Part 3

Biogeography of the Living Forms of Muskrats

Chapter 12

The Muskrat of Eastern United States and Southeastern Canada, *Ondatra zibethicus zibethicus*

CENTRAL IOWA may be used as a focal point in treating the common or eastern muskrat, the subspecies *zibethicus,* in relation to its geographic range in North America. This is near the southern edge of recent (Wisconsin) glaciation in Iowa and the southern edge of what was once the great lake and marsh country of the midwestern prairies. Farther south in the state, the terrain looks increasingly like that of Missouri, with its gullies and wooded hills. From Hollister's (1911) published record of *cinnamominus,* or the great plains muskrat, from Marion County, Iowa (which lies about 55 miles SSE of Ames), it may also be seen that central Iowa may once have been about the western boundary of the range of *zibethicus,* though the present range of the latter subspecies is known to extend from central Iowa hundreds of miles northwestward into South Dakota, if not westward into Nebraska.

THE GLACIAL LAKE AND MARSH REGION OF NORTHWESTERN IOWA, SOUTHWESTERN MINNESOTA, AND EAST CENTRAL SOUTH DAKOTA

The Ruthven and Estherville observational areas (chapters 5 and 6) rather typify the glaciated wetlands of the north central region of the United States except for the changes that accompany the gradation of the northern prairies into the northern great plains. The marshes of northwestern Iowa are but remnants of those existing before settlement by the white man. Throughout the 6,000,000 acres of tall grass prairie comprising the original marsh-interspersed agricultural lands that were chiefly located in that part of the state, practically each 40-acre tract had at least one pothole (Bennett, 1938). The first settlers had sufficient upland prairie to farm so that they did not attempt

drainage. Then, by the late thirties, Iowa had left only about 50,000 acres of more or less marshy wetlands, mostly in state ownership. Artificial drainage on a similar scale has occurred in parts of southeastern Minnesota and eastern South Dakota. As a rule, however, more extensive marshy areas remain within the next several hundreds of miles northward and northwestward from the Ruthven and Estherville areas.

In the Ruthven area are other bodies of water besides those kept under intensive observation. Trumbull Lake and Lost Island Lake, of 1,190 and 1,260 acres, respectively, are open water, wind-swept lakes having little emergent vegetation, hence frequented by few muskrats except in sheltered places. In the falls of 1936 and 1939, the shores of these lakes were heavily used by miserable transients, fighting among themselves, feeding upon bivalves and fishes, and otherwise betraying their insecurity.

Contrasting changes over the years are illustrated by Barringer's Slough (about 1,000 acres) and Dan Green's Slough (340 acres). The latter was from 1932 through 1935 in splendid condition for muskrats, having the equivalent of about 315 breeding pairs in May, 1935. In the years following, the vegetation deteriorated, presumably as a result of high water levels maintained by a dam and the activities of a large population of carp. By the spring of 1936, Green's Slough had a lodge-dwelling population of about 132 pairs plus bank dwellers. For the next decade and a half, hardly any muskrats lived on or about the main body of water. On the other hand, Barringer's Slough was habitable for muskrats only in limited places during the thirties, when its status varied from that of a dry marsh to an open water lake. In the forties, a combination of natural and artificial changes made it the best muskrat marsh in the Ruthven area, although it did not then maintain its muskrat populations at any noticeably uniform level.

The Spirit Lake-Okoboji area near the Minnesota state line consisted mainly of the summer resort type of waters, with occasional fair to excellent muskrat habitats in bays or adjacent marshes (Sigler, 1948).

The Big Sioux River drainage, which has its source in northeastern South Dakota, north of Watertown, and extends southward to its junction with the Missouri River at Sioux City, Iowa, is now well within the known range of *zibethicus*. How long this has been the case is undetermined. This drainage system included part of my Brookings County (South Dakota) hunting, fishing, and trapping grounds, 1915–28 (see Appendix F). South Dakota naturalists whom I then knew believed that *cinnamominus* was the resident subspecies. In the later years of my trapping, after I had had some college training in zoology, I observed many individual muskrats that, on the basis of size and coloration, might have been more convincingly assigned to *zibethicus* than to *cinnamominus;* but some also looked like *cinnamominus*. My present guess is that the population consisted substantially of intergrades.

The terrific droughts of the early and mid-thirties all but wiped out the resident muskrats over county-wide areas, and repopulation presumably took place chiefly through movements from *zibethicus*-dominated areas downstream, perhaps from as far as northwestern Iowa. A single highway victim picked up north of Arlington, South Dakota, August 27, 1939, was identified as *zibethicus* by Dr. H. H. T. Jackson of the U.S. Fish and Wildlife Service.

THE CENTRAL PRAIRIES OF SOUTHERN IOWA AND NORTHERN MISSOURI AND THE "HILL COUNTRY" TO THE SOUTH AND EAST

As the northern prairies extend down toward south central Iowa, the resident muskrats become more and more stream-dwelling. Still farther south, muskrats live in oxbow marshes or artificial lakes much as they do in the more northern glacial marshes and lakes, though subjected to shorter and more benign winters. Trends noted in southern Iowa, northern Missouri, and southeastern Nebraska were toward greater dependence of the muskrats upon corn or soybeans, increased raiding of gardens and orchards, year after year maintenance of elaborate burrow systems in hard clay subsoil. Southern Iowa muskrats living in rivers or ditches from which most vegetation has been washed away from the banks may almost have to get up into cultivated fields to feed and, once finding themselves in the midst of an edible farm planting, they certainly can take advantage of it. I never saw elsewhere the intensity of foraging on windfall apples that I did in southern Iowa in October and November, 1933, but neither did I ever see elsewhere so many and such big orchards in close proximity to small streams well populated with muskrats.

At peak levels, the southern Iowa muskrat densities for comparable small stream (other than ditch) habitats appeared to be about the same as in central Iowa. A farmer-trapper in Davis County caught about 80 muskrats per mile in the fur season of 1933–34 from a small corn-bordered stream. Southern Iowa ditches are inferior to central and northern Iowa ditches for muskrats roughly to the extent that they are fed by surface flows rather than by tiles. Many southern Iowa ditches are merely straightened natural streams.

Skunk River, which has shown close to optimum attractiveness and habitability for muskrats south of Cambridge in central Iowa (Chapter 11), becomes less favorable for muskrats as it grows larger, flowing southeastward to enter the Mississippi River near Burlington. At its wider places, muskrats have much the same problems of living as they have along the Mississippi River bordering the eastern side of the state. Their best habitats along lower Skunk River are oxbows or the mouths of small tributary streams. This also typifies the situation along the central to lower reaches of the Des Moines River, Iowa River, and Cedar River of southeastern Iowa.

In southwestern Iowa, the larger rivers are smaller than in the southeastern part, except for the Missouri River itself. The Missouri River offers, I would say, less habitat to the muskrats than does the

Mississippi River bounding the opposite side of the state. Among the more important of the Missouri River oxbow marshes of southwestern Iowa are Lake Manawa, south of Council Bluffs, and Forney's Lake, north of Thurman.

When I saw it in mid-October, 1947, Forney's Lake was heavily grown to yellow water lilies as well as emergent vegetation in places, but muskrats were scarce, reputedly because of a recent die-off. Lake Manawa, looked over in mid-October, 1948, had a zone of about 50 yards of exposed mud-margin. Nearly all of the muskrats were restricted to one shore, which had heavy marginal growths of narrow-leaved cattails and burrow systems and corresponding lodges at about 50-yard intervals. A 2-acre tract of dead cattails (probably killed by previous high water) had, at the time of this visit, 29 muskrat lodges of varying sizes and freshness, and the shore growths of cattails were crossed by muskrat trails and riddled with diggings.

