

Of 179 dead muskrats listed in the Goose Lake field notes, from mid-October, 1952, through March, 1953, 21 had died under circumstances that could not be satisfactorily appraised. Of the other 158, 113 had died demonstrably or almost certainly from the hemorrhagic disease (whether eaten upon by predators or not) at old disease foci and 22 more at what I came to regard as possible old disease foci. One dead muskrat had been dug out of a frozen lodge by a raccoon, but, of hundreds of raccoon scats looked at during the period of disease mortality of the fall and winter of 1952-53 at Goose Lake, only a single scat accompanying the above dead muskrat contained muskrat remains. Nine other dead muskrats had been eaten upon or played with by foxes, four of them in the stretch of shore zone first swept by disease in the fall. Two of the dead muskrats examined had been victims of intraspecific strife. Four had been trap cripples. Seventeen could have been functional though handicapped animals killed by predators. The latter included one surprised outside a lodge and killed by a fox and another killed under similar circumstances by a dog. Of the 15 that had seemed the likeliest victims of mink predation, per se, at least five had suffered enough from exposure to lose the ends of their tails from freezing.

About 70 muskrats survived the winter of 1952-53 on Goose Lake. As of late May and early June, 1953, 28 well-maintained territories were recorded, which would mean a total population of about 60 adults, and a similar figure was arrived at for late June. It may be said that, in general, the winter survivors stationing themselves in known disease foci died (five dead were found in these places in April) and that the others lived securely. Two of 59 mid-April to early May mink scats contained muskrat remains, and both muskrat-containing scats came from a notorious disease focus.

By midsummer, practically all muskrats living in or very near old disease foci had died, thus leaving about 50 adults residing in the safer places. Most of the latter adults and their season's young got along splendidly in lush vegetation and adequate water until

the food-rich shallows of the south part again dried up in late September. Most of the young animals and some of the adults then moved to the main body of water remaining, that of the relatively food-poor north half of the marsh.

The midfall population of 1953 amounted to about 230, including few, if any, immigrants from surrounding dry streams, insofar as the marsh was well outside all the travel routes taken by adjusting and wandering stream-dwellers. About 90 of the 230 still lived in food-rich shallows up to the middle of October. By November, scarcely more than a dozen were left in the shallows, the others having moved, for the most part, into the wetter but food-poor north half. Here, the newcomers had sufficient space in which to keep out of serious trouble with their fellows that got there first, though healed fight wounds on five of 71 specimens trapped on the wet marsh in mid-November did not bespeak wholly peaceful relations. Two of the most chewed up muskrats were noted to have been living very much alone.

Twelve of 18 dry-marsh mink scats datable to the period of probable greatest deadliness (with zero or lower temperatures on the nights of December 15–16) contained muskrat remains. By late December, only a lone, very large muskrat appeared to be alive in the dry and hard-frozen south half, and minks were diligently boring into the two principal groups of dry lodges in which the last of the other dry-marsh muskrats had persisted in trying to live.

Severe local dying from the hemorrhagic disease had begun at two of the deadliest old disease foci shortly after these had been repopulated by muskrats in the course of the September adjustments. Later in the fall, dying had started at two more old foci lying adjacent to the main body of water of the north half. By the first of November, an epizootic had been advancing on three fronts (from three different disease foci) into some 30 acres of wet marsh having a concentration of 200 or more muskrats. Dying also had started at another old disease focus on the opposite side of the marsh from the advancing three-front epizootic.

Seventy-six certain or very probable disease victims were recorded for the above period of fall and early-winter dying, and the evidence suggests mortality from disease of about 40 more. All of the recorded victims except two were found at or not far from notorious old disease foci. As usual, the outstanding disease focus of the Goose Lake studies – that of the east central shore mentioned so frequently in accounts of previous dying – became a site of mortality when reoccupied by muskrats in the fall; 29 dead were found here, of which 24 were datable to late September and October and the other 5 to early November, after which this part of the shore zone remained unpopulated by muskrats. Two other consistently deadly foci were occupied by muskrats at about the same time, but their new occupants were not known to have started dying until several weeks afterward;

the dying then slowly gained headway until no more muskrats were left alive by mid-December. Eight dead were recorded at one place and 12 at the other, mostly after freeze-up. The two disease victims dying away from known foci were occupants of the same lodge and burrow system; while more may have died here undetected, this local dying was neither very drastic nor part of any sweeping epizootic.

Exceptionally significant data were obtained from a disease focus that had been the site of a locally severe die-off in the late summer and fall of 1947. It had then remained muskrat-vacant for five years, until the fall of 1952, with muskrats living securely on all sides of it. Its muskrats had died out again during the winter of 1952-53 and it had remained muskrat-vacant once more, until the fall readjustments of 1953. Then, from late September to early November, 1953, this place and its immediate vicinity became completely depopulated, most of its 22 recorded victims dying in October. This constituted the second example at Goose Lake of a lethal disease focus retaining a distinctive infectiousness for five years in the absence of muskrat culture media of the hemorrhagic disease.

