Chapter 5

The Ruthven Marsh Area, Northwestern Iowa

THE SALIENT FEATURES of the marshes of Clay and Palo Alto counties comprising the Ruthven study area have been described by recent authors (Bennett, 1938; Hayden, 1943; Low, 1945; Provost, 1948); and the locations of the principal bodies of water in relation to each other are shown in Figure 5.1, reproduced from Hayden's map.

Although most of my work on muskrats was centered on a stateowned wildlife refuge, 450-acre Round Lake, data of supplementary value were obtained elsewhere in the vicinity. Next to Round Lake, the best-studied areas included about 300 acres of Mud Lake owned by the Mud Lake Fur Farm and the potholes of a 392-acre state-owned tract known as Dewey's Pasture.

THE YEARS OF PRELIMINARY INVESTIGATIONS, 1932-34

My experience with the Ruthven marshes began in the summer of 1932. The muskrat was not at that time one of the species being systematically studied under the Iowa wildlife research program, but it did draw attention because of its relation to waterfowl habitat. During the summer of 1934, when intensive field work on the muskrats was initiated, I accomplished little more than to lay groundwork for the detailed studies of the years to follow. However, information furnished by Dr. Logan J. Bennett (letter, April 1, 1938) and Joe Kautzky, Jr. (letter, March 23, 1938) helped a great deal in piecing together the Mud Lake picture for the years preceding and following my own studies on that marsh.

Mud Lake

By 1932, when Bennett began his waterfowl researches at Mud Lake, the marsh had regained a satisfactory water level after having gone dry in 1931. He estimated a 1932 fall population of about 200 muskrats, which would appear to have resulted from a spring population of about 20 pairs.





From my own observations, I would think that the equivalent of about 100 pairs should be close to the breeding population at Mud Lake in 1933. Bennett estimated the fall population at about 1,500, a likely figure following a 100-pair breeding population on a food-rich 300-acre tract. Minks were abundant, and four females with young were recorded for the marsh during the summer. Only one of

93 May to August mink scats contained muskrat remains, but other evidence was found of fairly heavy local feeding upon young muskrats.

No legal muskrat trapping was done at Mud Lake during the fall and winter of 1933–34. By midwinter, a zone essentially unoccupied by muskrats extended out about 150 yards from shore. The shallowwater muskrats had, by then, either withdrawn to bank burrows or congregated in the deeper marsh. This zone of abandonment had hundreds of lodges and feed houses. Although most of them showed unrepaired mink borings, slight evidence of muskrat mortality was found except in one tract. There, 46 of 58 winter mink scats from lodge latrines contained muskrat remains. This high incidence was ascribed to vulnerability of muskrats trying to winter under difficult conditions, but it could have represented instead the responsiveness of minks to a local die-off from the hemorrhagic disease (Errington, 1954b). The wintering population of minks was estimated at between 8 and 12.

The breeding population of Mud Lake for the spring of 1934 was originally recorded as the equivalent of about 400 pairs, but I would now say that about 1,000 animals (including unmated males) should have been closer to the truth. There were many manifestations of crowding in the summer months, with conspicuous groups of mixedage muskrats to be seen on lodge butts and rush rafts. Dead young muskrats were frequently noticed at the dens of two female minks having young about the marsh, but remains of muskrats were found in only three of the 64 mink scats examined for the period of June through September. The 1934 fall population of muskrats at Mud Lake was calculated at between 3,200 and 3,400, of which 2,528 to 2,790 were reported trapped. (The figures on trapping catches varied with the source of information.) At any rate, the muskrats were abundant for the habitat and probably comprised an overpopulation, even if this were judged solely on the basis of the extensive "mowing" of emergent vegetation that occurred in late summer.

Round Lake

Neither data nor estimates are available for Round Lake for 1932, but, in 1933, I worked to a considerable extent on this marsh. The general breeding-season signs in 1933 were similar to those of 1936, when an adult population the equivalent of 80 pairs was actually determined. The 1933 fall signs, however, were indicative of a much higher density than in 1936 and were more conspicuous than those shown by known populations of between 500 and 750 in the falls of 1937 and 1938. The 1933 fall density was therefore estimated at about 800.

Two female minks reared families about the marsh in 1933, and a third female was found killed by another mink. Mink predation upon the muskrats was obviously light: two of 126 mink scats for June, July, and August contained muskrat remains. There is reason to think that a moderate population of muskrats lived securely in good habitat.

In 1934, Round Lake showed such evidences of overpopulation as "mowing" of emergent vegetation on a large scale. The breeding population for this year was considered a little lower than one accurately determined for 1939, which would make it about the equivalent of 180 pairs for 1934. The fall population for 1939 also affords an index that might be applied to 1934. After certain emergency losses had taken place, the fall population for 1939 was determined at less than 1,300. Insofar as habitat conditions for rather similar breeding populations had been considerably better in 1934 than in 1939, it may be judged that the fall population may have been correspondingly higher in 1934. I would say that the 1934 population should have been possibly 200 muskrats higher, or a total of about 1,500.

Three female minks with young lived around the marsh, and substantial quantities of muskrat remains were seen in the fecal deposits outside the mink dens, though no exact figures as to incidence of muskrat remains in the mink scats are at hand for June and July, the months of greatest vulnerability of the young muskrats. Two of 37 mink scats for September contained muskrat remains.

The muskrats wintering 1934-35 were not subjected to legal trapping but did suffer illegal exploitation through spearing. Remains of 14 dying in winter and early spring were found.

INTENSIVE STUDIES OF OVERPOPULATIONS, 1935

I spent the most of the daylight hours from May through July and part of August, 1935, on Mud and Round lakes. For all of the intensiveness of particular phases of the studies, methods for determining total populations for the marshes had yet to be well worked out, and figures for the over-all spring and fall densities had to be determined by less satisfactory means.

