

Chapter 6

The Estherville Marsh Area, Northwestern Iowa

THE ESTHERVILLE AREA of Emmet and Dickinson counties somewhat resembles the Ruthven area, which lies to the south. It has, for agricultural Iowa, a considerable variety of glacial lakes, marshes, and sloughs. The Estherville area, too, was first observed personally in 1932, though I did not systematically work it until 1939, when it largely superseded the Ruthven area as a major site for intensive investigations of marsh-dwelling muskrats in northwestern Iowa. After 1940, I visited the area only at long intervals (once to three times a year), but infrequency of inspections was in large part offset by the cooperation given by E. M. Wogen, then of the State Conservation Commission, who made special efforts to obtain specimens and information for the study. I also received much help and information from the C. A. Barnes family who lived next to Cheever Lake — the series of marshes on which my intensive studies were mainly centered.

The 282 acres of state-owned property known as Cheever Lake was once divided, in a treatment of mink predation upon its muskrat occupants, into the Main, Northwest, and Northeast marshes (Errington, 1943). For purposes of the present chapter, further subdivision and the inclusion of certain outlying wetlands is desirable because of the complexity of the population data obtained for 1939. This was a year of complications imposed by a summer and fall drought upon heavy populations of muskrats.

In Figure 6.1, the once-designated Main Marsh may be subdivided into Central Marsh and Southeast Marsh, which are adjacent bodies. Central Marsh is the largest and deepest of the whole Cheever Lake series, totaling about 180 acres characteristically covered by thin to moderate stands of hardstem bulrush (*Scirpus acutus*) and with parts of its numerous bays grown heavily to cattails, wild rice, sedges, reeds, and yellow water lilies. Southeast Marsh, perhaps 15 acres in area,

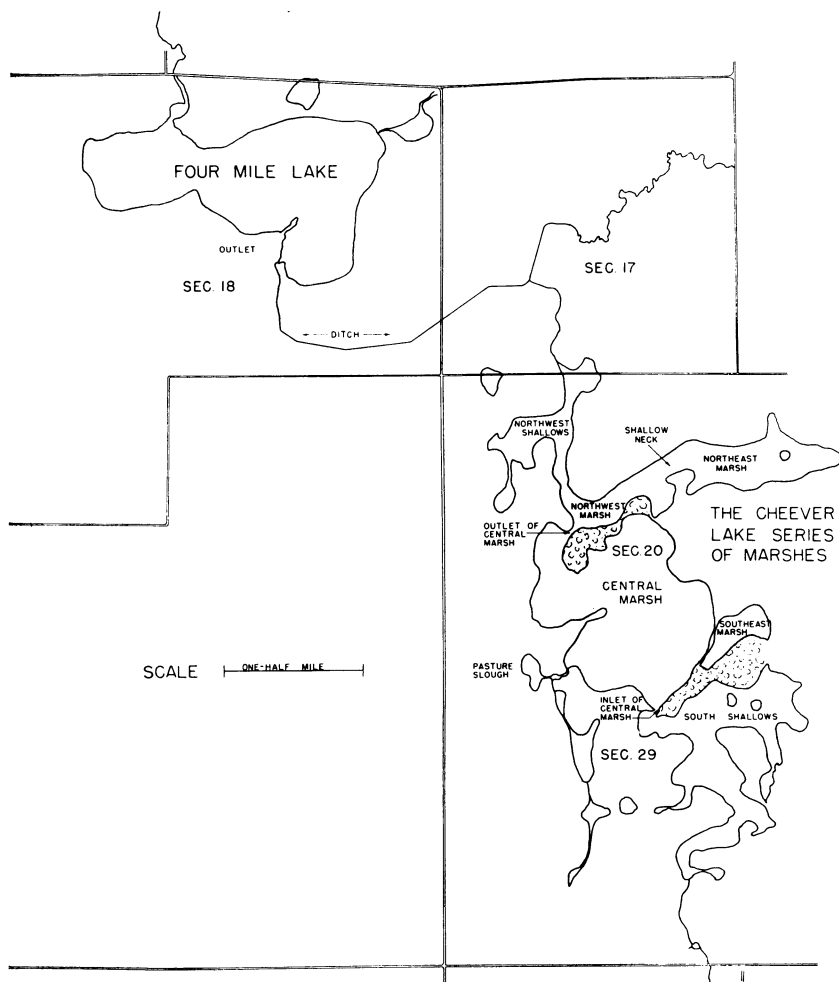


Fig. 6.1. Map of Cheever Lake and Four-Mile Lake and associated wetlands, near Estherville, northwestern Iowa.

is shallow, with an irregular open-water center and heavy marginal growths of cattail and burreed; it is separated from Central Marsh by a narrow strip of land, which is in part an ice-ridge. To the south of both Southeast Marsh and Central Marsh, and connected to the latter, is a 67-acre tract, partly in private ownership and partly state-owned; it may be referred to as the South Shallows. West of Central Marsh and separated from it by a few hundreds of yards of cultivated land and pasture is a small pasture slough. Northwest Marsh, of about 29 acres, is connected to the northwest corner of Central Marsh by the outlet channel from the latter; it is mostly quite shallow, lined by cattail, bulrush, sedge, and burreed fringes. Northeast Marsh is separated from a northeast lobe of Northwest Marsh by a neck that

soon goes dry as the water level recedes; it is about 44 acres in area, long and narrow in shape, and with burreed, cattail, and other marshy emergents surrounding an open-water center. Another marsh, Northwest Shallows, privately owned and 30 acres in area, extends to the west and northwest of the state holdings and is connected during high water with a northwest lobe of Northwest Marsh; it usually has excellent food resources for muskrats in its cattail and bulrush growths but is among the first to go dry in the Cheever Lake series of marshes.

Water levels of the Cheever Lake series varied much from year to year, from complete drought exposure to the maximum permitted by natural drainage in wet seasons. Stands of wild rice bordering Central Marsh varied as water levels changed, and species of *Scirpus* gained and lost dominance locally over the years. It could be seen that, prior to 1939, stands of river bulrush (*Scirpus fluviatilis*) grew and declined in the centers of Northwest and Northeast marshes and in shallow water at the north end of Central Marsh.

Most of Cheever Lake was a wildlife refuge in the early years of the study, only the southernmost part being open, in season, to hunting and trapping by the public. In 1942, the entire state-owned area was reclassified as Public Shooting Grounds, and all of this was likewise subject to legal trapping except on temporary fur-refuge units.

Cheever Lake in its aggregate of marshes has long been known as a muskrat marsh. It had sufficiently heavy populations in 1935 to incite agitation for opening the refuge to trapping and to cause the State Conservation Commission to suggest that investigations of the muskrats be conducted there. The muskrats did not actually build up without suffering human exploitation, for the refuge — situated in a four-section block of land, away from roads — was much violated by spearers, if not trappers, operating at night. At any rate, it had a great many muskrats for years.

Four-Mile Lake, 219 acres of state-owned Public Shooting Ground situated about a mile and a half northwest of the Cheever Lake series, was kept under limited observation as a check area. Occasional visits also were made to the High Lake and Mud Lake chain of waters east of Wallingford and to some in the vicinity of Spirit Lake, as well as to other wetlands within a radius of about 20 miles of Cheever Lake.

THE INTENSIVE STUDIES OF 1939 IN THE CHEEVER LAKE SERIES OF MARSHES

Following dispersal from wintering quarters in March and early April, 1939, the young-producing spring population of the Cheever Lake series of marshes was recorded as the equivalent of 332 pairs on 380 acres: 48 pairs on South Shallows, 28 on Southeast Marsh, one on the pasture slough, 16 on Northwest Shallows, 69 on Northeast Marsh, 41 on Northwest Marsh, and 129 on Central Marsh. Data on numbers of locally resident adult females not producing young in 1939 are lacking, but, if we assume that these comprised 5 per cent of the total — a figure not out of line with data obtained elsewhere — we would

get a total of 347 adult females, or, in round numbers, about 350. Applying a ratio of 55 per cent males, we would get a total of about 430 of that sex. The total adult population, as of the time of establishment of breeding territories, would then be about 780.