Experimental trapping was carried on, mostly November 10-14, to remove those muskrats that were in greatest danger from the contagion then spreading. Accordingly, the trapping of 76 animals virtually depopulated the tracts lying between the disease foci and the best-situated muskrats having a minimal chance of surviving the winter. The latter remnant was estimated at about 30, as of early December. The other muskrats then alive on the marsh may not have exceeded the lone animal in the dry south shallows and possibly one or two still maintaining an isolated lodge near one of the disease foci.

Of the total of 76 muskrats trapped, 5 were adult males, 5 were adult females, 40 were young males, and 26 were young females. Of 18 late-fall disease victims yielding sex and age data, 4 were adult males, 5 were young males, 5 were young females, and 4 unsexed young. Only 3 of the 80 young in the sample were judged to have been late-born, with times of birth assigned to early August. None of the young females of the sample had conceived young in 1953. All 5 adult females had conceived 3 or 4 litters, the mean being 3.4 litters per female. For 17 litters, the assigned birth months were: 3 litters in April, 5 litters in May, 5 litters in June, and 4 litters in July.

The estimated 30 muskrats alive on wet-marsh Goose Lake after the 1953 experimental trapping consisted of three population groups. One group was in the food-poor central part having up to a foot of water at freeze-up. The second group was strung out along the muddy east edge of the wet marsh and it lived partly in lodges containing large quantities of stored duck potatoes. The third group was at a place having neither the deeper water nor good food resources.

The water froze to the bottom of the marsh in all wintering sites during the second half of January, 1954, despite deepening of the strategic burrow systems by muskrats responding to the crisis. Almost

suddenly, the accessible food of the former wet-marsh became exhausted, except in the mud lodges of the east edge that had been stocked with duck potatoes. It was only at the latter that any evidence of muskrats being alive was found in late winter.

Responsiveness of the local predators to muskrat flesh followed familiar patterns. The numerous raccoons were unable to exploit either the drought-exposed or the diseased muskrats to any important extent. Latrines made up of thousands of raccoon scats were examined in the field from August through December, 1953, without finding any muskrat remains. Red foxes fed upon at least two muskrats at disease foci. As usual, the minks were the predators specializing on the handicapped and dead muskrats, but they found little muskrat flesh available to them until freeze-up. Even the drought-exposed muskrats of the south shallows were not known to have suffered losses from the minks until the ground froze solidly. No muskrat remains were found in 69 mink scats deposited from October through mid-November in the dry marsh, compared with remains in 14 of 20 scats for the middle to the end of December, in 10 of 33 for January, and in 8 of 9 for February.

Minks probably killed the last muskrat trying to winter in the long-dry but food-rich south part of the marsh, as well as two other muskrats abandoning the frozen wet-marsh lodges to move into well-vegetated shallows of the edge. They also were known to have killed two of the frost-evicted muskrats on the ice.

During the winter of 1953-54, at least nine muskrats died from the hemorrhagic disease at sites 50 to 150 yards distant from major disease foci. Some of the dying away from known foci may be explainable in terms of victims contracting the disease while visiting sites of earlier mortality, but it is by no means certain that this was invariably the case. Mink scats examined at or near sites of disease mortality contained muskrat remains in 5 of 26 for late November, in 25 of 69 for December and January, and in 20 of 35 for February. Most of the feeding of minks upon muskrat flesh in February was in response to dead muskrats becoming easily available inside lodges softening during a prolonged thaw.

Neither minks nor disease seemed to be involved in the serious wintering troubles of some of the muskrats. In mid-January, while the air temperature went as low as 15 degrees below zero Fahrenheit, a group of muskrats sat huddled within a partly open small lodge, too beaten by hunger and cold to repair the lodge. Other muskrats ate away about all that they could reach of the inner walls and tops of their dwelling lodges, even those having great quantities of mud mixed with the vegetation used in building. The two animals killed by minks on the ice had almost nothing but sand and harsh plant debris in their alimentary tracts. Some of the last muskrats observed to be alive were coming out on the wet ice during a thaw, to dig and gnaw on the top of a marsh-edge lodge composed chiefly of mud,

and these had first so thoroughly eaten out the interior of the accustomed dwelling lodge that the sides broke through in two places. Nevertheless, these muskrats (which were so tame from hunger that they permitted watching of their activities from a distance of a few yards) did rehabilitate a once-abandoned shore lodge having stored duck potatoes, and there apparently was some successful wintering at this lodge.

Although water did not return to Goose Lake in time to save the wintering muskrats from deadly crisis, the rains of May and June, 1954, well filled the marsh and left it in splendid condition — with but a lone muskrat in residence by the middle of June. The origin of the lone animal is uncertain but the evidence suggests a winter survivor. What appeared to be this same individual spent the whole summer in the vicinities of two of the deadliest disease foci on the marsh.