Mud Lake

At Mud Lake, a 1935 breeding density the equivalent of 0.65 pair per lodge was arrived at through close watches in sample areas. This applied to a total of 546 lodges would give 355 pairs (or adult females), and, following sex ratio data currently available from the vicinity, a total of about 750 adults, as of late spring. The latter does not have the value of a census figure, but I am unable to improve upon it. My feeling is that there were higher breeding densities in the observational samples than indicated but that error from this source could be offset by the existence of some local groups of sparsely populated lodges, especially in two shallow bays. A 1935 fall population of about 2,300 at Mud Lake would appear consistent with a reported trapping catch of 1,900.

A program of experimental tagging of young muskrats was begun at Mud Lake (Errington and Errington, 1937), and 129 young in 30 litters were thus marked from May 25 to June 23, 1935. The techniques first tried had serious shortcomings, but the tags stayed on well enough to establish the identity of certain litters (especially litters of which parts were kept in separate nests). A single tagged animal was taken as a subadult by a trapper in the fall.

Of 54 litters handled from one to five times during the period of May 17 to June 23, when the studies were centered on Mud Lake, 24 litters judged to have been complete averaged 6.9 young at very early ages. Nine samples of litters alive at about one week averaged 6.8 young; 21 samples at about two weeks, 5.9 young; 10 samples, two and one-half to three weeks, 6.6 young; and nine samples, three and one-half to four weeks, 4.2 young. The sharp decrease in mean size coincided with relaxation of parental care and with freer ranging by the young.

Diagnosed mortality from natural causes suffered by the above litters was almost entirely due to drowning and to attacks by other muskrats. Five of a litter of at least eight 23-day young and two of a litter of four 27-day young were drowned during a cold rain (Errington, 1937c). Among the victims of chiefly intraspecific strife, one litter having five young at 25 days was annihilated within the next fortnight; another of five at 18 days lost two within the next two days.

Elsewhere on the marsh, the collapse of about a third of the emergent vegetation in late spring and early summer left many muskrats vulnerable to horned owls. Prior to this crisis, no muskrat remains were found in 209 horned owl pellets gathered from the woods about Mud Lake from early spring, 1933, to early spring, 1935, despite a higher population of muskrats in 1934 than in 1935. After the failure of so much of the marsh cover, one of 43 pellets from March 31 to May 16, 1935, contained remains of young muskrats; five of 16 pellets from May 17 to June 1 contained muskrat remains (young animals in four and an adult in the other); and eight of 12 pellets from June 2 to July 15 contained remains of 11 recognized individual young and an adult (Errington, Hamerstrom, and Hamerstrom, 1940). Only one family of young minks was known to frequent Mud Lake in 1935; nothing is recorded of its food habits.

Round Lake

The most reliable direct counts of muskrats obtained at Round Lake in 1935 under conditions of good visibility gave 94 adults per 50 lodges, or a breeding density of 1.88 per lodge, as of early May. The total adult population for this season for the total of 286 lodges (excluding feed houses) may be computed pro rata at 538, plus 9 known bank dwellers, or about 547 adults. Using the same sex ratio (52.8 per cent males) as for Mud Lake, we would get 289 males to 258 females. A revised estimate gave about 650 adults, including about 310 females.

Verl ("Jack") Black, an expert trapper with experience on some well-populated Iowa marshes, told me that he estimated a population

of about 2,000 when looking over Round Lake in the fall of 1935. I have no record of my own final estimate of the time but know that Black's was hundreds of animals higher, and I now feel that his was the more nearly correct. My considered view is that the actual 1935 fall population for the marsh was around 1,700, insofar as it was apparently (judging from the comparable sign) a few hundreds higher than a 1939 population that was determined to have been a little below 1,300.

Two hundred and ten young muskrats in 63 litters were tagged experimentally at Round Lake from June 25 to July 22, 1935. Of these young, 27 were tagged in the middle of July by means of an improved technique; the other tagging was sometimes efficacious, sometimes not. Forty-nine of the 210 tagged young yielded data of some sort.

Special efforts were made to keep track of the tagged animals as long as possible. One study in the northeast part of Round Lake entailed daily examination of all lodges, feeding places, and litters of young on a tract of 15.8 acres for 19 consecutive days, July 6 to 24. Other sample tracts were closely observed for lesser periods of time, including 9.3 acres in northwest Round Lake, from July 16 to 22.

The northeast sample tract of 15.8 acres and the northwest one of 9.3 acres were selected for the most intensive studies because they had the heaviest breeding densities on the marsh — the equivalents of 22 and 15 pairs, respectively, as ultimately determined. In terms of musk-rats per acre, these breeding densities do not look impressive as maxima, but in actuality they constituted, because of the mediocre quality of the existing habitat for muskrats, what I now regard as some of the top-heaviest overpopulations that I ever studied.

The reproductive fortunes of the 22 adult females and associated males of the 15.8-acre study area of northeastern Round Lake were not accurately measured prior to July 6. The field notes for the period of intensive study indicated a minimum of 48 large young that by then had been weaned and established in the area as free-living individuals. Of these 48, four were found dead, leaving a minimum of 44 that might be regarded as having good chances for survival. Sixteen large young, which were referred to in the notes but not counted in the above total because of possible duplications, could have included additional individuals. It is still more likely that a number of other large young were sufficiently wary and able as divers to keep out of sight at the times of the daily visits.

Limited movements of free-ranging young across the boundaries of the northeast study area were known to have occurred. While no outside records were obtained on 8 tagged animals that reached ages of independence within the area, 7 outsiders were recorded short distances inside. Six of the latter had been tagged considerably less than 100 yards from the places where later seen, but the seventh (an ailing albino) was found dead 200 yards from its original quarters.