Carcasses of four adult muskrats dying between late March and late April were found, all in shore zones. One of these could have been a victim of the hemorrhagic disease worked with in later years but not specifically identified as early as 1939. The written description of this specimen now suggests visceral hemorrhages. Two of the other three had the appearance of transients killed by minks, and eight of twenty-one contemporaneous mink scats contained muskrat remains. The local mink population was quite low: a female with her family of young and possibly one or two adult males.

The most intensive field work was begun on July 15, by which time the water levels were low. The shallower parts showed much territorial adjustment, extension or modification of home ranges, and some outright abandonment or depopulation of given tracts through mink predation upon drought-exposed family groups.

A maximum postbreeding population of about 4,200 adults and young was estimated on the basis of the Cheever Lake data at hand, as of the middle of June. Of 62 litters for which the times of birth were recorded, 3 were born in the first half of April; 9, second half of April; 10, first half of May; 9, second half of May; 22, first half of June; 6, second half of June; 1, first half of July; and 2, second half of July.

By late fall, truly resident muskrats remained on the partly wet Central Marsh and, to a lesser extent, on the dry Northeast and Northwest marshes. Wanderers at times discovered and lived in abandoned lodges and burrow systems of dry marshes, but these may be ignored in population computations. The 1939 fall summaries arrived at for the three still-occupied marshes were about 1,680 muskrats for Central Marsh and about 53 and 32 for the Northeast and Northwest marshes, respectively, or a grand total of about 1,765.

The main marshy components of the Cheever Lake series are grouped for convenience of treatment.

South Shallows and Southeast Marsh

Only four acres of the South Shallows remained covered with water on July 23. The wet tract lay south and southeast of the inlet to the south end of Central Marsh and had five functional territories. Farther to the east and south, the marsh bottom had been so long exposed that five former breeding territories were completely depopulated and 20 others were recognizably near abandonment. About half, then, of the original 48 territories of the South Shallows were already lost or seriously impaired. Mortality was noted in five places. The specimens examined were of young of one month to two and a half months of age and dead since before the middle of July.

Late July brought an intensification of the drought crisis here.

Decided changes in the amount of water in sight were recorded even in the space of days, July 23 to 27. August rains (including one rain of four and a half inches) reflooded most of the marsh bottom by the end of that month, but the bottom was wholly exposed again before October.

An inspection on September 29 revealed that many wanderers were living in South Shallows from 200 yards to a half mile from the inlet of Central Marsh — most signs being light, superficial, and distributed with little reference to given lodges — most being, in fact, in dense vegetation along shore. A few animals were digging and heaping dry vegetation as if they intended to stay. Nearer the inlet were two well-maintained lodges and heavy general signs. An estimated 20 muskrats lived here at this time. Evidence was also seen of somewhat more muskrats living out in the adjacent south part of Central Marsh than could logically be accounted for in terms of Central Marsh territories and the young produced there.

At this time, nearly all of the muskrats scattered over the dry South Shallows were adults, as were a number of wanderers congregated along a quarter mile of the south shore of Central Marsh, on both sides of the inlet. A considerable proportion of the young from several South Shallows territories near the inlet evidently succeeded in establishing themselves between late July and the middle of September in the deeper waters of Central Marsh lying a convenient distance to the north; and these seemed to be about all of the muskrats of the South Shallows escaping the lethal consequences of the drought.

By the last of October, the signs of both wanderers and residents were much reduced in South Shallows, and there were fewer wanderers trying to live along the south shore of Central Marsh. A passageway through the dry inlet continued to be well-beaten, however. The single dead animal examined was of an adult male, bitten under a kidney by another muskrat. Seven of 11 contemporaneous mink scats contained muskrat remains. By November 18, practically all of the living muskrats of South Shallows were localized and "dug in" about 200 yards southeast of the inlet. Scattered wanderers remained alive until the cold weather of January, 1940, or later. Spring thaws exposed muskrat nests and tunnels in roadside snowdrifts nearly a mile to the south.

The pasture slough with the lone territory (which lay northwest of South Shallows and west of the southwest corner of Central Marsh) dried up early in the summer, but it had living young as late as early July. It was in the last stages of abandonment on July 23 — though abandonment may have been due as much to trampling of lodges by livestock as to the drought exposure, itself.

The situation at Southeast Marsh was rather like that of South Shallows, except that the drought crisis came later in the summer. All of the 28 original territories of Southeast Marsh were functional in mid-July, though many were by then partly drought-exposed. This resulted in considerable local readjustment and some known mortal-

ity. A newly-weaned young muskrat found on shore was a mink victim, and a single mink scat contained muskrat remains. By late July, evidence could be seen of a substantial drift of both adults and young from the west side of Southeast Marsh for distances up to 300 yards into the adjacent waters of Central Marsh. By late August, the movement became quite pronounced, and, by the first of November, scarcely any muskrats were left as residents along the west side of Southeast Marsh.

Studies of the above movements were made in some detail. Eight family groups living in Southeast Marsh along or near the strip of land separating that part from Central Marsh included in their original home ranges the adjacent stretch of Central Marsh. This left them in a position to move considerable distances into Central Marsh without trespassing. Apart from this transfer of family groups, numerous young from 13 other Southeast Marsh territories lying within about 200 yards of Central Marsh moved into the latter from late July to early September — mostly in late July as the water receded.

Some adults of the 200-yard zone lying nearest to Central Marsh did not extend their home ranges into the latter. These animals, plus animals of all ages living in Southeast Marsh outside of the 200-yard zone next to Central Marsh, were living by late August and September much where they had been in early and midsummer, except that they mostly abandoned the lodges in favor of trails, nests, and burrows in the dense vegetation fringing the banks.

A strife-torn live adult was seen hiding in the vegetation between Southeast and Central marshes on July 29. A probable mink victim of about five weeks of age was found August 28, and five of six fresh and recent mink scats contained muskrat remains. Despite their patent vulnerability, many of the Southeast Marsh muskrats maintained themselves in their original home ranges and territories for weeks after the disappearance of the surface water. As late as September 29, the numbers still alive farther than 200 yards from Central Marsh were judged from signs to be but slightly fewer than the numbers surviving August there.

The further decline of Southeast Marsh muskrats occurring in October represented little successful re-establishment elsewhere. There were in November passage trails across the marsh to the shore of Central Marsh and typical evidence of last-stage occupancy in places where muskrat signs had been conspicuous in September. On November 1, an animal was witnessed making a 140-yard journey across the mud bottom of the center of Southeast Marsh. A freshly dead adult male was found lying on its stomach, its back covered with muskrat-inflicted wounds and muskrat feces. The ultimate depopulation of Southeast Marsh took place, as in the South Shallows, with winter-killing or departure of the last wretched wanderers.

Northwest Shallows, Northeast Marsh, and Northwest Marsh

The heaviest drought losses by midsummer on the Cheever Lake series occurred in Northwest Shallows, dry since late May. A note of

July 16 describes the massing of most of the living animals (nearly all adults or of adult sizes, the remnant population of 16 original territories) in perhaps five acres of dense burreed and bulrush at the extreme west edge of the marsh. The animals were living in a food-rich place crisscrossed by trails; they improvised nests for shelter where convenient; and they were largely independent of the lodges formerly used. In the center of Northwest Shallows, a single territory continued to be maintained, and four lodges near by (one having a dead adult outside) showed limited use. The whole east half of Northwest Shallows, or that nearest a dry channel leading to one lobe of Northwest Marsh, was muskrat-vacant. The channel itself had only old signs, as if many animals had moved out weeks earlier. On July 23, a six-weeks young, which could have come from the Northwest Shallows as logically as from anywhere, was seen flattened at a road intersection about a quarter of a mile to the northwest.