The stream-dwelling muskrats of southwestern Iowa seemed more susceptible to drought than those of the southeastern part, the southwestern streams being rather characterized by deep channels and steep banks, both in natural and straightened watercourses. Within the banks of the larger streams — comparable in size to Squaw Creek and Skunk River near Ames — there were few real pools in sight during the dry fall of 1947. Oxbows, however, had good muskrat signs, though they were mostly going dry.

According to Bennitt and Nagel (1937), northern Missouri had more muskrats than the southern part at the time of a survey made, 1934–35. Muskrats by then had been decreasing for years, partly in consequence of the drainage of 1,800 to 2,000 square miles of marshy land that had taken place since early in the century. This left most of the suitable muskrat habitat restricted to the bayous, chutes, drainage ditches, and a remnant of swampy land — less than 10 per cent of the muskrat habitat originally present. But, in recent years, many artificial lakes and great numbers of farm ponds have been created both in southern Iowa and in Missouri, and these furnish considerable muskrat habitat. The muskrats of the ponds having good stands of cattails and other marshy emergents live as they do in oxbow or glacial marshes. Missouri's largest lake, the artificial Lake of the Ozarks, covers over 60,000 acres and has some muskrat habitat and muskrats in places. The Ozark region also has thousands of springs, including many big ones, and these and associated brooks and larger streams have places where muskrats live, usually at low densities.

The subspecies *zibethicus,* though limited in Kansas to the southeast corner (Hibbard, 1933; Black, 1938; Cockrum, 1952), intergrades with *cinnamominus* over most of the eastern part of the state or that known as the Central Lowlands. Black referred to the Flint Hills, dividing the Central Lowlands from the Great Plains to the west, as being the greatest barrier or break in the distribution of all forms of vertebrate life in Kansas.

I have been unable to find definite proof of *zibethicus* in Oklahoma, but it, or at least its intergrades with *cinnamominus,* should occur in the northeastern part of that state, as in southeastern Kansas. Blair (1939) wrote that the muskrats in the Ozark region would probably be referable to *zibethicus.* Relating to the Oklahoma part of the Ozark biotic district, Blair and Hubbell (1938) wrote of clear, cold, largely spring-fed streams in a dissected plateau, of much underground drainage and an abundance of sinks and caves. Dellinger and Black (1940) felt that *zibethicus* was increasing in the Arkansas Ozarks. A recent paper by Sealander (1956) shows that *zibethicus* is nearly statewide in distribution in Arkansas, except in the extreme southeastern part of the state. Expansion of the rice-raising industry and irrigation has created much new favorable habitat.

Southward through Arkansas into Louisiana, the wetlands become more and more those characteristic of the Gulf States, with cypress swamps and bayous and, of course, the widening Mississippi River. I cannot trace the thinning of the range of *zibethicus* through Louisiana on the basis of available information, but Lowery (1943) reported that muskrats were not uncommon in the fresh-water lakes around Baton Rouge. At that time, the Louisiana State University Museum had 24 specimens, and the specimens showed intergrading between *zibethicus* and *rivalicius.* O'Neil (1949) referred to an approximately 200-mile gap between the ranges of *zibethicus* and *rivalicius.*

Eastward and southeastward from southern Missouri, the range of *zibethicus* may be chiefly classed as river bottomlands or as the dissected Ozark-Appalachian "hill country." Some of the rivers are large, and great floods of the Ohio and Mississippi rivers, in particular, have their own ecological impacts on muskrats and muskrat environment. Frison (1938) referred to southern Illinois as the part of the state having the lowest production of muskrat pelts, explainable by unstable water levels and absence of marshes.

In 1930, I saw some of the muskrat habitat of central Kentucky at about the same time that Bailey (1933) worked there. He then noted a scarcity of individuals but a general distribution along streams and in ponds and marshes. Mostly, the muskrats lived in banks and fed upon shore vegetation. In a county described as typical of the eastern mountainous section of Kentucky, Welter and Sollberger (1939) took several specimens from a creek where the banks were worn smooth by the animals. The muskrats were very common at a pond, from which they made daily visits to corn fields over well-traveled paths. The hills were steep and eroded, and the narrow valleys were subject to flooding.

Tennessee is still well within the geographic range of the muskrat in southeastern United States but may hardly be considered as offering much good habitat. According to Kellogg (1939), *zibethicus* formerly occurred in most of the streams and ponds. Muskrats were reported as getting scarce in Fayette and Shelby counties after the drainage of

the cypress swamps. A few muskrats were trapped each year in the marshes around Reelfoot Lake, which was formed by earthquake, 1811–12, in the Mississippi Valley of northwestern Tennessee and southwestern Kentucky. Kellogg found them fairly common during October, 1937, along the Cumberland River and tributaries west of Indian Mound.

Dr. Vincent Schultz, formerly of the Tennessee Game and Fish Commission, has given me a great deal of information concerning the recent status of muskrats in the state. From a letter and enclosures of September 26, 1951:

> It appears from these figures . . . that the best muskrat habitat is in the East Tennessee Valley portions of the Plateau Slope of West Tennessee and the Mississippi Bottoms. . . . Throughout my travels in all Tennessee counties I have never seen a good cattail marsh like one finds in the Midwest. In fact, I have never seen a muskrat house but have been told that they occur in the sawgrass of Reelfoot Lake. . . . The soils of the Plateau Slope of West Tennessee . . . are very sandy and erode easily. . . . I have been informed that . . . [muskrats] occur only where stumps, sod or other materials hold the soil in place.

Komarek and Komarek (1938), in working with the mammals of the Great Smoky Mountains of the Tennessee-North Carolina boundary, found muskrats foraging in a cane patch as well as feeding on riverbank willow shoots. The Highlands Plateau, lying southeast across the western tip of North Carolina from the Great Smoky Mountains and having similar climate and biota, has a few muskrats. Odum (1949) mentioned their occurrence on small artificial lakes in the region.

Wiebe (1946), in exploring possibilities for improving conditions for migratory waterfowl on the great artificial impoundments of the Tennessee River in northeastern Tennessee, discussed the extreme water fluctuations due to human manipulation, and one may readily keep muskrats in mind as well as waterfowl. Annual drawdown in storage reservoirs for flood control may exceed 100 feet but in mainstream reservoirs is generally less than 10 feet. With reference to pools of relatively constant level for improving waterfowl habitat on the TVA, Wiebe also wrote that these had the additional advantage of providing a stable habitat for muskrats.

THE SOUTHEASTERN EDGE OF THE MUSKRAT'S GEOGRAPHIC RANGE IN THE UNITED STATES

Freeman's (1945) distributional map of *zibethicus* in Mississippi shows that the modern range of the subspecies includes about the northeastern two-fifths of that state. He expressed a view that the animals probably first entered the state in relatively recent years via the Tennessee River and slowly spread southward. They have been artificially stocked in at least four of the southern counties. Yeager (1941), giving an historical account of the fur animals of the Delta

region of northwestern Mississippi, an area of 8,000 square miles of bottomland between the Mississippi and Yazoo rivers, never knew muskrats to have been present there. James R. Henry (letter to Dr. H. M. Harris, March 14, 1949) did find a few muskrats of this subspecies at the northeastern tip of the Delta "in small lakes and ditches in the Moon Lake region of Coahoma County and in the Coldwater River south of the Arkabutla Dam in Tunica County." The Moon Lake muskrats built lodges and at one time were fairly numerous, though reduced in numbers in 1946–47.