Of a total of 73 young closely studied on the northeast area during the 19-day period in July, only 11 were judged on fair evidence to have been reared. A loss of 16 may be more or less chargeable to human disturbance or tagging, but, even allowing for this, a "natural" mortality of 46 of 62 is still extremely high. A fungus skin disease due to *Trichophyton mentagrophytes* (Errington, 1942b) and intraspecific attacks were the major agencies of loss.

One litter of five 13-day young was bitten to death by an adult – on circumstantial evidence, by a female about to give birth to a litter of her own. The lodge was remodeled, the dead young covered up therein, and, on about the following day, a new litter was born to the nearest adult female (other than the mother of the murdered young) living in the vicinity. This had all the appearances of aggressive action to gain possession of what had been at the time the best habitation in the neighborhood. Three days after the killing, I leveled the lodge in search of the buried young, following which a new lodge containing the very young litter was built up 45 yards away.

Another lodge just outside the 15.8-acre northeast area was apparently taken over and rebuilt by adults other than the rightful possessors, on the day after the destruction of a litter of 8 young of four days. In this instance, the killing was done not as an act of parental competition but by cannibalistic young of the litter preceding the litter destroyed. Another litter of 7 new-born young did not last as long, the young cannibals having well cleaned it up by the day after its birth.

Equally deadly to the victims, if reflecting less viciousness, was the rebuilding of a lodge by a mother that brought her own young to it after covering with debris the then-living abandoned young of a litter belonging there. Also, the eating of some very small young by larger young followed the abandonment and death of half of a split litter of 8; the other 4 of the litter were well attended in a lodge 60 yards away.

The hazards awaiting weaned young trying to live under crowded conditions are illustrated by data on intraspecific attacks in and about the 15.8-acre area. An animal slightly less than two months of age was found sitting on a rush raft, so dazed from head wounds that it was easily caught by hand; after tagging and release, it was seen two and one-half hours later, still sitting and still dazed. The biggest and most vigorous young of one tagged litter was found dying at 31 days, its tail bitten through and nearly severed at the base. One of about 40 days was found dead in a lodge, hindquarters slashed. Two suspected strife victims of between 50 and 60 days were seen rotting in the water.

The total productivity of the northeast 15.8 acres may be calculated as the 11 young believed to have grown to independent ages during the July period of intensive study, plus the 44 of older ages having good chances for survival, plus the unknown number of older ones that were reared without being recorded. Possibly, the number of the latter might fairly well offset the number of the others that died in late summer or early fall after having been last observed. At any rate, a local increase totaling 55 young for the equivalent of 22 pairs would seem, under the circumstances, about what might have been expected.

The northwest sample area of 9.3 acres having the equivalent of 15 breeding pairs was partly surrounded by wide expanses of open range, into which the weaned young usually succeeded in moving before being tempted to prey upon helpless litters or getting into trouble with their elders. Except for one young that recovered from slight wounds inflicted by another young, no victims of intraspecific attack were found in the area during the intensive study, nor during nine visits made before or after this period. In fact, only two dead young were found in here: one drowned and the other dead from what looked like a light accidental blow to its nose.

There were 10 helpless litters being cared for in the 16 lodges of the northwest sample area, with much splitting and shifting of litters taking place. Members of one litter of 14 days were found distributed in four adjacent lodges. As this happened to be the situation at the time of the first inspection of the area in nine days, it could hardly have resulted from human disturbance. In one instance, a new-born litter was moved into a lodge very shortly after the lodge was vacated by a mother moving her 16-day litter to the next lodge, 55 yards distant. Two members of another new-born litter were found, placentae still attached, 45 yards from the lodge containing their 7 litter mates. It was apparent that much intermingling of adults occurred, but, with the larger young "out from under foot," the overlapping of territories did not promote anywhere nearly the friction observed in the northeast area.

The northwest area was unquestionably a very productive one for Round Lake in 1935. An early checkup on May 5 revealed seven litters of small young in 24 lodges lying within or just outside the area. Breeding also continued late, litters being born July 29, August 5, and August 24.

I find it most difficult, if only because of the variety and complexity of situations existing at Round Lake in 1935, to generalize accurately on the fortunes and responses of the muskrats of that marsh for that year. Yet, so many equivalents of experiments were set up through the operation of natural factors that attempts at generalizations should be particularly in order.

Eight dead adults and 77 dead or dying young were individually referred to in the notes for the middle and latter parts of the summer of 1935, and, of these dead, the young of course represent but a small fraction of the numbers dying. Of the litters handled, 6.9 per cent were infected and virtually wiped out by *Trichophyton* (Errington, 1942b). Seldom were more than one or two young actually found dead of whole litters patently dying from the fungus skin disease or found dead among the helpless litters being preyed upon by large young muskrats. Most losses were indicated by final disappearance of the young. Decomposition, settling to the bottom of the marsh, burial under the piles of vegetation manipulated by muskrats, and scavenging (especially by partly grown muskrats and by the small painted turtles, Chrysemys picta bellii), all served to obliterate remains of dead young quite rapidly.

Among the more informative specimens were three of four newborn young dead of exposure on a flooded nest; a breast-slashed young of about five weeks on a deep-water rush pile occupied by two adults; an unweaned young of 20 days backed into a blind chamber in a lodge and twice bitten through the head by an adult; and two young of 16 days killed in a shore-zone lodge by a mink, one bitten through the head and the other through the shoulders.

For comparative purposes, Round Lake may be divided roughly into east and west halves for the spring and summer of 1935. There were no mink dens with young along the shore of the east half (which was mainly bounded by a graveled road, much frequented by dogs), but along the quieter west shore were no fewer than five female minks with their families. Until the breaking up of the mink families, only an occasional big mink (of the size of an adult male) worked around the east shore. The two halves had rather similar numbers of occupied muskrat burrows and, considered broadly, were also somewhat alike in topography and vegetation.