By the last of August, massing in the west half of Northwest Shallows was no longer apparent, but muskrats did live in certain old lodges and in some lodges newly constructed on the dry marsh bed. The signs suggested transients more than persistent residents, as individuals stayed about a given lodge for but a few days at a time. By the last of September, what were probably the true remnants of the Northwest Shallows population were hundreds of yards to the south, massed at the edge of the then dry lobe of Northwest Marsh, nearest the channel constituting the natural passageway between the two marshes. The signs of these massed animals were restricted (as earlier they had been in the west half of Northwest Shallows) to dense vegetation furnishing cover as well as food.

In Northwest Shallows, an old male was found dead on September 29. The signs indicated that it was a transient that got into trouble with the single other muskrat present. From November to midwinter, the muskrats of which signs could be seen on occasion were evidently wanderers. Before spring, Northwest Shallows ceased to be the habitat of living muskrats.

Northeast Marsh originally had 69 territories in 1939. It became, in effect, partly isolated sociologically as the drought crisis progressed. Territories of the elongated marsh tended to be distributed near shore, side by side, in a way permitting extensions toward the deeper center without undue trespassing on property rights of animals occupying the neighboring territories. In contrast, the territories of a shallow bay abutting the junction between Northeast Marsh and Northwest Marsh tended to be circular in form and packed into a dense block of burreeds and bulrushes. No considerable movement on the marsh bottom was here possible without crossing territorial boundaries. The occupants generally stayed where they were, in a sense imprisoned and enduring far more drought exposure without readjustment than did their more freely-moving fellows living to the east. The jammed-together territories (twenty-one in all and, except for those bordering the open water, localized in no more than five or six acres of vegetation) formed an evident obstacle to either footloose movements or to

orderly extensions of home ranges from the west end of Northeast Marsh to the adjoining lobe of Northwest Marsh. That the muskrats were crowded is illustrated by my witnessing, on July 28, thirteen muskrats (an adult, a subadult of about three and a half months, six young of about three months, and five young of about seven weeks) leaving a loosely constructed small lodge when it was opened for examination.

The muskrats resident in the crowded junction were not drought-exposed for as long as were those of the shallow east end of Northeast Marsh, and they had access to equally good if not better growths of food plants. Nevertheless, primarily because of their population tensions and fewness of alternatives of action, they were subject to greater crisis at given stages of the drought.

In Northeast Marsh away from the crowded junction, one territory was abandoned without compensating extensions or adjustments, and three others were badly deteriorated, as of July 20–21. In the junction, itself, opportunistic minks cleaned out an exposed territory and heavily raided three neighboring ones. Six victims between six and 10 weeks of age were found in the drought-exposed lodges. An early-July lot of 28 mink scats from the wetter parts of the marsh contained no muskrat remains, compared with representations of this prey in 11 of 46 scats deposited mainly in the drying junction. From the middle of to late July, 20 of 40 scats from or near the junction contained muskrat remains.

What seemed to be massing of Northeast Marsh animals east of the territorial blockage at the junction was observed as early as July 28. The August rains relieved the crisis at the junction temporarily, and, on August 28, the population there looked much as it had a month before. Eight of 17 mink scats for August contained muskrat remains, mostly denoting close scavenging by the minks — large quantities of bone splinters, tail bones, muddy fur, and debris in the scats. The vulnerability of the occupants of the junction did not appear to be as acute as it had been in late July.

By September 28, the junction was again drought-exposed. An adult female was found dead in a sitting position, too putrid to reveal cause of death; it was thought at the time to have been a strife victim. A subadult partly eaten by a mink was found just west of the junction. Eight of fifteen September mink scats contained muskrat remains.

The muskrats were not at this time wholly comfortable in the more favorable parts of Northeast Marsh — an adult male was found dead with muskrat-inflicted wounds — but these parts showed a great deal of evidence of residents “digging in” rather than attempting to move out. Of course, there was some cross-country movement out of here as well as from other drought-exposed places. Farmers living on surrounding land told of encountering muskrats everywhere in the fields. Territory-by-territory estimates totaled 53 resident muskrats for Northeast Marsh, as of September 28. By November 1, the situation was little changed so far as the dug-in residents were concerned,

except that winter was approaching. One of three fresh and recent mink scats contained remains of a small "kit" muskrat. By November 19, there may have been somewhat fewer muskrats than on November 1, but surely the losses in the interim had not been heavy.

In early January, 1940, it was seen that poachers were violating the dry Northeast Marsh. They dug out some of the best lodges and left no muskrats alive in about half of the area of the marsh. Two animals found dead were a subadult dying of strife wounds and an adult female killed by a mink. C. C. Lille and L. D. Wright (State Conservation Commission) and I took seventeen muskrats as specimens from still-occupied habitats: four adult males, four adult females, seven young males, and two young females. Four of these specimens had fresh or recent strife wounds, and five others had older healed wounds. The animals ranged in condition from thin to fairly fat, with the majority being lean but in good shape and having fed upon shoots and rootstocks of burreed. The adult females had countable placental scars for the 1939 breeding season. From these, it could be seen that two of the animals had conceived two litters each and that the other two had conceived three litters each.

The evidence suggested that about a half-dozen muskrats survived the winter of 1939-40 on Northeast Marsh.

The drought chronology of Northwest Marsh was similar to that observed for Northeast Marsh, but Northwest Marsh had decidedly the poorer food supply over most of its area. Hence, its 41 original breeding territories were rather restricted to a fringe of cattail, burreed, bulrush, sedge, iris, cordgrass, and the like. As this border zone became drought-exposed, the muskrats had the alternative of erecting lodges for living quarters in the deeper water of the center (where little food except duckweed was obtainable) or remaining in their drying burrows and lodges closer to the good food. Many muskrats moved into the wetter parts to live but "commuted" to feed near shore.

It happened that the deepest part (and one of the richer from the standpoint of food) of Northwest Marsh lay adjacent to the junction with Northeast Marsh, and a certain converging of local muskrats here further reinforced the barrier to through passage presented by the close-packed territories of the Northeast Marsh on that side of the junction. This converging was a response of muskrats originally living in well-defined territories of the surrounding shore zone. As the population worked toward the central water, territorial boundaries coalesced until they were no longer perceptible, and the center became essentially common range. Even so, the muskrats establishing themselves nearer the center (the equivalents of 16 families) comprised something of a sociological unit, the members of which displayed tolerance toward each other's presence and activities. On the other hand, there was no reason to think that any significant numbers of outsiders were tolerated, except perhaps some young moving in from late July to September.

Massing of former residents of Northwest Shallows in the connec-

ting lobe of Northwest Marsh also appeared due in part to an abundance of local animals (the equivalents of seven families) in residence in the outer edge of this lobe. This outer edge had a dense cattail growth and, accordingly, some of the most attractive food on the marsh. The outlet from Central Marsh had a still more extensive cattail growth with muskrats (the equivalents of four families) in it, but these muskrats were not especially crowded — although it was true that two of the Central Marsh territories discouraged the passage of strangers through the outlet until September.

When, in late September, the outlet territories lost their identity, movements without effective impediment took place over common trails from the south part of Northwest Marsh to the edge of Central Marsh lying to the south. And when there was a backwash of the transients massed about the outlet of Central Marsh, large numbers congregated in the outlet cattails and in the adjacent cattail growths of Northwest Marsh.

The most conspicuous July and August losses at Northwest Marsh were noted in or near the crowded junction with Northeast Marsh and may be identified with the general crisis there. Two long-exposed lodges were dug out and their occupants collected, July 28: two adult females and four young aged from five to about ten weeks.

Another site of losses was in the shallow cattail-grown part of Northwest Marsh between the outlet from Central Marsh and the channel leading to Northwest Shallows. A mink-killed young less than a month old was found in mid-July and six of seven mink scats contained muskrat remains. The respite afforded by the August rains was such that, by the end of that month, the muskrats were living in the cattails much as they had been a month before — except for the massed transients from the Northwest Shallows. The transients somehow disappeared, probably to engage in cross-country wandering. The less populated sides of the marsh, with their inferior food supply, also had muskrats in late August about as they had in late July.