The report by Freeman is most informative concerning *zibethicus* in Mississippi. Drainage systems having the most muskrats are the Tallahatchie, Big Black, Tombigbee, and Surcanotchee rivers and their tributaries. When beavers live along a stream, more muskrats are found around the beaver ponds than on other parts of the same stream. He recognized no barriers or limiting factors to prevent muskrats from inhabiting the wetlands of the entire state of Mississippi. Big Black River, which has muskrats in its upper part, flows through several counties that do not have them. The Chickasawhay River has a good population on some of its tributaries north of Waynesboro, then flows more than 100 miles through a muskrat-vacant country before reaching the Jackson County marshlands. Pearl River has muskrats above Jackson, but it is 175 miles between these and the *rivalicius* muskrats in the coastal marshes to the south. Practically the same food plants are to be found along the southern Mississippi streams as along the stretches frequented by muskrats farther north.

Yeager (1937), writing of 1920–26 fur yields from a farm in Webster County in the middle of the *zibethicus*-occupied part of Mississippi, mentioned muskrats as occurring in small numbers in an area where corn and oat fields extended to the creek banks.

Eastward from Mississippi, the range of *zibethicus* includes nearly all counties in Alabama, but Arant (1939) and, later, Barkalow (1949) reported the subspecies as being scarce in the southern counties. The latter author doubted its presence in some counties, even in 1942 after continued general increase. According to Beshears and Haugen (1953), Alabama has approximately 10,000 farm ponds impounding an estimated total of 35,000 acres of fresh water, and the muskrats have become established in many of these ponds. Arant wrote that this form had extended its range in southern Alabama after Howell (1921) had not found it there.

Howell found it difficult to understand why *zibethicus* did not range all of the way down to the coast, for environmental conditions seemed as well suited to it in southern as in northern Alabama counties. He cited a trapper of long experience, C. W. Howe, as stating that muskrats first appeared near Linwood, Pike County, in 1906, and became quite plentiful on the upper Conecuh River between Troy and Union Springs, where none could be found in 1898. Howe found unmistakable signs of muskrats in 1912 along Little River, which is about 50 miles NNE of Mobile. In the spring of 1916, he saw

a single stray individual still farther south, at Twelve Mile Island in Mobile River.

Hamilton (1943) shows the mapped range of *zibethicus* as covering only about the northwestern two-fifths of Georgia and South Carolina and the western half of North Carolina. As muskrat habitat, the Piedmont region and the southern Appalachians may be compared with that of eastern Tennessee – of generally marginal character but still having places where limited numbers of muskrats might live. In Georgia, the muskrat is an important fur resource in the Piedmont only (Jenkins, 1953).

The nearly muskrat-vacant parts of Georgia and the Carolinas do have some muskrats outside of what may be regarded as their established range. William P. Baldwin, Jr., of the U.S. Fish and Wildlife Service, informed me (letter of January 28, 1949), for example, of finding *zibethicus*

> in South Carolina at the Jack's Creek impoundment of the Santee National Wildlife Refuge, Clarendon Co., located on a portion of the newly constructed Santee-Cooper reservoirs. . . . E. B. Chamberlain, Curator of Vertebrate Zoology of the Charleston Museum (S. C.) . . . stated that the eastern-most S. C. record of muskrat that he had was one taken a few miles west of my location, on the Santee River prior to flooding of the reservoirs. This general area is approximately 90 miles inland from the Atlantic Ocean, and well above the limit of tidal action; it is possible that the new reservoirs may facilitate the rat's spread to within 30 miles of the coast. In this area the rats exhibit the usual scarcity associated with marginal populations.

The absence of true muskrats from southern Georgia and all of Florida has long mystified naturalists. In the spring of 1929, I saw representative parts of this region in the course of field trips with that observant outdoorsman, H. L. Stoddard. As we waded swamps and streams, we made comparisons with northern muskrat habitats and tried to think of explanations for the range of the species thinning out and ceasing in the Southeast. In 1948 and 1954, we talked about this again, still without arriving at any convincing explanations.

I recalled the Wakulla River and bordering cypress swamp in northern Florida and felt that, if these had been located a few hundred miles to the northwest, they surely would have had muskrats. In southern Georgia, I saw a great amount of terrain that never would be classed as good muskrat country, but I could not see why it should not have some muskrats along its streams. The ecological counterparts of the region in Virginia would not have large numbers of muskrats but probably would have some, much as in marginal stream habitats of Tennessee. The upper reaches of the rivers flowing into the Gulf of Mexico through southern Georgia and northern Florida have their muskrats, but the animals dwindle and disappear about half way to the Coast.

Many authors refer to the little so-called round-tailed muskrat *(Neofiber)* as taking the place of *Ondatra zibethicus* in Florida wet-

lands. I do not feel that this is strictly true, and any implications of competition between *Neofiber* and *Ondatra* are fallacious. *Neofiber's* range is almost confined to most of Florida and to the Okefinokee Swamp area of southeastern Georgia. Jenkins told me in conversation in 1956 that the distance separating the ranges of *Ondatra* and *Neofiber* was about 100 miles. (For a description of the habits and ecology of *Neofiber,* the reader may be referred to Harper [1927] and Schwartz [1953]).

Baldwin, in his aforementioned letter of January 28, 1949, emphasized coastal and downstream tidal fluctuations, lack of wide expanses of sustaining habitat during catastrophic periods, and scarcity of certain vegetative communities as factors limiting the distribution of muskrats in the Southeast (see Appendix G).

True muskrats, *Ondatra zibethicus,* once did live in what is now Florida, during the Pleistocene (Sherman, 1952).

THE UPPER MISSISSIPPI VALLEY AND EAST CENTRAL PRAIRIES

The Central Prairies extending eastward from central Iowa to the Mississippi are more or less dissected. They have chiefly stream-dwelling populations of muskrats except in artificial impoundments and in the oxbow marshes of the larger stream valleys. East of the Mississippi in the northern and central parts of Illinois, Indiana, and Ohio, evidences of recent glaciation are more apparent, but the main muskrat habitats are still of stream types or stream-derived.

The upper Mississippi River furnishes good examples of certain types of habitat. From 1932 to 1935, I made a number of field trips in the vicinity of Lansing, northeastern Iowa, and spent a considerable part of the summer of 1940 working on that river or its bottomlands. Throughout my Lansing investigations, I had the advantage of the advice and sometimes the company in the field of an excellent riverman, W. E. Albert, Jr., then of the State Conservation Commission. On several occasions, I inspected parts of the Upper Mississippi Wildlife Refuge with Ray Steele, the manager.

In the early thirties, before the profound changes resulting from engineering manipulation of the upper Mississippi, the best local muskrat marshes were then, as now, bottomland oxbows, though the species lived in varying numbers along many of the smaller ramifying stream channels and up the mouths of side creeks draining from the higher land. Densities of muskrats were sometimes very high on the better oxbows during years of abundance.

A memorandum from Aldo Leopold dated December 9, 1941, refers to a catch of forty muskrats from a three-acre pond in Henderson County, Illinois, across the river from Burlington, Iowa. "There were 7 houses in this pond, but a large number of additional rats inhabited bank burrows. The pond is bordered on one side by the railroad bank, hence opportunities for bank burrows are especially good."