Mink predation upon the young muskrats was as pronounced in the west half as it was negligible in the east half. Mink scats could be seen literally by the quart about the latrines of the rearing dens, and the weathering muskrat fur stood out in heaps. Samples totaling 114 mink scats were gathered from May to August, 1935, and 41 of these contained muskrat remains – an exceedingly high incidence for the warm-weather months during a period of no serious environmental emergencies.

The losses from skin disease were likewise heavier in the west half, and this also had a bearing upon the severity of the mink predation suffered (Errington, 1943). But, disease and mink predation notwithstanding, the mean fall densities looked about the same on most of the comparable subdivisions of the marsh that had been either minkhunted or practically mink-free. One exception was noted: on 20 acres of marsh where the summer mink pressure had been most severe, the fall population was probably lower by two or three muskrats per acre than the 10- to 15-per acre densities estimated for adjacent parts of the marsh.

The data from the two halves of Round Lake for 1935 revealed other evidences of intercompensations or automatic adjustments in rates of loss and gain. On the east half, where losses from agencies other than intraspecific strife had not been great, breeding had ceased by midsummer. This half had a number of conspicuous aggregations of mixed ages of young throughout July. Thirteen were caught and tagged on one old lodge butt alone, and many others on this butt escaped capture. Five additional gathering sites of miscellaneous groups of adults and young were mentioned in the field notes, mostly in the northeast study area.

The sexual states of adult males collected for specimens while in close association with such mixed groups suggest that the continued

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proximity of large numbers of young may have affected the psychology, hence the physiology, of the males and thus brought about an early sexual quiescence. One of two adult males collected on June 27 and two of three collected on July 25 and 26 from the densely populated tracts of the east half had testes that were much reduced in size, whereas four specimens of adult males collected between June 25 and July 28 from the less populated west half were in normal breeding condition. Breeding continued through August in the west half.

In those parts of the marsh where continued late breeding was prominent, the basic stimulus may be identified with a relative lack of population tension. Nearly all of the late-summer litters (or commonly the third or fourth of the season for individual females) were born on sections of the marsh where either the known early summer mortality of the young had been highest or where lessened tension may be ascribed to unimpeded movements of young outward into relatively underpopulated parts of the marsh. Appreciably fewer young of active sizes were intimately associated with adult animals in the long-producing west half than in the east half, where breeding ceased so early.

In the east half, and especially in the northeast study area, it was many weeks before the majority of the weaned young had access to any livable quarters except those in the midst of population aggregates dominated by short-tempered adults. Here, the weaned young, having but limited opportunities for movement away from the area, lived warily as unpopular trespassers, the survivors among them contributing to prevailing population tensions as well as drawing attacks from their elders.

In late summer, the harassed muskrats of the northeast study area were living in what had been the most food-rich part of Round Lake until midsummer. It was doubtless not a matter of chance that so many adults had wedged in their breeding territories where the vegetation had then been most attractive to them. The behavioristic manifestations of the resident adults may therefore be regarded as a resultant of (1) a greater tolerance of crowding induced by an originally superior food supply and of (2) the heightened tensions following both overuse and natural deterioration of important tracts of the habitat available to them, plus (3) irritations because of the presence of weaned young while new litters continued to be born, and plus (4), conceivably, the psycho-physiological influence of an impending cyclic low (Errington, 1954a; 1957).

Cover conditions had been generally backward on the marsh up to the last week of June, with bulrushes sparse and reeds only about two and one-half feet out of the water. By the end of the first week of July, emergent vegetation had made much better growth, especially in the center, and muskrat lodges were being built at an accelerated rate. By the middle of July, it was becoming more and more apparent that fair-sized young were moving deeper into the marsh where the newly emergent vegetation was thicker.

One particularly substantial drift of young was from the outer-

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most edges of the northeast study area and from an area immediately to the north, where emergent stands died or were cut down by the muskrats to such an extent that the bulk of the muskrat population situated within 200 yards of shore almost had to move. By August 3, most of the animals engaged in this adjustment were living in heavier, previously unoccupied rushy growths 300 to 400 yards from shore. No evidence of foot-loose abandonment of home ranges was noted in connection with the drifting toward deeper parts of the marsh. The drift was of the nature of mass extensions of ranges into marsh that was essentially virgin habitat.

Rather similar drifting of young occurred during the summer from the northwest study area, which had avenues of travel to deep water vegetation on three sides. At the same time, there was very little sign of activity in west-central Round Lake out from the places having the characteristically heavy losses of young through predation and disease.

INTENSIVE STUDIES DURING THE DROUGHT EMERGENCY AND APPARENT CYCLIC LOW OF 1936

Dissociation of variables linked with drought, heat, disease, and the little-understood phenomenon called the "10-year cycle" is admittedly hard to do. Drought had a big part in the wholesale reduction of muskrats that occurred in Iowa and in states to the north and west in 1936. Directly and indirectly, it was responsible for the loss of millions of muskrats. It all but wiped out the species over countywide areas in the western half of the north central region.

I long attributed primarily to the 1936 drought the lowest net rates of gain (either in relation to density or not) observed for both the Round Lake and Mud Lake populations. Yet, the data looked upon from the perspective of recent years show that only a small proportion of the Round Lake residents could have been seriously affected by drought between the spring and fall of 1936. There the food, cover, and water conditions remained well within known limits of comfort and tolerance of at least the lodge-dwelling muskrats. At Mud Lake, the situation differed in degree, with drought being a more important factor on the east third than on any sizable tract at Round Lake, but a summer gain surely depressed below 100 per cent may not be convincingly explained more than partly in terms of drought.

The summer of 1936 was hot, but, if it be argued that excessive temperatures (up to 117 degrees Fahrenheit and often day after day above 100 degrees) may have accelerated mortality or damped reproduction, similar statements could be made of the summer of 1934, when rates of net population gain figured out in the vicinity of 300 per cent for both marshes — and these latter gains appeared to have reflected considerable density-depression as well.