September brought the real changes. By its end, the animals originally blocking movement through the junction of Northwest Marsh with Northeast Marsh had largely abandoned the junction, though by late August the blockade had looked stronger than ever. Following this partial abandonment, the signs of seemingly footloose individuals appeared in increasing quantities for a time, and this was observed in many places about once-abandoned lodges and burrows for the whole length of Northwest Marsh. The disintegration of so many territorial boundaries and the pouring of massed transients through the junction was traced back to about the middle of September. Contemporaneously, the territories of the outlet either broke down or were bypassed (evidences of both were noted), and the massed muskrats overflowed into and about adjacent Central Marsh, to the accompaniment of clashes with the residents.

During the month of October, the greater proportion of those muskrats invading Central Marsh via its outlet withdrew to the

heavy cattails of the outlet and the south and southwest edges of Northwest Marsh. Not only were the residents of the invaded part of Central Marsh savagely intolerant, but the yellow waterlily and miscellaneous shore growths of that place were also less attractive than the food supply remaining for muskrats in Northwest Marsh, lack of surface water in Northwest Marsh notwithstanding.

Little that could be called peace existed for the Northwest Marsh muskrats after early September. They were drought-exposed, mink-hunted, and strife-torn. Mortality noted for September and October included four adults and three young, of which one young was a mink victim. Four of five mink scats contained muskrat remains. Feeding upon an adult or subadult by another muskrat was revealed by muskrat scats made up of muskrat fur. Two muskrat specimens were collected: a young female in good condition and without wounds and a wandering adult female having abdominal strife wounds infested with maggots.

A population estimate of about 32 was made for Northwest Marsh on September 28, and, except for the backwash of transients from the outlet of Central Marsh, the numbers of animals staying there seemed not to change importantly in November and December. Two specimens collected in January were adult males, one in fair shape and without wounds and the other thin and strife-torn. The backwash of transients disappeared, presumably to wander cross-country and to spread along the shores of Central Marsh.

Later in the winter, all the muskrats of Northwest Marsh either died or left.

Central Marsh

With its deeper water and a fair food supply and its location in the midst of outlying drought-exposed marshlands, Central Marsh attracted many newcomers during the late summer and fall crises. As previously indicated, however, it was not exactly a haven for the needy, and desperate strangers were greeted by teeth of the residents. Residents died, too, as the drought worsened. Indeed, the numbers of residents dying or leaving far exceeded the numbers of muskrats successfully coming in to establish themselves.

By mid-July, two territories of the original 129 had been depopulated without compensating gain elsewhere, and many others showed deterioration, adjustments, and movements from drying to wetter parts of the same territories or home ranges. Along the southeast shore, a row of territories extended into both Central Marsh and Southeast Marsh from the strip of land separating the two. As was also brought out earlier, movements by the occupants of eight territories took place here without apparent difficulty, from drying Southeast Marsh into wetter Central Marsh; and the latter marsh absorbed most of the young reared in 13 other Southeast Marsh territories. The territories here and along most of the shore zone of Central Marsh were of the elongate type extending from bank burrows out into the marsh, side

by side; they permitted much more freedom of movement as the shallow parts became drought-exposed than did territories of the circular type that were crowded together.

The Central Marsh circular territories that were close enough together to impede deep water adjustments were chiefly at the northwest corner next to the outlet leading to Northwest Marsh and in a shallow tract a few hundred yards east of the outlet. These not only imposed problems upon those muskrats trying to live in circumscribed home ranges but also discouraged movements of the fall transients massed in or about the outlet.

As exemplifying what might be expected of an elongate territory, there were, in mid-July, dry and abandoned lodges on an exposed mud flat 80 yards from the water's edge, and, 100 yards out in the water, a nest used by the family group. Temporary structures were strung out in between. Trail signs between the abandoned lodges and the new nest reflected the gradual, unimpeded changing of living quarters in response to exposure of the shore zone. Feeding and other activities of adults and young continued to be noted along this trail for some time after the major adjustments were over.

In contrast, two blocked-off territories in the dry outlet had evident family groups that stayed where they were despite long drought exposure, living in barely moist burrows or in nests in the vegetation, digging in the powdery bottoms and fighting the newcomers from Northwest Marsh. These occupants of the dry outlet held recognizable territories until they, in the second half of September, either left as wanderers themselves or were overrun by the animals massing to the north.

In a shallow tract east of the outlet, a stretch of about 600 yards of poor shore-zone habitat crowded with muskrats (27 territories) was separated from superior deep-water habitat (lying 300 to 400 yards out from shore) by 11 strong, well-used territories. Immediately to the east of the crowded stretch there were no blocking territories between shore and deep-water bulrushes, and here the occupants of 4 shore territories patently "commuted" distances of 200 to 300 yards out to the richer feeding grounds.

The maximum summer population of Main Marsh must have been around 3,000 muskrats of all ages. Considering the numbers involved, nothing very exceptional happened to this population until July. It had some of the troubles attendant upon high densities, manifested in part by slackening of breeding in June. A single runty young that looked like a sufferer from the deadly *Trichophyton* skin disease (see Chapter 5) was observed on July 17. On July 22, while opening a few deep water lodges, I found a young of weaning size dead from unknown cause. Another dead, this one of about five weeks, had a muskrat-slashed face. These samples of data suggest much adjustment mortality taking place unobserved before the beginning of the intensive studies in the middle of July. By then, aggregations of adults and mixed sizes of young could be seen on rush rafts, similar to those

seen late in or after the breeding seasons during the high-density years at Round Lake.

Of two adult males collected from deep water, July 18–19, one was becoming sexually quiescent. Of three adult females collected, one had not conceived in 1939, one had had its last young early in the summer, and one had had its last young probably about the middle of June.

A shore territory in late stages of abandonment was dug out July 25 and its population remnant collected: an adult male and two young of about seven weeks. A young mink victim was found near shore. Two other dead muskrats were found in dry lodges, including a recognized adult. Remains of a young muskrat were found in a horned owl pellet, though the local horned owl diets were running almost entirely to marsh birds.

Away from the southeast shore and the route of ingress of muskrats from Southeast Marsh, young muskrats were known to drift into Central Marsh during late July, August, and the first half of September, chiefly via the natural inlet and outlet. The young thus attracted to the deeper waters in substantial numbers were essentially the offspring from a total of 35 breeding territories of South Shallows and Northwest Marsh that were situated within 200 yards of Central Marsh.

Late summer movements of young animals about drying territories situated farther than 200 yards from Central Marsh appeared to be more random, with an unmeasured but probably minor ingress into Central Marsh occurring in connection with cross-country wandering.

The August rains had the effect of prolonging the late July status of the Central Marsh muskrats until about the middle of September. Adjustments within shallow water territories were noted, many young animals (whether locally reared or not) moving toward the central bulrushes, there to sit around on floating nests. In one place, the muskrats that had stationed themselves between 150 and 200 yards from shore in late July moved several hundreds of yards deeper into the marsh during August. Large-scale remodeling of lodges and bank burrows was also carried on while the benign living conditions of August prevailed.

A local population crisis resulting from the heavy southward invasion of drought-evicted muskrats via the outlet was at its height by late September. On the evening of September 27, around 30 muskrats per acre were counted in the five acres of Central Marsh lying nearest the outlet. This might be judged a top-heavy concentration of adults and subadults anywhere, the more so here because of shortage of good food and because of acute population tensions. The peripheries of the marsh, where residents and invaders most frequently met, were scenes of continuous conflict — sometimes fights could be seen simultaneously in different places.

In this tract, the signs indicated that the resident animals tended

to avoid the shore which was practically taken over by the invaders for several hundreds of yards on both sides of the outlet. This rather characterized the behavior of residents even when the better food was on shore. Insofar as it was restricted to the stretches of shore dominated by strangers, it may logically be interpreted as the behavior of animals desiring to stay out of trouble.

The unhappiness of the invaders is evinced by their withdrawal in October from the most congested and strife-ridden shore of Central Marsh, back through the outlet into Northwest Marsh. However, many transients still continued living along the shore of the northwest corner of Central Marsh well into November. Four of five specimens collected from this group, November 18–19, were battered adults. In the fall, the corn fields lying northwest of the marsh had conspicuous numbers of wandering muskrats that might be attributed in large part to the backwash from the outlet.