The site of the old Iowa State Game Farm on an island above

Lansing was also a splendid place for muskrats when I first saw it in 1932, and trappers took several hundred muskrats that fall from, or from the vicinity of, 68 acres of state-owned bottoms. This was one of the areas that flooded and lost its productivity for muskrats after installation of lock dams and the nine-foot channel.

In the summer of 1940, the river habitat differed greatly according to localities. For some miles below the dams, conditions for muskrats were in many ways similar to what they had been before the nine-foot channel. Virgin timber had not been cut, and on the whole, about two-fifths of the original bottomland stand remained. Areas extending about a mile below the dams were subject to rapid fluctuations of one and a half to two feet due to "pile-up" as water was let out of the dams. Numerous small, shallow areas were covered with muskrat lodges and grown to sedges, reeds, and some cattails, but with bottoms of sandy rather than mucky consistency. Depths of the marshy impoundments varied from a few inches to about seven feet, depending upon the configuration of the channels and islands before flooding. Some of the partly submerged stump areas (from which the trees had been cut in the course of the engineering program) were literally dotted with lodges in bulrush, sedge, and smartweed areas. I saw one tract of about three square miles in early May in which the winter's lodges and feed houses must have averaged twenty or more per acre. The stumps were important in providing anchorage for lodges, and I could see many shallow burrows extending up under stumps that did not have lodges.

Less spectacular muskrat retreats were seen in small sloughs and marshes on islands. These and oxbow marshes along the shore were often well grown to burreeds and cattails much as were comparable glacial marshes of the northern prairies. They furnished far better habitats than the shaded ponds and bayous of virgin timber. Muskrats lived either in lodges or in shallow burrows. Streamlike channels through wooded parts usually had few muskrats, and the wide, lakelike tracts above the dams had muskrats only in the banks. As muskrat habitat, the drastically altered upper Mississippi River bounding eastern Iowa showed about all gradations from the very poor to the very good, with most of it being very poor and the superior places being sharply localized.

(Appendix H relates to special local studies of upper Mississippi muskrats.)

The streams of northeastern Iowa may be considered fairly typical of those of the nonglaciated or driftless area of southwestern Wisconsin and southeastern Minnesota. In July, 1940, these had about the populations of muskrats that one would expect to find in rocky brooks and small creeks having occasional pools and little muskrat food besides watercress *(Nasturtium officinale)* and the bank vegetation of pastured or wooded streams. The best habitats were situated in downstream stretches, which graded off into Mississippi bottomland bayous. Some of the upper stretches would have no midsummer signs of musk-

rats in one- or two-mile samples, often not even in attractive-looking places. One stream having a width of about 25 feet and a prairie-like appearance had family groups of muskrats at 200- to 300-yard intervals. Some cattail-bordered artificial ponds near a state fish hatchery had muskrats. In a three-quarter-mile stretch of what was known as one of the best trout streams in Iowa, only one place — a big pool under a rocky ledge — had any muskrat signs.

On the Wisconsin side of the Mississippi, the bottomlands of the Wisconsin River offer big-river type of habitat — good and poor — for many miles, with tributaries similar to those described for northeastern Iowa. Upstream in the Mississippi drainage, many of the best muskrat habitats are river marshes — not only oxbows but border zones and bends of wide streams grown to cattails and like emergents and sometimes covered with muskrat lodges. The Minnesota River, flowing generally eastward through southern Minnesota to join the Mississippi at St. Paul, has some of the best examples of these river marshes, which in some years are practically saturated with muskrats.

In the fall of 1932, I saw near Shakopee, Minnesota, one of the highest densities of lodges of my experience and learned the next year from Dr. R. G. Green of the University of Minnesota that this area had suffered great losses from epizootics of undetermined etiology. McCann and Highby (1942) wrote of the Minnesota River bottoms as being literally dotted with occupied muskrat lodges in the fall of 1941. In late summer, 1948, I made observations on these river marshes and found them to be in attractive condition for muskrats, though decidedly underpopulated. Concerning unfavorable situations, Highby (1941) wrote of tremendous losses of Minnesota muskrats through freezing during the winter of 1939–40, following the long, dry Indian summer that was observed to have had such drastic consequences for the Iowa muskrats.

Eastward into the central Wisconsin sand plains, muskrats may or may not occur in abundance. Hamerstrom and Blake (1939b) introduced one of their papers with the following description of a drained area near Necedah:

> Central Wisconsin is a typical example of footless drainage in the Lake States. Once with more marsh than dry land, the country was ditched about twenty-five years ago in an ill-starred agricultural venture. The marshes were drained and duly planted to crops but the expected profits — except to the land speculators — failed to materialize. Farms were abandoned one by one, fires ate out most of the peat, and the job was called a failure.
>
> From the standpoint of the water-loving furbearers it was more than a failure; it was a disaster. With the marshes and swamps gone, the streams straightened . . . they had only ditches to turn to. . . . [On 10,000 acres, 200 miles of ditches comprised] almost the only remaining habitat for muskrat, beaver, otter, and mink. . . . A review of the seasonal cycle clearly shows the weakness of the drainage ditch environment: spring dispersal of a small breeding nucleus over a greatly expanded range; in summer the range drying up, population on the move but making a strong recovery none the less; by late autumn muskrats many and well distributed; winter decimation. . . . Ditch heads and short laterals were the preferred breeding grounds in spring. As

the season advanced the water in these places dwindled to small pot-holes. . . . A few fairly stable breeding areas were provided by such favorable spots as beaver ponds, deep holes in bends or behind drift jams, and some of the deeper main ditches. . . . The most probable cause of the winter decrease lies in an unbalance between food and water supplies. In the ditches cited as an example, the two main foods — bur-reed and pondweed — die back in winter and do not have fleshy roots. Root foods were almost wholly lacking in the water and along the banks. Ice reached the bottom during the winter. . . . Such a condition, while it does not kill every wintering muskrat, unquestionably reduces carrying capacity to a fraction of its potential.

The extensive activities of beavers in damming all types of central Wisconsin ditches and thus indirectly creating muskrat habitat had been described by the same authors in an earlier paper (Hamerstrom and Blake, 1939a).

From July, 1929, through June, 1932, I carried on field studies on many areas in south central Wisconsin (Errington, 1945). While my work was not centered upon muskrats, I covered my study areas with sufficient of an ex-trapper's viewpoint so that I generally knew fairly well the status of muskrats in representative stream areas and glacial lakes. Some of the big lakes — Mendota, Monona, Kagonsa, Koshkonong, for example — had bays or outlying waters grown to cattails and bulrushes and comprising very good muskrat habitat. In general, the muskrats were present or absent about as one might expect from the quality and extent of the habitat available to them.

In the neighborhoods of Beaver Dam, Fond du Lac, and Oshkosh are many muskrat marshes, including some operated commercially as fur-producing units. The site of one of the pioneering ventures in marsh management — the well-known aquatic nursery of Clyde B. Terrell — is at Oshkosh, and "rat-ranching" on privately owned or leased wetlands is a substantial industry.

One area with which I became particularly familiar during my 1929–32 Wisconsin residence was the marshy zone of the southwest corner of 200-acre Lake Wingra, in the University of Wisconsin Arboretum. This corner had a stand of cattails, and between it and a big spring to the southwest lay a boggy tract grown to willow, alder, and birch. The fairly abundant muskrats lived in a variety of habitats, from those of continuously flowing brooks and spring pools to those of the true marsh. In winter, steaming wet spots could be seen in some places away from the principal spring. The less favorably situated muskrats came out in the snow to forage or to wander along the lake shore or be killed by dogs or traffic on the paved streets nearest the marsh and bog. When I again saw this place in late April, 1949, the marshy southwest corner looked about as it had two decades before, but the bog had a much thicker and taller growth of willows and alders and had become more of a northern-type swamp.