Further discussion of the possible operation of the cyclic mechanism in 1936 had best be reserved until later in the book, after the various kinds and shades of evidence have been assembled, winnowed, and appraised. That something special happened may nonetheless be recognized, something not to be dismissed in ordinary terms of weather, habitat, or epizootiology.

Mud Lake and Dewey's Pasture

About 100 of the 300 acres of marsh controlled by the Mud Lake Fur Farm were dry by the fall of 1936, and only 40 of the dry 100 acres still had living muskrats. The season's catch was 501 muskrats (letter, Joe Kautsky, Jr., March 23, 1938), of which 42 were reported taken from dry marsh (letter, John Garlisch, November 17, 1936). Virtually the entire population was caught, which would figure out at a November density close to 460 muskrats on the 200 acres of wet marsh. The fall population of 2.3 animals per acre for the wet marsh apparently had not been significantly affected by the drought. On a pro rata basis, a reduction of the dry marsh population to less than one-half muskrat per acre would mean a net lowering of the Mud Lake population by almost 200.

The mistake should not be made of thinking that the greater numbers of muskrats trapped on the wetter 200 acres might simply have reflected immigration from the part drying up in summer and fall. The territories or home ranges had been packed together in such a way as to have permitted little free movement, and, in the dry marsh, well-used home ranges had been consistently occupied despite more favorable food and water conditions in the wetter but already occupied parts of the marsh. Only a very small proportion of the animals trapped in the better grades of habitats showed the wounds and poor flesh indicative of trespassers, whereas all of six muskrats from the dry eastern end that I examined on November 11 were thin and chewed up. The principal trapper, Verl ("Jack") Black, judged that 90 per cent of the muskrat pelts taken from the dry marsh were damaged (letter, November 16, 1936).

The 1936 spring breeding density for Mud Lake cannot be figured out with better than fair satisfaction, but sufficient work was done to judge (1) that the population of adult females of the dry but still occupied 40-acre tract had suffered only moderate reduction through drought up to the trapping, (2) that, on the basis of specimens examined, possibly 18 of the 42 muskrats trapped on the dry 40 acres were adult females, and (3) that these dry 40 acres had an original population more or less representative of the holdings of the Mud Lake Fur Farm. After making allowance for some drought loss of adult females on the 40-acre sample, the evidence would suggest the equivalents of between 160 and 200 pairs – probably nearer the former – as the spring population for the total of 300 acres of the Mud Lake Fur Farm.

Lying north of and adjacent to Mud Lake, the 392-acre state-owned waterfowl breeding grounds known as Dewey's Pasture had slightly over 100 acres in marshy potholes. The 1936 breeding population of muskrats was estimated on the basis of summer signs as the equivalent of 20 pairs. The potholes went dry from June to August, with vulnerability of the muskrats to minks becoming critical just after disappearance of the surface waters. No muskrat remains were seen in about 200 mink scats dated to June and early July, but 20 of 27 scats deposited from the middle of July to early October did contain muskrat remains. However, all of 4 dead young muskrats found could have died from causes other than mink predation, and one had been eaten upon by another muskrat. There was also evidence of much outright abandonment of the dry potholes in late July – though fairly substantial remnants occupied some old quarters for weeks afterward. The remnant animals included not only formidable, property conscious adults but also individuals seen to be immature, diseased, and otherwise handicapped. The last resident muskrat in Dewey's Pasture was apparently killed by a mink early in October.

Round Lake

Much illegal spearing of muskrats through the lodges had taken place on Round Lake during the winter of 1935–36. The field notes for a visit of May 13, 1936, suggest disease losses, as well. Two neighboring east-side lodges had winter mink latrines on them, and all of about 90 scats contained muskrat remains, which is the sort of thing one sees following a local epizootic. On May 23, a recently dead adult was found in one of the lodges near the winter mink latrines, further suggesting the continuation of a local epizootic. In the south central part, an adult male was found floating on June 17 and adult females on June 24 and 27, all sufficiently fresh to show what was then noted as visceral inflammation.

The entire marsh was kept under intensive observation during the 1936 breeding season, with the objective of obtaining data on as many as possible of the muskrat litters born. Not all of the season's litters actually were handled, but thorough inspections of mapped and numbered lodges (in which the majority of the litters were regularly quartered) were made at about weekly intervals, or as often as full circuits could be made.

A breeding population the equivalent of 80 pairs was determined from, among other data, the location of litters. This, considering the evidence of surplus adult males, should mean a total of about 170 adults present, as of the middle of May.

Mink predation on adults was conspicuous in April and May, but the brunt was borne by shore-dwelling transients. Eighteen carcasses of victims were found, and those for which sex was ascertained were males having many wounds received from other muskrats. Sixty-one of 106 mink scats deposited in April and May contained remains of adult muskrats. By June, the surplus males had been eliminated, and the incidence of muskrat remains in the scats dropped to 7 in 84.

The total of 120 litters accounted for at Round Lake in 1936 should be revised upward. The best procedure in trying to arrive at valid figures as to the actual number born would seem through pro rata calculations. The breeding histories of 51 of the adult females were followed with reasonable confidence in the completeness of the data obtained on the numbers of litters born to them during the breeding season. The remaining 29 of the total of 80 adult females could well have given birth to and reared undetected litters in bank burrows. Of the 51 adult females most satisfactorily kept track of, 2 were classed as nonbreeders, 13 as one-litter females (including 3 that died before the possibility of further conceptions), 23 as two-litter females, 11 as three-litter females (including one dying while pregnant for the third time), and 2 as four-litter females. If these 51 and their total of 100 litters be accepted as representative for Round Lake in 1936, then the grand total of litters would be 157. The mean size of 43 complete litters was 6.3, which would give a grand total of about 990 young born.

Four of the original 80 adult females were accounted for as having died during the breeding season. It is possible that some of the 13 unsexed adults found dead between late spring and fall also had been females, or that other adults (including females) had died without my knowledge, especially when concealed in bank burrows. Perhaps about 70 adult females were surviving by fall.