Further indications of the troubles of the mainly shore-dwelling invaders were the following: 12 individuals found dead here from late August to November 19 included at least 6 adults and were mostly victims of intraspecific strife. Two of the 12 died in ways that now suggest the hemorrhagic disease. Two subadults were killed by minks, and 22 of 40 contemporaneously deposited mink scats contained muskrat remains. And much traveling of muskrats on the ice of late fall was noted.

Adults resident on Central Marsh by late fall were the occupants of 112 summer territories that either remained functional throughout the drought or were restored by the adjustments at the southeast part. Of 75 residents taken for specimens in early January, 1940, by Lille, Wright, and myself, 4 were adult males, 5 adult females, 44 young males, and 22 young females. The ratio of 13.2 young per surviving female included immigrant as well as locally-reared young. The statistical adequacy of such a small sample might be questioned, but it probably is fairly representative, judging from our other data on sex and age ratios from northwest Iowa marshes similarly affected by the 1939 drought.

The ratios from the 75 trapped residents applied to 112 territories would give early winter figures of 112 adult females, 90 adult males, and 1,478 young, or a total of 1,680 muskrats entering the winter. This figure was derived without reference to transients and nonbreeding females.

Computations of the number of young immigrating to Central Marsh and successfully establishing themselves may be attempted. Ten July specimens dug out of drought-exposed lodges — just before the late-summer centripetal drifting of young occurred — were an adult male, 2 adult females, and 7 large young, or in the ratio of 3.5 young per adult female. There were 71 dried-up territories (23 about Central Marsh itself, 25 in Northwest Marsh, 13 in Northeast Marsh, and 10 in South Shallows) from which the young moved centripetally into the deeper water of Central Marsh without being accompanied by

the adults. The 3.5:1 ratio used as an indication of the young that were present to move from each of the 71 dry territories (leaving the adults behind to die, or later to wander and then probably to die, anyway) would give a value of about 250 young in this category. The 250 subtracted from the total of 1,478 young calculated to be fall residents would leave about 1,230 young reared in the 112 successful territories of Central Marsh.

Returns, for effort expended, of the specimen trapping in January, 1940, were sufficiently poor to show that the Central Marsh population had been greatly reduced by illegal spearing known to have been carried on prior to our trapping; and it may be doubted that more than 100 animals wintered. Living conditions for these were only fair over most of the marsh, for the water levels seldom exceeded a foot and a half at freeze-up — though few signs were seen of any except evident transients being forced to come out on the ice. Most of the truly resident animals had access to bulrush rootstocks under the ice and to bullheads massed in the channels of the lodges. Twenty-seven of 66 examined stomachs of January-trapped specimens contained fish remains, in addition to bulrush material (Errington, 1941a). The Central Marsh specimens were in good flesh, but the high incidence of animal matter in their diet suggests that they were not finding easy feeding, and, in sexual development, they were about a month behind the specimens from the more food-rich Round Lake.

SUPPLEMENTARY OBSERVATIONS IN THE ESTHERVILLE AREA DURING THE 1939 DROUGHT

Four-Mile Lake had a thick border of cattails and bulrushes and a 1939 breeding density the equivalent of about a pair per 50 yards of shore zone. With no territories near the open water center, this figures out as about 100 territories for the marsh. By November, conditions looked bad because of low water, and wanderers could be seen sitting or running on the ice, but nearly all of the original territories were still occupied. The data suggest an average productivity of about 5 young per original territory, with some 200 adults remaining alive up to freeze-up and later. The total fall population of about 700 was sharply reduced by winter-kill and poaching—the legal trapping season having been kept closed to protect the drought-handicapped muskrats.

The plight of late fall and early winter wanderers was particularly illustrated by data obtained east of Wallingford, from the open water Mud Lake and High Lake. The shores of these lakes were gathering grounds for luckless adult muskrats leaving their dry territories too late in the season for successful re-establishment of living quarters elsewhere. Dr. Jessop B. Low, then of Iowa State College, noted similar behavior on the part of muskrats about open water Lost Island Lake and Trumbull Lake, near Ruthven. On the whole, such muskrats were thin and battered, living in improvised nests on shore or in holes in the ground. As cold weather came on, they died in con-

spicuous numbers from strife wounds, mink and canid predation, hunger, and exposure. Traffic victims were commonly to be seen on the main highways of the counties having many lakes and marshes.

About Mud Lake and High Lake east of Wallingford, the shore-dwelling transients were as opportunistic and indiscriminate in their feeding as one might have expected for desperate animals (Errington, 1941a). They preyed upon sluggish bullheads and Bell's painted turtles in the shallow waters over the beaches and ate away the flesh from exposed parts of the fish and turtles frozen in the ice. Frogs and clams were also utilized as available, but the most available food consisted of population-stunted bullheads, present about the lake margins in thousands, alive and dead, and fed upon accordingly by whatever hungry creatures, muskrats included, could take advantage of them.

As concerns the hungry transient muskrats of the shores, any advantages that they found there must be judged to have been only ephemeral, for they suffered near-annihilative mortality before the weather became really cold.

THE EMERGENCY YEAR OF 1940 IN THE ESTHERVILLE AREA

A survey, May 1-2, 1940, of the Cheever Lake series showed 50 well-used sets of burrows and maintained lodges that could be classed as breeding territories. All were on Central Marsh, no sign of regular use being apparent on the dry or nearly dry South and Northwest Shallows, nor on the Northeast, Northwest, and Southeast marshes. Eight dead muskrats, representing winter and spring mortality, were found: four (including a winter wanderer with a frozen tail) that had been partly eaten by minks, a male and a female dead possibly from disease, and two specimens that were too putrid to suggest cause of death. Eight of 32 mink scats contained muskrat remains.

On July 17-18, there were 34 plainly recognizable territories on Central Marsh and three in Northeast Marsh. Three others in Southeast Marsh showed signs of abandonment after having been established in late spring and early summer. At this time the marshes were drier than they ever had been in 1939, and the remnants of surface water of Central Marsh continued to shrink, to disappear completely in October.

The occupants of the three Northeast Marsh territories got along comparatively well in a dry but food-rich habitat. By October 22, after about four months of drought-exposure, signs of what could be identified as the corresponding three family groups were still distinguishable, localized as they were in widely separated places. This entire population was trapped for examination in November by Morris Hardman of the State Conservation Commission: three adult males, three adult females, five young males, and four young females. The adult females had an average of two early-season sets of 1940 placental scars averaging six scars to a set. In view of the relative isolation of these territories and the lack of passage signs leading to or away from them, the Northeast Marsh population was considered

to have been self-contained. Successful rearing of a fourth of the young conceived, or an average of three per adult female or breeding territory, may be indicative of what to expect in the north-central region when excellence of food resources may partly offset the disadvantages of an all but waterless habitat. A single July mink scat found in Northeast Marsh contained remains of a large, young muskrat. No other mortality was noted here, and the fifteen trapped specimens were in good flesh and without strife wounds.

The wetter though ecologically unfavorable Central Marsh was the scene of mounting crisis for the muskrats from midsummer to winter. Maximum postbreeding densities, as of late July, were estimated at about 400 adults and young. The local mink population was a female with her young, plus a very few adult males.

There probably was considerable loss from the hemorrhagic disease on Central Marsh, and late summer and early fall carcasses of three adults and two subadults may, without certainty, be thus assigned. A drought-exposed muskrat family suffered severely from the minks in early July, which accounted for most of the seven muskrat representations in 128 mink scats from July. No muskrat remains were found in 114 August scats, though the water level gradually went down throughout the month. Up to September, the general muskrat population responded safely to the drought by moving centripetally toward the wetter parts of the marsh. In September, several badly-situated family groups were severely preyed upon by the minks, but only two of a sample of 43 contemporaneous mink scats contained muskrat remains.