The celebrated Horicon Marsh east of Beaver Dam in southeastern Wisconsin was once drained along with so many other fine waterfowl and fur-animal habitats. Later restored by public agencies, it serves as state and federal wildlife refuge and also as a fur-producing area.

Since the fall of 1946, the Wisconsin Conservation Department has been investigating problems of muskrat management on 10,000 acres of state-owned marsh. These studies have been centered to a considerable extent on measuring mortality and productivity of muskrats on given areas of marsh and the responses of the species to experimental manipulations, particularly to the level-ditching measures that are in common use on private "rat ranches" (Anderson, 1948; Mathiak, 1953, 1956). In April, 1949, Mathiak showed me representative parts of Horicon Marsh, on both state and federal holdings. Practically all types of marsh characteristic of the region were to be seen on around 30,000 acres that were then wet. In the southern part were big expanses of open water interspersed by growths of emergent, shallow-water vegetation. In the northern part, a new road grade had a nearly dry stand of cattails and reeds on one side and a flooded tract of dead willows and floating cattail clumps on the other. The road grade, itself, was packed with tracks of evidently transient muskrats.

Conservation department reports from Horicon Marsh by Mathiak and W. C. Truax reflect many phenomena of sorts that may be noted about major marsh areas. The listed acreage of muskrat habitat increased from 3,150 acres in 1946 to 4,200 acres in 1947 as a result of higher sustained water levels. For the fur season, 1946–47, 8,209 muskrats (0.92 per lodge or one per 2.6 acres of habitat) were harvested, compared with a catch of 9,535 (0.62 per lodge or one per 2.3 acres of habitat), 1947–48. For 1946–47, it was estimated that two-thirds of the resident population had been harvested, compared with only one-third in the 1947–48 season, which would indicate populations of around 12,300 and 28,500 muskrats, respectively. The trapping yield for the 1948–49 season was 24,654, despite a considerable period of low water. Ecological contrasts between 1948 and 1949 were very sharp, as large tracts of flooded marsh in the south end lost their emergent vegetation in 1949. On the other hand, the deterioration of muskrat habitat in the south end in 1949 was offset by bringing formerly dry areas into production. The 1949 catch was 28,678.

Horicon Marsh has been the site of losses of muskrats from both tularemia and hemorrhagic disease, according to Dr. A. M. McDermid, then Veterinary Pathologist for the Conservation Department (letter and memorandum, August 29, 1946). An epizootic of the two diseases occurred there at least in March and April, 1946. Losses from the hemorrhagic disease were observed at times during later investigations but not on any very serious scale. I saw evidence of local dying during a week spent with Mathiak in April, 1954. Some private "rat ranches" lying to the north of Horicon Marsh were known to have suffered heavy losses of muskrats from hemorrhagic disease in the fall of 1947 (Clyde B. Terrell, letters of December 2 and 9, 1947). Mathiak and other Wisconsin fur-animal investigators with whom I talked in April and December, 1949, and during the 1954 visit, told me that losses on some private marshes had continued to be serious.

In Illinois, the highest catch of muskrats per trapper is in marsh

areas of Lake and McHenry counties (Frison, 1938). These counties are in the northeastern tip of the state, where the lake chains are a continuation of those of southeastern Wisconsin.

Most of northern and central Illinois offers muskrats the sort of living conditions that are also characteristic of Iowa streams. Yeager (1942; 1943) did much work on drainage ditches of black prairie farm lands of east central Illinois, where he considered ditches basic habitat for the muskrats. The Illinois prairie has a total of about 6,500 ditch miles, or one mile of ditch per 2.5 square miles of land, not including creeks, rivers, etc. The ditches vary from 6 to 60 feet in width (average 12 feet) and from 3 to 12 feet in depth (average 6 feet). Fewer than 10 per cent have running water at all seasons except during years of evenly distributed rainfall. Many dry up completely during very dry seasons. Yeager gave examples of maximum catches averaging up to 73 muskrats per mile of ditch, 1940–43.

Brown and Yeager's (1943) illustrated bulletin on fur resources describes characteristics of each of the several physiographic regions of the state as well as the muskrat habitats found therein. These authors wrote that, for the two trapping seasons of 1938–39 and 1939–40, the greatest production of marsh muskrats came from the glacial lakes region of northeastern Illinois, where the yield averaged about 50 per square mile. Although stream habitats were generally less favorable than marsh habitats, total catches of stream muskrats in Illinois exceeded those of marsh muskrats insofar as a much larger range was occupied by the stream-dwellers. The comparatively low catches of two to five muskrats per square mile over southern and much of western Illinois were explained in terms of the intermittent character and lack of aquatic vegetation of the streams, as well as by heavy trapping. Water polluted by oil sludge or residues from coal mines damaged in varying degrees the muskrat habitats along the Rock, Galena, and Upper Illinois rivers and in the oil centers throughout southern Illinois.

Bellrose and Brown (1941) compared the status of muskrat habitats of lakes in the Illinois River Valley. They brought out that the vegetation upon which muskrats depended for food and shelter was limited chiefly by seasonal changes in water levels. Lakes with stable water levels (impounded waters, particularly) had less abundant vegetation of emergent types than did lakes with semi-stable water levels. Semi-stable bodies of water therefore contained the more muskrat houses. Cattail communities, although making up only 0.2 per cent of the aquatic and marsh plants in the lakes mapped by these authors, supported more muskrat houses per unit area than did the other plant communities. River bulrush was of great value to the muskrats and one of the most abundant of marsh plants.

Bellrose and Low (1943) wrote of the effects of floods and droughts on the survival of muskrats in the above types of bottomland waters. Characteristically, the lakes that lie on either side of the Illinois River are shallow and flat-basined. With normal river stages, they

have little or no current. These lakes vary in size from a few to 6,500 acres. Three of them — Douglas, Rice, and Chautauqua — have been among the most productive of muskrats in the Illinois River Valley. Rice Lake, in 1940, had 413 acres of river bulrushes and 317 acres of American lotus. Lake Chautauqua had a periphery of 140 acres of marsh smartweed *(Polygonum muhlenbergii),* several hundred acres of black willow *(Salix nigra),* and about 45 acres of duck potato. Douglas Lake was principally a river bulrush marsh of some 1,300 acres.

Ecological changes following the permanent artificial flooding of a tract of wooded bottomland at the confluence of the Mississippi and Illinois rivers have been summarized by Yeager (1949). After eight years of flooding of timbered areas, the trees were dead. Buttonbush was more tolerant, about 40 per cent surviving except when deeply submerged. Cattails, duck potatoes, and sedges were the most common marsh plants invading the flooded bottoms, with smartweed, wild millet, and rice cutgrass growing on wet soil. Heavy growths of coontail and leafy pondweed, often covered in fall by masses of duckweeds, appeared in clear-water sloughs and lakes during the first four years of flooding. In 1943, 1944, and 1945, severe floods destroyed the submerged and emergent aquatic vegetation, but by the fall of 1946, several species were recovering.