It did seem that, after the elimination of surplus males through minks and strife in April and May, most adults lived securely until the water level of the marsh went down in July and exposed some of the bank burrows. As a rule, the occupants of the banks withdrew safely to deeper water, but 7 of the 8 adults believed to have been living in the exposed burrows of a 300-yard stretch of shore were apparently killed by minks, and lesser losses were detected in two other places. Thirty-four of about 160 mink scats collected for this period from the 300-yard exposed stretch contained remains of muskrats, mostly of adults.

Considerable movement of muskrats about the countryside was induced by drought in late summer and fall, but there was no reason to think that the relatively well-situated Round Lake population participated in it to any significant extent – least of all the resident adult females, which are always among the more reluctant to give up established home ranges as long as living conditions are tolerable.

A late fall sample of 175 residents (taken as specimens for the investigation by Verl Black, Roy Walrod, and myself) consisted of 18 adult males, 29 adult females, 72 young males, and 56 young females. (Six other specimens collected at this time were easily recognizable as wanderers from their poor and battered physical condition.) On the basis of the above ratios, a total living population of about 70 resident adult females should have been associated with about 45 adult males, 175 young males, and 135 young females, or a grand total of about 425 resident muskrats at Round Lake, as of November, 1936. The removal of 175 specimens would have left about 250 of the resident population to enter the winter. If any wanderers became established, they were present in but negligible numbers. It may be seen that the total of about 310 young of the year calculated for the 1936 fall population would comprise less than a third of the calculated number of young that had been born. By far the greater part of such a decline should have been due to mortality, for the tagging of 123 young in 52 litters gave evidence that few young had left the marsh. Of 13 young muskrats tagged on Round Lake during the summer of 1936 and recovered in the following fall and early winter, only one evidently took to wandering. It was trapped at a drainage ditch about four miles from its birthplace.

The causes of mortality of 90 young were well ascertained. Fifty-one were, directly or indirectly, victims of the skin disease previously mentioned, but this sample surely is much overweighted, even considering that 12 per cent of the litters were infected. It was true that infections of the skin disease proved to be invariably fatal to victims showing gross manifestations before the age of two weeks, and that few litter members escaped if the disease appeared among them at such an early age (Errington, 1942b); also that, as infection in a litter could be recognized days before any actual dying, the mere disappearance of animals thus ailing could be interpreted as evidence of their deaths. But the five of the ninety that were found dead from strife wounds probably did not represent a proportionate amount of those dying through this agency — especially near two rather crowded shore zones occupied by some patently intolerant adults.

Three female minks had young in dens about Round Lake in 1936, and also present was a huge male (sometimes observed at close quarters in its favorite retreat) that specialized on the transient male muskrats frequenting the shore in the spring. The killing of 8 young muskrats, including a litter of 6 small ones, was specifically traced to the minks. Only 3 of 153 mink scats for May and June contained muskrat remains, and these remains were of the above litter of 6. After drought had exposed the shallower parts of Round Lake in July, 47 of 194 mink scats contained muskrat remains. For August through September, with the passing of the period of greatest drought vulnerability, no muskrat remains were found in 76 mink scats. For late fall, when some ingress of drought-evicted muskrats from other places occurred, 4 of 21 mink scats contained muskrat remains.

By late September, most of the lodges were within 50 to 150 yards of shore, and, even in the central part, the heaviest concentrations were within 300 yards of shore. The total of habitable lodges was something over 175. A month later, the mud margin extended about 200 yards out in the marsh, and, by freeze-up in early November, the maximum depth of water was about a foot and a half.

THE INTERMITTENT STUDIES OF 1937

In 1937, I was too busy in central Iowa to make more than occasional visits to the Ruthven area; hence the time spent there was largely devoted to obtaining data illustrating population trends. For information contributed by others, particular thanks are due to Dan Nichols of the State Conservation Commission and to Dr. Clarence A. Sooter, then of Iowa State College.

The Ruthven Marsh Area, Northwestern Iowa

Mud Lake

At Mud Lake Fur Farm, John Garlisch, the caretaker, told me that, in 1937, he saw only one muskrat there up to April 27. Considerable repopulation occurred later in the spring, bringing the Mud Lake breeding population up to an estimated equivalent of about 17 pairs. A 1937 fall catch of 130 (letter, Joe Kautzky, Jr., March 23, 1938), plus an estimated 30 escaping the trapping at Mud Lake, would indicate a fair amount of ingress of breeding animals.

Round Lake

Despite a low water level and freezing to the bottom over much if not all of Round Lake in the winter of 1936–37, the survival rate of the muskrats appeared to have been quite high. Indeed, the usual habits of the muskrats living in channels and air spaces under the ice rather than in the lodges at such times gave them good protection from illegal spearing. (The main violators of the refuge were apprehended with nine muskrats in possession. They were said to have tried again, but, after spearing only three in three nights, concluded that there were not any muskrats left.) But living conditions for some of the wintering muskrats were unfavorable, and some wandering was observed. Muskrat remains were found in all of eight winter mink scats examined.

Mink-eaten bodies of 5 muskrats were found in late April, and these seemed to have been typical transients. Thirty-six of 114 mink scats for this month contained muskrat remains. Ten other winter and spring dead were found, of which the deaths of 7 were originally ascribed to drowning during a windstorm. That diagnosis may have been faulty, for, despite the absence of references in the field notes to recognized lesions, the general evidence suggested that a local epizootic may have killed the occupants of a reed patch, the lodges of which later disintegrated through wave action.