By October 21, approximately 40 used lodges on Central Marsh were concentrated in a wet area of less than six acres. This concentration appeared to follow an orderly adjustment within old territorial boundaries. Successive stages in the centripetal movement of family groups could readily be traced through lodges and nests built farther and farther out, over total distances up to a quarter mile in some cases. At the last stage of occupancy, the used lodges were in the apexes of territories shaped like long equilateral triangles extending back to the dry shore zone and its old lodges and burrows. The surface water disappeared on October 22, and the muskrats abandoned the marsh. Mass movements were also noted at about this time from marshes of similar status in the vicinities of Spirit Lake and Wallingford.

Just before the muskrats abandoned Central Marsh in October, drought-exposed and concentrated groups suffered very heavy mink predation. Of 98 mink scats examined in October, 23 contained muskrat remains. Heavy rains during the last few days of the month brought the water up to about the level of late summer, and living conditions for muskrats looked greatly improved, but, except for fewer than a dozen evident transients, freeze-up found no muskrats remaining on the marsh. None of 18 mink scats for November contained muskrat remains, but three possible mink victims among the land-

active transients were recorded. Four more transients were taken for specimens: an adult male, two adult females, and one young male. The adult females (origin unknown) had two 1940 sets of placental scars each, averaging 8.5 scars per set. An occasional transient continued circulating about the marsh and adjacent fields until early winter. By January, the depopulation of the entire Cheever Lake series of its muskrats was complete.

Neighboring Four-Mile Lake had in 1940 about 30 breeding territories, of which seven were abandoned by mid-July. The drought affected the Four-Mile muskrats less severely than those of the wetter Central Marsh of Cheever Lake. About 12 of the original territories at Four-Mile Lake were still functional on October 23 when the drought reached its greatest intensity. The fall population was calculated at about 60 animals or slightly less than the number of adults present in the spring. So far as I could determine, the marsh was minkless all summer and fall. By December, the rushes in most parts occupied by muskrats were well drifted over with snow, thus giving the animals substantial protection from cold.

Wogen obtained for examination a series of 12 specimens taken by trappers in November from Mud Lake and High Lake, east of Wallingford, where conditions were rather typical of drying north-west Iowa lakes and marshes. All except one of these specimens were thin animals, mostly shore-dwelling transients. Six of the 12 were adults, of which 2 were females. One of the adult females had 11 placental scars in two sets dating back to early in the 1940 breeding season; the second had 23 placental scars in three 1940 sets.

THE EARLY YEARS OF POPULATION RECOVERY OF MUSKRATS IN THE ESTHERVILLE AREA, 1941 AND 1942

The 1941 breeding population at Cheever Lake was of immigrant animals, exclusively, insofar as no muskrats survived the preceding winter on that series of marshes. It amounted to the equivalent of seven pairs, all localized in Central Marsh. The marsh levels were well restored by winter precipitation and remained in good condition for muskrats until midsummer, a dry spring notwithstanding.

Following another long period of more or less dry weather, a heavy rain in mid-September brought up the water to cover about two-thirds of Central Marsh. The other Cheever Lake marshes still had bottoms exposed except for puddles. The near exposure of Central Marsh in late summer did not appear to result in any particular complications for the low population of muskrats resident. By late November, some mortality was apparent. A subadult victim of a mink was seen. An adult male, in poor condition and likely a transient, was probably a mink victim, also. Four of 19 fall and early winter mink scats contained muskrat remains.

The evidence (chiefly from the 1942 spring census) indicates that about 65 muskrats wintered at Cheever Lake, 1941-42, and that the 1941 fall population may have been about 70.

Four-Mile Lake was less affected by dry weather than Cheever Lake, and its combination of food and water was favorable for muskrats throughout most of 1941. The breeding population was the equivalent of 19 pairs, or about 45 individuals. Trappers took during the open season a known total of about 140 muskrats, of which the carcasses of 81 were examined: 5 adult males, 9 adult females, 40 young males, and 27 young females. The 9 females included one that had not conceived young in 1941, 3 that had a single litter each, 3 that had two litters each, and 2 that had three litters each. From the available sex and age ratios and the reported trappers' catches, the fall population for Four-Mile Lake may be calculated as about 160, of which most of those surviving the trapping also survived the winter of 1941-42.

Wogen (letter, March 14, 1942) reported that all of the muskrat lodges on Cheever Lake and approximately half of those on Four-Mile Lake showed unrepaired mink borings. This did not appear to have any particularly lethal significance to the muskrats, for the survival of the wintering muskrats was very good. At Cheever Lake, the strongest possibility is that the muskrats simply abandoned their lodges and retired to bank burrows—which, in view of the location of their lodges (mostly within 150 yards from shore, and usually much closer), they could easily have done.

In 1942, heavy spring and early summer rains brought the water of the Estherville marshes up to high levels. At the same time, Cheever and Four-Mile lakes had their most attractive stands of vegetation which at Cheever Lake meant chiefly more and thicker bulrushes in the shallow north parts of Central Marsh. On the other hand, High and Mud lakes and associated waters east of Wallingford showed deterioration from the point of view of the muskrats.

On Cheever Lake, a 1942 breeding population the equivalent of about 35 pairs (about 75 adults) lived mainly in Central Marsh and in lodges built the previous fall fairly well out in the water. The few bank territories also were in places that showed use late in 1941. A total of 491 muskrats was reported trapped by the public in the late fall of 1942, of which the carcasses of 191 were collected and sent to me by Wogen. This sample consisted of 12 adult males, 11 adult females, 93 young males, and 75 young females. A fall density of about 660 may be calculated, assuming that adult losses had been immaterial (as they seemed to have been) during the breeding season and that no great amount of movement took place into or away from the marshes. Farmers noticed muskrats appearing in September in Northeast Marsh, but this is regarded as merely an adjustment within the Cheever Lake series.

Of the 11 Cheever Lake adult females examined for placental scars, one had not conceived in 1942; 2 had conceived single litters each; 3, two litters each; 3, three litters each; and 2, four litters each. The seasonal chronology of the above 25 sets of placental scars: 10 in spring and early summer, 10 in midsummer, and 5 in late summer.

The 1942 data on breeding densities at Four-Mile Lake are too inferior to permit satisfactory expression numerically. From the sparseness of signs (of only three territories) seen during an inspection of a half-mile of the best shore zone on June 12, and the wintering figure of about 20 previously calculated, an estimate surely not much in excess of the equivalent of 10 pairs may be made. But the trapping catch for late fall, 1942, was reported to Wogen as 429! A sample of 93 carcasses was sent to me for examination: 6 adult males, 7 adult females, 45 young males, and 34 young females.

Unlike the appraised situation at Cheever Lake in 1942, a heavy late summer and fall movement of mixed-age animals is believed to have taken place into Four-Mile Lake, via its outlet, from a drainage ditch near by, to bring the pre-trapping population up to between 700 and 800, probably nearer the former. Whether they were born and reared on the marsh or not, the 80 specimens of young included 9 or 11.3 per cent "kits" or probable August young. And, whatever its origin, the sample of 7 adult females included 2 that had conceived a single 1942 litter each; 2, three litters each; and 3, four litters each. Of the 20 sets of placental scars, nine were assigned to spring and early summer; six, to midsummer; and five, to late summer.

Similarities in the 1942 data from Cheever and Four-Mile lakes may lead one to ask whether there may not have been substantial though undetected ingress into Cheever Lake in late summer and fall, as well as that indicated for Four-Mile Lake. Probably there was undetected movement into Cheever Lake from its environs. However, Cheever Lake was more out of the usual routes of travel of muskrats leaving the ditches. Then, again, the spring densities, as recorded, were not nearly so much out of line with the trapping season catches at Cheever Lake as at Four-Mile Lake.

THE HIGH-DENSITY YEAR OF 1943

The spring of 1943 was one of exceptionally high breeding densities, not only in the good habitats of Cheever and Four-Mile lakes, but also in the food-poor waters of the High Lake-Mud Lake series where the animals were practically restricted to the banks. In the latter series, samples of lake shores looked over in May had functional territories distributed at about 100-yard intervals.