The Kankakee marshes of east central Illinois and northwestern Indiana before the era of agricultural drainage were among the great habitats of aquatic wildlife, including muskrats, of the continent. According to Ling (1935), two trappers caught 7,634 muskrats from a tract of 1,000 to 1,200 acres, between November 1 and December 20, 1912, when the marsh froze over. They speared 1,300 more in a few days after freeze-up. Ling considered this a good muskrat marsh but not exceptional. A companion article by Bridges (1935) stated that, when La Salle discovered the Kankakee in 1679 at its source near South Bend, Indiana, it was perfectly described by its Indian name, "slow river flowing through a wide marsh." The marsh extended back from one to 14 miles from the banks of the Kankakee River in two great tracts: One was the "lower" or Grand Marsh of about 400,000 acres, and this remained flooded throughout the year. The "upper marsh" of about 600,000 acres was usually but not permanently flooded. In the summer of 1935, Bridges, visiting the area long after the old Kankakee marshes had been "drained and ploughed out of existence," referred to some fair-sized areas having been restored to a marshy condition.

EAST CENTRAL AND NORTHEASTERN UNITED STATES AND SOUTHERN ONTARIO, UP TO NEW ENGLAND

Eastward from Illinois, the prairie types of terrain soon change to those of the hardwoods, which originally covered most of southern Michigan, northern and central Indiana and Ohio and extended eastward into Pennsylvania and New York.

The Upper Peninsula of Michigan, which ecologically may be re-

garded as a continuation of northeastern Wisconsin, had at least one site of a pronounced response of muskrats to a diking and flooding program. According to a Fish and Wildlife Service news release, "Muskrats 'steal the show' at Seney Waterfowl Refuge," more than 10,000 pelts were taken in the fall of 1940 and spring of 1941 from parts of a 93,000-acre tract that previously had been regarded as inferior muskrat habitat. In the Huron Mountain region, studied intensively by Manville (1948), the muskrat is common in lakes and streams. There were 10 chief inland lakes from 10 to 775 acres in size in a block of 41,050 acres. The Huron Mountains themselves are described as an isolated range of granitic knobs and ridges.

Leedy (1948) described the ecological changes resulting from settlement of Ohio by the white man. Originally, that state was 95 per cent forested, with marshes occurring chiefly in the northern part. In addition to the cutting of the forests, the drainage of wetlands greatly altered the habitat for wildlife, including muskrats. Wood County alone has more than 2,000 miles of open drainage ditches, and the muskrats feed on corn, soybeans, alfalfa, and other crops grown in adjacent fields.

The muskrat marshes about Sandusky Bay, southwestern Lake Erie, are among Ohio's best known. Anderson (1947) reported a catch of 10,191 muskrats for the 1945–46 fur trapping on the holdings of the Winous Point Duck Club. Of a 4,400-acre area, 2,800 acres were marshy, having narrow-leaved cattails, river bulrushes, reeds, sedges, millet, and blue-joint grass. During the previous five years, cattail declines varying from 65 to 83 per cent on the different units had occurred. Tracts 20 acres in size that formerly had been covered by cattails became barren of muskrat food plants in this period.

Northeastward across Lake Erie from Sandusky Bay lies the Point Pelee National Park of Canada and the site of a biological investigation by Dr. C. H. D. Clarke in the spring of 1942. In his mimeographed report dated January 20, 1943, he wrote that "agricultural development has been so great in the Lake Erie region that Pelee Point is the only wild area left in Essex County [Ontario], and by far the best sample of the Southern Hardwood forest formation left in Canada." Following a résumé of the known history of muskrat populations beginning with the winter of 1919–20, he summarized his findings:

> The Point Pelee Marsh, including ponds, has an area of some 3,000 acres. Its water level fluctuates with Lake Erie. . . . [Open] ponds and wet meadows, extremes unfavorable to muskrats, reduce the actual first class muskrat range to about 1,000 acres. On this range it is doubtful if the population has ever greatly exceeded 5,000. . . . Really high populations occur only when the water level is high. . . . Decreases in the muskrat population come about through lowering of water levels often combined with restrictions of their winter foraging ability by freezing of underwater passages.

Also in southern Ontario is a privately-owned artificial marsh for which trapping and other records have been kept for many years

(Hewitt, 1942). The 1,250-acre marsh was dominated by cattails and bulrushes, and food (corn, potatoes, carrots, and marigolds) was also supplied artificially through the ice. The records show catches of 575 on 1,000 acres in 1930, 1,464 in 1931, 1900 in 1932, 2,125 in 1933, 2,222 in 1934, 2,416 in 1935, 3,121 in 1936, 5,227 in 1937, 6,351 in 1938, 7,815 in 1939, 5,250 in 1940, 7,300 in 1941, and 8,191 in 1942. Only for five winters are lodge counts available: 1,974 lodges for 1934, 2,383 for 1935, 2,770 for 1936, 4,041 for 1937, and 4,452 for 1938. The five lodge counts, if plotted on coordinate paper, line up much like the mid-slope of the Verhulst-Pearl-Reed logistic curve, with the probable upper asymptote beginning to appear just before the near-peak catch of 1939.

Northeastern Ohio and northwestern Pennsylvania afford some decided contrasts in muskrat habitats. The marshes and swamps themselves vary greatly. Some are tree-fringed with open-water centers and boggy margins; some, heavily grown to water lilies and swamp shrubs grading off into deciduous swamp forest of elm, ash, and maple; some show stages from pond lilies through bog heath to coniferous forests of black spruce and tamarack (Aldrich, 1943). The Pymatuning Lake reservoir of the northwestern corner of Pennsylvania has many muskrats at times, though conditions are not always favorable because of fluctuations of water levels. Douglas E. Wade (letter, July 30, 1940) referred to much movement of the species along the shore of this reservoir, as well as along small natural streams, during the drought summer of 1939.

During a ride through Pennsylvania in the spring of 1949, I was able to make some observations of muskrat habitats, and these were supplemented by information given me by biologists familiar with the region. There were some muskrats along almost all watercourses, but the general densities were sparse. Nothing resembling good muskrat habitat was seen along the larger rivers that were subject to repeated floodings, involving rises in water up to 15 or 20 feet. The creek-like tributaries in fertile farming country had accessible growths of scrub willow and cattails and often the corn of adjacent fields. They looked comparable to Keigley's Branch in central Iowa (Chapter 10). As the country grew more mountainous, the smaller streams had few muskrats. This could also be said of the larger streams, like the Yough River in southwestern Pennsylvania. Along the latter stream, however, there were some locally fair to good habitats. One was at the mouth of a tributary having stream-edge willows, and similar vegetation, and a little flood plain looked as if it might have had fair habitat had the water not been so foul with sewage and mine wastes.

The higher stretches of streams were rocky and nearly devoid of muskrat foods, and it could easily be seen why there should be a wide belt of nearly muskrat-vacant terrain along the crest of the Allegheny Mountains. While such a barrier would not be entirely impassable to muskrats at all seasons, it should be sufficient to discourage cross-country movements from one side of the divide to the other.

Lying between Pennsylvania and Kentucky, West Virginia has few marshes, but stream habitats in which muskrats live may be found in many places, as where corn or other agricultural or garden crops are planted near the water or where there are beaver-flooded areas. Swank (1949) described the role of beavers in increasing the habitat available for muskrats in the West Virginia mountains. There did appear to be some conflict between beavers and muskrats when the muskrats tended to burrow through dams during periods of low water, and ponds in which beavers were not active were often drained as a result of muskrat burrowing. However, it was evident that many muskrats lived with the beavers in the beaver lodges, though most muskrats lived in burrows in the banks. The muskrat lodges that were built in beaver ponds were the typical structures that muskrats build in marshy areas. One beaver pond had five muskrat lodges from which twenty-one muskrats were trapped in one season, but this was an exceptional pond. It was five years old, about three acres in area, and had extensive growths of emergent plants.