Conditions on Round Lake were favorable for direct observations in the last week of April, 1937, and a census figure the equivalent of 86 pairs, or about 185 adults, is believed to have been accurate for the time. However, the spring dispersal was by no means over, and Round Lake was the likeliest source of the muskrats moving into Mud Lake, for more were known to have survived at Round Lake than elsewhere in the Ruthven area. Then, too, three of the animals tagged in 1936 at Round Lake were taken by trappers at Mud Lake and a neighboring marsh in the fall of 1937. Several other tagged muskrats were, according to "grapevine," caught during the same fall within a four-mile radius of Round Lake.

From tagging results, the early-summer distribution of lodges observed by Sooter (I have his notes and a map dated June 26, 1937), and information pieced together on location of used burrow systems, it may be estimated that the equivalent of 52 pairs – or approximately 60 per cent of the late April population – remained on the marsh. The fewness of visits to Round Lake in this year are hardly conducive to accuracy in calculating adult mortality, but, unless disease did undetected killing of adults, such mortality would appear to have been considerably lighter in 1937 than in 1936. Remains of only 2 dead adults could be assigned to the summer of 1937. For lack of more definite information, we may assume a spring to fall loss of a couple of adult females, thus reducing their number to the vicinity of 50.

In early winter, 1937, C. C. Lille and L. D. Wright of the State Conservation Commission trapped 208 specimens from Round Lake in connection with the investigations: 20 adult males, 24 adult females, 94 young males, and 70 young females.

This sample, because of the moderation of the trapping done in particular areas, is thought to have been overweighted with selectively taken adults, for the reason that a greater proportion of the fully adult members of a muskrat population may be caught in the first few days of trapping. We have data from Iowa samples totaling 3,720 fall-trapped muskrats that are both representative of practically total populations and informative concerning times of trapping of their component lots; these samples show a mean ratio of 3.61 young per adult in the early-caught lots, compared with a mean ratio of 4.43 young per adult in the over-all populations. Instead of the recorded ratio of 3.73 young per adult in the Round Lake specimens trapped in 1937, we may then, calculating from proportions, arrive at a ratio of 4.58 young per adult as being more nearly representative of the actual Round Lake population for that year.

The use of 50 surviving adult females as a basis for calculating the 1937 fall population from the sex and age ratios would give a total adult population of 92, including 42 males. With the corrected ratio of 4.58 young per adult, the number of young of the year would figure out as near 420 and the total population at near 515. The trapping by the Conservation Commission should have left about 300 muskrats to enter the winter of 1937–38.

Mink predation upon the Round Lake muskrats was clearly light in 1937 after the elimination of the vulnerable spring transients. No muskrat remains were found in about 86 mink scats deposited from May to August, nor in 81 fall scats. Three female minks with their young lived along the shore, close to the retreats of the majority of the resident muskrats.

Following the spring dispersal, the Round Lake muskrats of 1937 lived principally in lodges near shore or in bank burrows. Water levels were high not only in the spring but also throughout the summer. No important late-summer drifting of muskrats toward the center of the marsh took place, though the central vegetation remained in attractive condition and was only somewhat less dense than in 1935 and 1936, when centripetal movements had been conspicuous.

INTENSIVE STUDIES AT ROUND LAKE OF A MODERATELY LOW-DENSITY POPULATION LIVING IN FAIRLY GOOD HABTAT, 1938

The evidence indicates that the muskrats were well-situated on Round Lake during the winter of 1937–38. Though minks ate several muskrats in the traps of the state trappers, the general population of muskrats seemed to have been secure. None of 160 winter mink scats contained muskrat remains. For the spring months, 1938, one of 124 mink scats contained muskrat remains, and a single body of a mink victim was found, a male lying on shore.

A settled breeding population the equivalent of 64 pairs or about 150 adults was arrived at. Because of the low population, favorable conditions for observation, and the intensive nature of the work, this figure is regarded as being nearly exact.

Tagging was resumed, after lapsing in 1937, and 128 tags were placed on members of 26 litters between May 16 and July 7, 1938, principally to establish the identity of key litters in studies of growth rates and development (Errington, 1944).

Lille and Wright took 206 specimens for examination from Round Lake in December, 1938. The sites of trapping of all specimens were carefully mapped for purposes of the investigation by Horace L. Poole. Excluding two wanderers, 204 specimens consisted of 18 adult males, 20 adult females, 88 young males, and 78 young females. This sample, like that for 1937, is undoubtedly overweighted with selectively taken adults, as different parts of the marsh were subjected to only a single day of trapping. If calculations on the same proportional bases as in 1937 be applied to the 1938 data, the 1938 age ratio should be 5.36 young per adult, instead of the 4.37 young per adult in the actual series of 204 specimens.

The losses of adults during the summer were remarkably low. Only one dead (a male dying from wounds of intraspecific strife) was found. Three adult males were collected for specimens. For practical purposes, it may be assumed that about 62 adult females were still alive by late fall. On this basis, pro rata calculations would give a total resident population of 118 adults and — using the recalculated ratio of 5.36 young per adult — 632 young of the year, or a grand total of 750.

Sixteen young were shot for specimens during the summer, and a seventeenth escaped with probable fatal wounds. Of 62 other young known to have died, 32 were victims of the fungus skin disease; 12 of abandonment or other deficiencies in parental care; 5 of drowning, chiefly during a cloudburst; 3 of mink predation; and 8 of miscellaneous or unknown causes, probably including undiagnosed disease. In 1938, the incidence of litters infected with *Trichophyton* was a triffe higher (12.2 per cent) than in 1936.

Among the victims of undiagnosed disease was a subadult found floating on the water, still warm with body heat, with nothing demonstrably wrong with it except thoracic congestion. This, I now suspect, represented the pneumonic syndrome of the then unrecognized hemorrhagic disease.

Most of the intraspecific strife, cannibalistic feeding, desertions, and behavioristic irregularities of the year occurred in the northwest corner, the most heavily populated part of the marsh. Numerous young went ashore here – presumably as a result of intraspecific tensions, as this sort of thing did not often happen with well-situuated Iowa marsh populations. This was where the known mink predation took place.