The Cheever Lake breeding densities recorded for the spring of 1943 were only about half those of the first high-density year studied, 1939, and amounted to a total equivalent of 180 pairs. These were distributed as follows: 27 on South Shallows, 7 on Southeast Marsh, 15 on Northeast Marsh, 23 on Northwest Marsh, 8 on Northwest Shallows, and 100 on Central Marsh. This, on the basis of 55 per cent males shown by the 1942-43 trapped specimens, would give a total of about 400 adult muskrats. The population appeared to be secure, for, in walking the shores in late May, I found no remains of spring transients, and none of 13 fresh and recent scats from a large mink contained muskrat remains.

Plans for an experimental fur-refuge system were worked out with Wogen, and three areas were designated as those to be closed to trapping in the fall. One was about fifteen acres in area in the Northeast Marsh, selected as having the best combination of water and food for wintering muskrats. Another of approximately the same size was set up in the deeper part of Central Marsh. The third, of about twelve acres, included the south part of Central Marsh and the north, or deepest, part of the South Shallows.

The 533 trapped carcasses that Wogen sent me from Cheever Lake in November, 1943, consisted of 32 adult males, 34 adult females, 292 young males, and 175 young females. Wogen and I thought that the summer losses of settled adult females had been negligible; hence, the age and sex ratios of fall are applied without correction to the figure of 180 territories obtained for the spring. This, prorated, would give 180 adult females, 169 adult males, and about 2,414 young of the year, or a total of about 2,763 for the November pre-trapping population.

The reported catch was 2,352, and Wogen (letter, February 5, 1944) did not believe that a night of poaching on one of the refuge tracts could have resulted in the illegal taking of more than 25 to 30 muskrats. The number surviving the trapping at Cheever Lake appeared to be in the vicinity of 400.

The uterus was lost from one of the adult female specimens. Of the other 33, 3 had not conceived during the 1943 breeding season; 3 had conceived a single litter each; 11, two litters each; 12, three litters each; and 4, four litters each. The seasonal chronology of 77 sets of placental scars: 39 for spring and early summer, 30 for midsummer, and 8 for late summer. Thirty-one "kits" (August-born or later) were listed among the 467 young of the year, or 6.6 per cent of the total, compared with 4 or 5.2 per cent of the placental sets assigned to August.

Four-Mile Lake had in 1943 a breeding population the equivalent of 165 pairs, or (using the 55.4 per cent of males found for the 1942-43 carcasses) a total of about 370 adults. As at Cheever Lake, summer conditions were favorable at Four-Mile Lake, and no mortality was recorded. A fur-refuge of about 70 acres was set up at Four-Mile Lake and enclosed a sizable part of the best wintering habitat.

Thirty-four young in five litters were tagged on Four-Mile Lake in 1943 (Errington, 1944). Seven were recovered during the trapping, including six members of a litter taken as subadults living close together 100 to 150 yards from where they had been tagged.

Wogen accounted for a minimum of 1,815 muskrats taken in the 1943-44 trapping at Four-Mile Lake and sent me 308 carcasses: 22 each of adult males and adult females, 164 young males, and 100 young females. These ratios used without corrections for the 165 territories recorded during the breeding census would give an early November figure of 330 adults and 1,980 young of the year, or a calculated total of 2,310. A population of between 400 and 450 surviving the trapping

should be as much in keeping with the evidence as any computed figure.

Four of the 22 adult females examined from the Four-Mile Lake catch had not conceived during 1943; 5 had conceived one litter each; one, two litters; 6, three litters each; and 6, four litters each. The 49 litters were chronologically distributed as 15 for spring and early summer, 28 for midsummer, and 6 for late summer. The 6 for late summer were assigned to August, and the 12.2 per cent of the total that they represent may be compared with 24 or 9.1 per cent "kits" or August young in the sample of young of the year.

Environmental conditions for muskrats at Four-Mile Lake were substantially improved in 1943 through moderate flooding of heavily vegetated shallows. At Cheever Lake, there was similar improvement, but the proportion of the marsh thus affected was decidedly less than at Four-Mile Lake. To a considerable extent, the rise in water level at Four-Mile Lake actually created a new habitat, at the same time leaving unimpaired, if not improved, the habitat previously occupied up to (or near) capacity by the muskrats.

THE BEGINNING OF A POPULATION DECLINE, 1944

Continuing high water was accompanied by some changes in the Estherville marshes. Twelve-Mile Lake, a formerly densely-grown marsh lying south of Cheever Lake, lost its emergent vegetation almost completely. Cheever Lake was less affected than Four-Mile Lake, the latter of which showed considerable thinning of emergents and, especially, loss of cattails. Four-Mile Lake, however, remained in good condition for muskrats until the failure of a dam in the summer brought about the equivalent of a drought emergency.

The 1943-44 fur-refuge experiments at Cheever and Four-Mile lakes were instrumental in protecting and wintering a reasonably satisfactory stock of muskrats. The two small refuge tracts at Central Marsh appeared to function somewhat better than the one at Northeast Marsh because their location and the bank-dwelling habits of many of their muskrats decreased the likelihood of excessive exploitation by legal trapping at their boundaries. The larger refuge at Four-Mile Lake had a long trapped boundary on one side, but the animals living in its east half were secure from the trapping. So far as our knowledge goes, the survivors of the trapping season on the refuge tracts wintered with slight loss. On the other hand, the 1943-44 trapping was almost annihilative on those parts of both marshes open to legal exploitation.

By mid-June, 1944, the equivalent of 272 breeding pairs could be distinguished at Cheever Lake: 70 on South Shallows, 21 on Southeast Marsh, 55 on Northeast Marsh, 32 on Northwest Marsh, and 94 on Central Marsh. Because of the attractive 1944 condition of Northeast Marsh and South Shallows, and the unlikeliness of many muskrats surviving in them the winter before, it is believed that these marshes drew considerable numbers of muskrats from outside the

Cheever Lake series during the spring dispersal. Such newcomers presumably came from the well-populated east end of Four-Mile Lake as well as from local creeks and ditches. Using the 1943-44 sex ratio of 60.8 per cent males, the spring breeding population may be calculated at about 700 adults.

Four-Mile Lake had a "settled" breeding population in 1944 of the equivalent of 142 pairs, or possibly about 100 animals fewer than the number judged to have wintered. The sex ratio of 60.4 per cent males in the Four-Mile Lake catch for 1943-44 applied to 142 territories would give a breeding season figure of about 360 adults.

Mortality during the summer and early fall months was conspicuous at Four-Mile Lake even before the partial drying of the marsh. At Cheever Lake, losses through intraspecific attack and unknown causes were noticeable by June, but the marshes there did not appreciably deteriorate until fall. According to Wogen, much late-season shifting — attributable to local food shortages — took place. Animals massed in the then-attractive Northwest Shallows and in a string of rich sloughs extending several hundreds of yards northward.

Wogen sent me November-trapped samples of 190 carcasses from Cheever Lake and 225 from Four-Mile Lake. The Cheever Lake carcasses consisted of 11 adult males, 16 adult females, 89 young males, and 74 young females; those for Four-Mile Lake, of 23 adult males, 18 adult females, 103 young males, and 82 young females. No adult females in either collection passed through the 1944 breeding season without conceiving. Of those for Cheever Lake, 7 conceived two litters each; 5, three litters each; and 4, four litters each. For Four-Mile Lake, 6 conceived two litters each; 8, three litters each; and 4, four litters each. The 45 Cheever Lake sets of scars were dated: 20 for spring and early summer, 22 for midsummer, and 3 for late summer. The 52 sets of scars from Four-Mile Lake: 16 for spring and early summer, 31 for midsummer, and 5 for late summer.

No information on the total 1944-45 trappers' catches from these marshes is at hand, and any estimates as to fall populations must be prorated from spring densities and the specimen data. This might not be so difficult for Cheever Lake, where the chief adverse factor seemed to be the mounting population density. Allowance for a likely spring to fall reduction of about 10 per cent of the adult females should leave about 245 of the spring-resident females still present by November. Using the sex and age ratios of the carcasses, a fall population of about 413 adults and 1,871 young, or a round-number total of about 2,300, can then be calculated.