Handley and Patton (1947) list *zibethicus* as abundant in "streams, marshes, swamps, and ponds" in all counties of Virginia west of the Blue Ridge Mountains. The range of *macrodon* lies east of the Blue Ridge Mountains in that state.

The New Jersey coastal marshes comprise some of the best habitat of *zibethicus* in northeastern United States. The ranges of *zibethicus* and *macrodon* come close together here. Dozier (1947a) showed the range of *macrodon* as including nearly all of Delaware Bay, while Hamilton (1943) reported that specimens he examined from Cape May were typical *zibethicus.*

Cottam and Bourne (1938) gave the total area of tidal marshes extending along the coastal region from New Hampshire to Maryland as approximately 625,000 acres. Most of these marshlands have been ditched for purposes of mosquito control, with highly variable effects on their muskrat occupants (which shall be taken up later in the treatment of *macrodon).* Well inside of the geographic range of *zibethicus* in New Jersey, splendid fresh or brackish marshes for waterfowl and muskrats have been created by diking salt marshes.

A substantial amount of research has been done on the muskrat in the great marshes of western New York. Johnson (1925) wrote that no other single area of like size in the state compared with the Montezuma and Cicero marshes in muskrat production. Both Dozier (1945) and Heit (1949) regarded the fertility of the underlying black muck as probably an important reason for the superior physical condition of many of the muskrats that they handled in the Montezuma area, especially insofar as such fertility was reflected in growths of cattails and other characteristic marsh vegetation. Johnson's page 225 and Map 5 at the back of his bulletin show that the smallest muskrats and those with the thinnest pelts were found in the northern part of the state, including the Adirondack region, while medium-sized to small

muskrats were found in the southeastern part, including the Catskill region. He made no separation of mountain-dwelling muskrats and those of the lower valleys and wetlands of the same parts of the state, but one may easily see, in view of the inferior nature of much of their habitat, why the muskrats should tend to be undersized.

NEW ENGLAND AND SOUTHEASTERN CANADA

Dice's (1938) map of the biotic provinces of eastern North America shows that the region here to be discussed lies very largely in the Canadian biotic province. From northeastern Minnesota, northern and central Wisconsin and Michigan, and southern Ontario (except along Lake Erie), it extends eastward and northeastward to cover much of New England and southern Quebec and all of New Brunswick and Nova Scotia. Dice pointed out that New Brunswick does not differ greatly from northern Michigan in vegetation or in mammalian fauna and that the muskrat is one of the mammals ranging over most or all of the Canadian biotic province. Differing from prairie wetlands and east central forests, poorly drained situations in the Canadian biotic province have white cedar *(Thuja occidentalis),* balsam fir *(Abies balsamea),* tamarack, several species of spruce, with occasional hardwoods. If we visualize New England as something of a continuation of the rougher terrain of New York, we should also be able to appraise fairly well its general habitability for muskrats.

New England does have some good muskrat areas. The lower stretches of many rivers have marshy edges, either occurring naturally or as a result of human manipulation. Of the New England tidal marshes, the majority would appear ecologically similar to those of Long Island, New York, which have been published upon by personnel of the New York State Museum in discussions of mosquito control (Glasgow, 1938). The salt marshes have been largely ditched in a way not intended to drain in the usual sense but to hasten the outflow of tidal waters, and this engineering manipulation often did not fundamentally change the salt-marsh vegetation (Taylor, 1938).

Lake Champlain, on the northwestern border of Vermont, has extensive marshes associated with it, the muskrats of which have been studied by Seamans (1941). Lake Memphremagog, extending into Quebec from north central Vermont is classed with Lake Champlain with respect to habitat types and size of muskrat catches, and the rest of Vermont has its small ponds and streams.

Gashwiler (1948) described much of the muskrat habitat in Maine as consisting of small lakes or ponds, sluggish streams, beaver ponds, flooded bogs, or sedge meadows. Takos (1943, 1944, 1947) carried on his intensive studies of muskrats in central Maine on about 120 acres of cattail marshes and three and a half miles of sluggish stream.

Muskrats were totally absent from Kent Island (about 115 acres), in the Bay of Fundy, New Brunswick, when the Bowdoin Scientific Station was established there in 1935. They first appeared, according

to Gross (1947) in 1941, and then built up to astonishing numbers — as many as 1,400 have been taken during the April trapping — despite the evident inferiority of the habitat in which the majority of the animals lived. (See Appendix I for a résumé of the Kent Island situation.)

Mainland populations of *zibethicus* in New Brunswick are similar to those of Maine, occurring as expected in suitable habitats (Morris, 1948). In Nova Scotia, not only is the subspecies usually common in freshwater marshes but it is also found along tidal creeks and nearly all inland watercourses having muddy banks and aquatic vegetation (Smith, 1940). Rand (1944) cited manuscript or mimeographed writings of R. M. Anderson and C. H. D. Clarke to the effect that muskrats were abundant in the area of the Cape Breton Highlands National Park, which is at the northernmost tip of Nova Scotia.

Sheldon's (1936) account of the mammals of Lake Kedgemakooge and vicinity in western Nova Scotia give the reader an idea of the type of terrain to be expected as we follow the range of *zibethicus* northward into eastern Canada. This lake (which appears as Fairy Lake on most maps, has a rugged shoreline broken by peninsulas and by rivers and brooks, which connect it with other lakes. Muskrats were common in lakes and in rivers having muddy bottoms and were observed using channels and runways made by beavers in the bogs.

The Gaspé peninsula lying north of New Brunswick and south of the St. Lawrence River is about as far northeast as the natural range of *zibethicus* extends. Jean Duguay, of the Quebec Department of Fish and Game, outlined for me the approximate ranges of *zibethicus* and of *aquilonius* in that province (letter and enclosure of April 1, 1949). In southwestern Quebec, the forty-eighth degree of latitude is close to the southern limit of *aquilonius,* but a wide zone of intergrading between the two subspecies may be expected southeast of James Bay. Anderson (1934) wrote that *zibethicus* is found around both sides of southern James Bay and that it ranges southeast to the St. Lawrence River.

SOUTH CENTRAL CANADA AND NORTHERN MINNESOTA

Although the southwestern side of Hudson Bay is within the range of *albus, zibethicus* appears to be the dominant subspecies occupying a tremendous expanse of the Pre-Cambrian Shield wilderness of northern Ontario. This block of range of *zibethicus* includes much country that is the "real North," where subarctic living conditions impose handicaps to survival as severe as in any area occupied by the several subspecies that we think of as "northern." From the District of Patricia — where the land is probably as wild as anywhere on earth — to the north shore of Lake Superior and into northeastern Minnesota and southeastern Manitoba, there is an almost continuous succession of more or less wooded rocky hills, rapids-filled rivers, and lake after lake. But like New England, northeastern New York, and the

southeastern tip of Canada, the habitats suitable for muskrats are much restricted to quiet waters having marshy emergent vegetation.