Except for the above, Goose Lake continued to be without muskrats until late September and early October, when about thirty animals moved in from a ditch via the flowing water of the outlet of the marsh. As of early December, the population was estimated from signs at about twenty-three, following known or suspected mortality from disease at or near four old disease foci. Food, cover, and water conditions were excellent, but most of the newcomers were hazardously located with respect to disease. By early April, 1955, signs of successful wintering could be seen in five places (including the vicinity of the deadliest disease focus on the marsh), and about eight muskrats were judged to have wintered. Two of these survivors were later found dead of hemorrhagic disease, and remains of four winter victims were noted. Nearly all dying occurred in or near the notorious old disease foci where most of the newcomers had settled in the fall.

The high population of nine minks regularly frequented Goose Lake and its immediate environs through December and January, 1954–55, and well into February. By February 23, only six minks were remaining, the other three having disappeared about the time that the breeding season of free-living minks started. These minks cruised the marsh sufficiently to take advantage of muskrats dying from disease, though they subsisted principally upon the meadow mice of the marsh fringes. Three of the fifty-two winter mink scats examined contained muskrat remains.

Of eight muskrat territories recorded at Goose Lake from late May through June, 1955, three were attributed to animals having wintered there and five to those having come in via the flowing outlet during the spring dispersal. The newcomers were distributed along the west side of the marsh, in the usual line of travel of muskrats entering from the outlet. One of the territories attributed to winter-resident stock was lost because of disease in mid-May. As of late June, four of the seven functional territories were doubtfully productive, and one seemed to be maintained by a lone animal. There was no evidence of anything to be called full-scale breeding, and possibly

as many as three of the four indubitably productive territories actually produced only single litters of young, born to lone females that had been pregnant when they established their territories.

The water level went down during a late summer and fall drought until only about 30 acres of the deeper marsh had water covering the bottom by late September. The muskrats then alive were localized either in a few newly-built central lodges or along a 150-yard stretch of east central shore zone. Adjustments in dry or drying habitat were — except for the death of the occupant of a lone-animal territory — unaccompanied by detected mortality, and it is thought that most of the young born in the productive territories were reared to independent stages.

A well-based population estimate of about 45 muskrats was obtained in mid-November, up to which time little loss had resulted from the drought conditions. Freeze-up came with no more than a foot of water remaining in the deepest places. Few muskrats were left alive by late December, when all of the food-poor remaining water was frozen to the bottom. By the end of the first week of January, 1956, all muskrats at Goose Lake were dead except possibly at one lodge; and certainly none got through a period of subzero weather beginning shortly after the middle of the month, with a minimum temperature of 23 degrees below zero. While the muskrats were still alive, they hollowed out the interiors of all maintained lodges, ate on the tops from the outside, and some did a considerable amount of foraging in drought-exposed food-rich shallows.

Two locally resident minks took advantage of the frost-evicted and starving muskrats. Muskrat remains were found in only 3 of 11 mink scats examined in mid-November, when the freeze-up crisis was just beginning; but 9 of 18 scats examined in early December and 15 of 19 scats examined for the last of December and the first week in January contained muskrat remains. By the middle of January, the minks were no longer visiting the dead muskrat lodges, but foxes were showing interest in them. Three of five mink scats deposited during the first half of March contained muskrat remains — representing two individuals whose bodies were thought to have become available to the minks with the spring thaw.

By early April, 1956, water was again covering about half of the bottom and, by mid-May, about three-fourths, or all of the deeper parts. Less than a month later, the entire marsh bottom was drought-exposed. It remained without surface water or muskrats throughout the summer and fall. It had a solid head-high growth of vegetation, with smartweeds and seedling cattails and bulrushes dominating the previously exposed mud flats.

By the spring of 1957, Goose Lake again had water over much of its bottom, and the marsh was in habitable condition for muskrats during summer and fall as well — but without muskrats. Then, in mid-October, muskrats reappeared, to build, almost simultaneously,

several groups of lodges in different parts of the marsh. The origin of the newcomers could not be traced, but it is suspected that they had come in from a large drainage ditch lying less than a mile to the west. From careful fall-to-spring estimates, it was concluded that about 35 muskrats had originally established themselves in the fair-to-good habitat that they had found available in late fall. Evidence of unauthorized human disturbance (presumably trapping) was detected in one part of the marsh in early winter, with an estimated reduction of about 10 animals; but, apart from this, the muskrat population wintered very well, despite the intrusions of three individually distinguishable minks into the lodges. No muskrat remains were found in 16 winter mink scats.

By spring, 1958, fresh muskrat signs were still to be seen in expected places, and about in expected proportions at each wintering lodge. A survival figure of about 25 would be consistent with the amount and distribution of current signs, as of the time that the ice melted. By May, however, only four territories were being maintained, including one territory judged to have been recently established by one or more recent newcomers to the marsh.