From the distribution of the 1944 breeding territories at Four-Mile Lake, I would judge that at least 44 were hazardously situated with respect to the crisis following loss of most of the surface water. It is probable that the spring to fall losses of adult females cut the original 142 down to about 90 and that the sample of young included the increase from both functional and lost territories. The November

population would then figure out at 205 adults and 920 young, or a total of 1,125.

The fur-refuge tracts at Cheever Lake afforded muskrats better wintering in 1944–45 than did the nearly dry refuge at Four-Mile Lake, but the Cheever Lake refuges were still much less efficacious than they had been in 1943–44. The refuge of Northeast Marsh, which qualitatively was in excellent condition for muskrats in 1944–45, proved too small for the most advantageous results. At Central Marsh, the bulrushes and other emergents deteriorated in apparent consequence of high water.

THE ACCELERATION OF A POPULATION DECLINE, 1945

By late May, 1945, it could be seen that the formerly outstanding muskrat marshlands of the Cheever Lake series were deteriorating to the extent of becoming rather open water lakes and sloughs. Privately owned, low-lying pastures, which normally were too dry to afford livable muskrat habitat, now became lush marshes in their turn. The status of Northwest Shallows changed in practically a single growing season from a muskrat-vacant tract of lowland to the most populous muskrat marsh in the neighborhood.

This ecological drama, with its local variations, occurred not only in the glaciated lake areas of central and northwest Iowa but also throughout the eastern Dakotas and western Minnesota northward far into south central Canada. In the Estherville area, only Four-Mile Lake, among those inspected annually, escaped the major changes introduced by the wet years, and it was subject to changes of the opposite sort after its dam failed in 1944. As of late May, 1945, it had water over most but not all of its bottom.

The 1945 breeding density at Cheever Lake totaled the equivalent of 67 pairs: 8 on South Shallows, 6 on Southeast Marsh, 17 on Northeast Marsh, 4 on Northwest Marsh, 13 on Northwest Shallows, and 19 on Central Marsh. Application of the ratio of 52.6 per cent males shown by the 1944–45 catches would give a total adult population of about 140. At Four-Mile Lake, the equivalent of 44 pairs was recorded, which, with the 1944–45 ratio of 55.6 per cent males, would figure out at about 100 adults.

Following the environmental extremes imposed by high water in the Estherville area, the summer and fall of 1945 brought a severe drought. Wogen informed me that all except Central Marsh at Cheever Lake went dry. He was unable to obtain specimens from Four-Mile Lake, which was so muddy at the opening of the trapping season on November 10 that the trappers quit.

Of 228 trapped carcasses from Cheever Lake (mostly from Central Marsh, where the drought-concentrated population was exploited), 13 were adult males, 13 adult females, 112 young males, and 90 young females. The ratio of 15.5 young per adult female certainly reflects centripetal movements of young more than it does the mean productivity of breeding females at Central Marsh. It may be judged, from the spring location of the territories, that those of Northeast

Marsh, Northwest Marsh, and Northwest Shallows probably lost most of their adults during the drought crisis. This would leave 33 or approximately half of the initial spring population of Cheever Lake females alive and present in the fall of 1945. Actually, it may be expected that a few of the adult females of the drought-exposed territories did get over to Central Marsh to stay there and also that a few of those resident at or near Central Marsh did die or leave. The sex and age ratios of the trapped carcasses prorated from 33 adult females would give 66 adults and 512 young of the year, or a total of about 580 muskrats for the fall population.

Of the 13 adult females, one did not conceive in 1945; 2 conceived a single litter each; 2, two litters each; 5, three litters each; and 3, four litters each. The chronology of the scars (nineteen sets assigned to early summer, twelve sets to midsummer, and only two sets to late summer) parallels the tightening of the drought emergency.

No satisfactory basis exists for assigning a numerical value to the 1945 fall population at Four-Mile Lake. In view of the drought exposure and the fact that people intending to trap became discouraged even before starting, there could hardly have been more than 100 muskrats remaining by November. The survival for the winter of 1945-46 must have been negligible, in contrast with which fair numbers got through the winter on a fur refuge of about 30 acres established in the east part of Central Marsh at Cheever Lake.

THE LOW-DENSITY YEARS, 1946-49

High water conditions again prevailed in the marshes of the Estherville area by the spring of 1946. Estimates of breeding territories or the equivalent of pairs for Cheever Lake totaled 38 as of early June: 2 on South Shallows, 3 on Southeast Marsh, 8 on Northeast Marsh, 3 on Northwest Marsh, and 22 on Central Marsh. The 1945-46 ratio of 54.8 per cent males would give a total of about 85 adults. At this time, I could find evidence of only two functional breeding territories on Four-Mile Lake, but some others were probably overlooked. Nevertheless, the density surely was very low — perhaps the equivalent of a half-dozen pairs or about 15 adults.

Cheever and Four-Mile lakes were closed to trapping in the fall of 1946, so no trap carcasses were available for examination. Conservation Officer Ralph Lemke told me that there were about 60 lodges of medium to large sizes on Cheever Lake during the fall and winter of 1946-47. At 5 muskrats per lodge, the total fall population of Cheever Lake may be estimated at about 300. For Four-Mile Lake, I would estimate the fall population at between 40 and 50.

By early summer, 1947, the Cheever Lake population was still more reduced. My estimate was the equivalent of 10 pairs, or perhaps 25 adults. At Four-Mile Lake, the population seemed higher: the equivalent of about 15 pairs, or perhaps 40 adults.

The trapping season on muskrats was closed for the fall and winter of 1947-48 over nearly all of Iowa. At Cheever Lake, the water was low in the fall, with only about two and a half feet remaining in the

deepest parts of Central Marsh. Lemke made an estimate of some hundreds of lodges and feed houses on the wet marsh, and a farmer living nearby counted about 100 large-sized lodges there. As nearly as I could find out, almost no muskrats wintered on dry Four-Mile Lake in 1947-48, nor anywhere in the neighborhood of Cheever Lake except on Central Marsh itself.

Northwest Iowa marshes had unusually few signs of muskrats in late May, 1948, even compared with the preceding two years. At Cheever Lake, a check of breeding territories of two-thirds of Central Marsh on May 28, 1948, gave the equivalent of 16 pairs. Prorated, this would give 24 pairs for the whole of Central Marsh. Not many muskrats seemed to live elsewhere on the Cheever Lake series, and I think that an allowance of another dozen would be ample. The breeding population could then be estimated at perhaps 70 adults.

Lemke said that most of the Central Marsh lodges of winter were taken out by the ice in the spring and that many muskrats were then seen on shore. Whether this resulted in any appreciable population crisis may not well be judged.

The hemorrhagic disease may be suspected of being at least partially responsible for the continued unfavorable status of many muskrat populations of northwestern Iowa and northward and northwestward. Prior to 1948, no victims from this region were positively recognized, but, on May 28, two were found dead along the northwest shore of Central Marsh at Cheever Lake, of which the one in freshest condition showed typical lesions.

During another inspection trip in late September, 1948, many muskrat signs were seen about the Cheever Lake marshes, but they were irregularly enough distributed to suggest summer disease losses. A muskrat-vacant, 100-yard stretch of shore zone still could be seen where the clearly diagnosed disease victim had been found four months before. The fall population for Central Marsh was calculated with fair satisfaction at a little over 500. An allowance of another 100 muskrats for Northeast and Northwest marshes might be permissible, which would bring the Cheever Lake grand total for the fall of 1948 up to about 600.

Water and vegetation looked favorable for muskrats at Four-Mile Lake during brief visits on May 28, September 28, and October 1, 1948, but this marsh appeared to have been devoid of the animals at these times.

In early summer, 1949, Cheever Lake and Four-Mile Lake were in attractive condition for muskrats but practically unoccupied. On June 6, the east half of Central Marsh at Cheever Lake was checked over, and a single functional territory was found there. I doubt that a dozen adult muskrats were alive on the whole Cheever Lake series. I made no further inspections of the Cheever Lake area after mid-autumn, 1949. Central Marsh at Cheever Lake and Four-Mile Lake were then in good condition, but the muskrat was still barely represented as a species.