Signs of only one female mink with her young could be found at Round Lake in the summer of 1938. The 3 mink-killed young muskrats were recently weaned; remains were found in 8 of 160 mink scats deposited in June and July. Five of 89 scats for August contained muskrat remains, and these remains were of approximately halfgrown animals. Four representations of muskrats in 35 September and October scats included remains of at least 2 individuals that were adult-like in appearance.

Water levels were well maintained throughout the 1938 breeding season. Perhaps the emergent vegetation over the marsh as a whole was somewhat less abundant than in the earlier years of the study, but general environmental conditions were not greatly dissimilar to what they had been each year following 1933, with the exception of the low water stages of 1936. Local changes could be noticed, for example, in the continued deterioration of the heavy stand of cattails of the east side, but this was partly offset by the extension of cattail tracts in the north center and northwest corner and the washing out of some of the reed clumps was accompanied by thickening growths of bulrushes.

INTERMITTENT STUDIES AT ROUND LAKE DURING A YEAR OF FALL DROUGHT, 1939

Little information may be extracted from the notes concerning the 1938–39 wintering of the muskrats at Round Lake. Minks were scarce; muskrat remains were found in one of 13 scats. In March and April, 1939, two mink victims were handled, both representative of the several transient muskrats seen to be living in flimsy nests along the shore. One transient muskrat, collected for examination, was a typical wandering male with painful-looking strife wounds. Three of 19 spring mink scats contained muskrat remains.

A good checkup of the breeding population, May 8 to 10, gave the equivalent of an even 200 pairs, or a total of about 425 adults. Because of the initiation of intensive studies at Cheever Lake (Chapter 6), visits to Round Lake were inadequate to trace mortality in detail. Apparently, only a solitary mink was regularly present in the summer; muskrat remains were found in 4 of 150 scats deposited in June and July and in none of 92 from September.

The year was characterized by a prolonged, dry Indian summer, turning into locally acute drought. Water levels in late fall and early winter were not as low at Round Lake in 1939 as they had been in 1936, but the population adjustments and mortality reflected drought crises far more spectacularly in 1939.

Lille, Wright, and Verl Black took 195 specimens (exclusive of six current wanderers) for examination in December: 16 adult males, 14 adult females, 96 young males, and 69 young females. The trapping was sufficiently intense in given tracts of marsh to yield a good cross section of the population living there; nevertheless, the age ratio was distorted by differential mortality of adults during the drought.

Offspring of the shallow-zone adults had tended to migrate centripetally and to establish themselves securely in deep-water habitats during the late-summer period of minimal friction, whereas the old animals had remained in residence along the exposed marsh borders until late fall. Then, when these old ones had finally relinquished their property rights and tried to make adjustments, it had been too late for them. They had been fought off by animals already resident in the better habitats, and they had suffered severe losses from intraspecific strife and from the special hazards of wanderers at this time of year.

Ninety-three of the original breeding territories had been wellsituated with respect to the drought, and, in these, the survival of adults had been high. In the shallow zone, most of the adults of the other 107 original territories ultimately had died or departed from the lake after having produced their season's young. Using 93 as the remaining and more or less centrally located population of adult females in combination with the sex and age ratios obtained from the trapping, we would get a corresponding number of about 106 adult males and about 1,080 young of the year, the latter being the offspring of both central and peripheral breeders. The grand total of about 1,280 arrived at for the marsh seemed to be in keeping with the external signs shown by an almost exclusively lodge-dwelling population in December.

CONCLUDING COMMENTS ON THE ROUND LAKE STUDIES

My real work in the Ruthven area terminated with a few brief visits in the course of 1940-41. In those years, the general trends of muskrat populations and muskrat habitat were both downward.

In midwinter, 1939-40, poachers violated the Round Lake refuge and drastically exploited the muskrats. It would be a good guess that many hundreds of muskrats were speared or trapped illegally, and the 1940 spring population was obviously much reduced - down to an estimated equivalent of 60 pairs or about 143 adults. The midsummer water level was similar to what it had been in most previous years of my studies, but, by late fall, it was considerably lower, exposing much of the shore zone. For unknown reasons, the emergent vegetation became much reduced (especially the central stands of bulrush and cattail), although the reed clumps appeared to be little changed, and the southeast corner had the best stand of bulrushes in years. The late fall population of muskrats was rather restricted to 225 medium-small lodges (194 actually counted, the balance estimated for inaccessible parts). These lodges were of the sort that, judged from my trapping experience, might have yielded an average of 3 muskrats each. On this basis, an estimate of about 675 muskrats as the fall population was made.

Something happened to the Round Lake muskrats during the winter of 1940–41 – just what is not at all clear. B. I. Severson of the State Conservation Commission reported that he knew of only 15 muskrats having been speared there (Taylor W. Huston, letter, March 4, 1941). The famous "Armistice Day Blizzard" was said to have destroyed many of the lodges, but I have no way of knowing how deadly this event was for the muskrats. Bodies of 3 mink victims were found on a spring inspection trip, and 7 of 15 mink scats contained muskrat remains. My estimate of the 1941 breeding population was the equivalent of between 25 and 30 pairs, probably about 55 adults.

Water levels fluctuated considerably at Round Lake from spring to fall, 1941, yet not enough to bring about any known crises for the muskrats. In general, emergent vegetation continued to be less dense and less widely distributed than in the early years of the study, being especially sparse in the deeper parts of the north half. No muskrat remains were seen in about 200 summer mink scats. By late fall, the visible signs indicated a low population, estimated at about 175.

I visited the Ruthven area in late June, 1958, and found that the marshes on which my intensive work had been done in the thirties were dry and conspicuously grown over with cattails. James G. Sieh, of the Iowa State Conservation Commission, kindly summarized for me (letter and inclosures of July 9, 1958) the information he obtained from Round Lake after discontinuation of my work there, and this material is excerpted in Appendix B.