I looked over a considerable area of northern Ontario in the summer of 1921, chiefly in the rugged Pre-Cambrian Shield between northwestern Lake Superior and Lake Nipigon and the immense coastal plain bogs and swamps of the Paleozoic Basin southwest of James Bay. Stretches of white water, with cascades and falls, were of frequent occurrence, and large rivers roaring through gorges invited neither residence nor passage of muskrats. Perpendicular rock faces (some rising from deep water to a hundred feet or more in height) of lake shores and islands could hardly furnish less attractive places for muskrats, especially where wave-beaten. An occasional bay with emergent vegetation or a widening of a river bordered by marsh plants sometimes did, sometimes did not, show muskrat signs. Small lakes with less precipitous shores had variable amounts of marshy or swampy edges, and some muskrats lived here as well as in numerous connecting channels or marshy spots in small muskegs. Robert H. Smith of the United States Fish and Wildlife Service informed me in 1948 that the Indians make locally good catches of muskrats about fifty or sixty miles west of James Bay, where there are some excellent wild rice marshes.

Muskrats are usually mentioned by mammal students working in the Pre-Cambrian Shield north of the Great Lakes, and when the subspecies is designated it is *zibethicus*. Clark (1938) referred to the subspecies as common in 1935 on Pancake River and small lakes and rivers in the vicinity of Pancake Bay, Algoma District, Ontario. A specimen I saw killed on a highway about seventy-five miles southeast of the Whiteshell Provincial Park, in the southeastern corner of Manitoba, in 1948, was almost certainly assignable to *zibethicus*. Snyder (1942) in his 1931 study of mammals in the Sault Ste. Marie region found that trappers there depended largely on muskrats in their fur harvests and that St. Joseph Island had some of the best muskrat marshes.

In 1950, I spent much of the second half of August in the Superior National Forest lying south of the Quetico Provincial Park, especially in areas recommended for study by Sigurd F. Olson and Milton H. Stenlund as being typical of the region. Lake 1 of the Kawishiwi River, an island-filled wilderness body of extremely irregular outline lying about twenty miles east of Ely, was intensively surveyed over a period of several days, and the locations of living muskrats were mapped. Only one tract of fair muskrat habitat was found in the area of about five square miles with which I became familiar, and that was in a three-quarter-mile stretch of sluggish stream in the midst of a swamp.

The above stream showed signs of perhaps a small family group per quarter mile, or of an estimated twenty muskrats along its length to the place where it dwindled in the swamp. The best food resources consisted of narrow-leaf cattail mixed with swamp shrubs, and this was the sole passably adequate wintering tract seen in the Lake 1

survey – and it was not so very good. What appeared to be a single muskrat lived at one of the rocky timbered islands adjacent to the mouth of the stream, and another lived a few hundred yards farther away; these left signs indicative of newcomers, probably subadults. About a mile out from the mouth of the stream was a third animal, probably also a newcomer and a subadult, then frequenting a beaver burrow in a shallow sedge-grown place between two islands. One other possible wintering site was found – a very poor one in a rocky shore, recognized by great quantities of clam shells surely dating back for many months, to spring if not to the preceding winter. This was about three-quarters of a mile from the mouth of the same small stream, and it had the appearance of a 1950 breeding territory occupied in late August by several muskrats, presumably members of a small family group. The total population of the five square mile sample area of Lake 1 should have been about thirty muskrats, as of late summer, 1950.

A two-mile stretch of the South Kawishiwi River (essentially a narrow lake) was worked without finding any sign of muskrats, whatever, though there were some attractive cattail growths in parts of the shore zones. One of the streams near Ely that Stenlund showed me looked like rather good habitat, with fringing growths of burreed, duck potato, and sedge, but the tract inspected had no current muskrat signs. Stenlund also showed me the best muskrat habitat of which he knew in the vicinity of Ely – a sluggish cattail-bordered stream at the east end of Shagawa Lake – and while this had some muskrat signs, it still was not much in comparison with what might ordinarily be expected.

The Superior region was rated by Dr. Paul R. Highby of the Minnesota Department of Conservation as the most unproductive of muskrats in the state (memorandum, May 11, 1948, Highby to Taylor W. Huston). Catches for 1946 averaged about one muskrat per square mile for Cook and Lake counties, about two per square mile for St. Louis County, and about four per square mile for Carleton County, which is the most southerly of these four counties; and the total catch for the four counties for that year was estimated at 18,750. Highby's observation (expressed in the above memorandum) of muskrat populations being sparse even in the "slow moving marshy streams between the lakes," where most of the catches are made, and my own failure to find evidence of many muskrats in the best places investigated during my 1950 survey, apparently relate more to the situation in late years. Olson, an ecologist of long experience and one intimately familiar with the region, recalled times when muskrats had been quite abundant locally.

From trappers' reports, I would judge that the hemorrhagic disease may have been in part responsible for this late scarcity of muskrats. One man told me of a fine marsh having many lodges but yielding few

muskrats during the 1949–50 fur season. After the melting of the ice, he saw many dead muskrats.

The north shore of Lake Superior is inhospitable for muskrats with wave-washed bare rock one of the chief features to be seen. The mouths of streams entering the lake may be gorgelike or flat, depending on their location, and with exceptions, have little quiet water or marsh-type emergent vegetation. One fair-looking muskrat habitat was noted inland from Split Rock, where bog and marshy growths bordered a stream. A beaver lodge was in sight from the road, and there could well have been muskrats in the area. From Duluth southwestward, the marshes, lakes, and streams took on increasingly the aspects of those of the hardwood-forested part of the state.

In late August, 1948, representative areas of the Pre-Cambrian country in southeastern Manitoba and adjacent Ontario, especially the Whiteshell Park, were looked over in company with Arnold Davey of the Game and Fisheries Branch of the Manitoba Government. Five years later, I spent a week in other parts of the Whiteshell.

Lake shores in the Whiteshell were principally of sloping granite outcrops offering little to attract muskrats and this, too, may be said of the islands out in the lakes. But, occasional dense growths of wild rice, and to a lesser extent of cattails and bulrushes, covered whole bays or small lakes, and there were in many places lake-shore fringes of emergent vegetation. Even some wind-swept margins had heavy growths of vegetation. Wild rice generally extended farthest into the deep water and protected bulrushes and cattails from the heaviest wave action. Masses of "goose grass" *(Equisetum fluviatile),* sweet flag, water lilies, and submerged plants grew in suitable situations — around the entire periphery of some of the lakes — where they would remain accessible to bank-dwelling muskrats having little other food.

One of the superior muskrat retreats examined — the outlet at the north end of Jessica Lake — was bordered by a willow swamp. The outlet, itself, was swift flowing in the center but with slow water along the sides, which had much reed, water lily, cattail, bulrush, sweet flag, and such vegetation, grading off into the typical swamp. The muskrat lodges were mostly newly built, of small size, and located near shore, though one was a summer lodge built into the base of a willow in the swamp. Deep-freezing seldom occurred in this sort of place, both for reasons of accumulations of snow and the nature of the muck underneath. A half mile east of the outlet lay something of a delta of a small stream entering the lake, and this was partly grown to a bed of wild rice, of remarkable thickness. Heavy stands of reed also dominated parts of this delta, and the swamp bordering the stream was at least a quarter mile wide.

Whiteshell Lake, which was decidedly more food-poor than Jessica Lake, had sparse bulrush growths and a few muskrat signs along most of its shore, with vegetation being fairly thick in a few places.

The best retreat seen for muskrats was about an island having some bank burrows and growths of cattail, bulrush, sweet flag, and reed between the island and the mainland. Fringing vegetation of the lake shore included locally heavy stands of reed but was chiefly of bulrush. Barren stretches of shore usually had no muskrat signs.

The muskrat catches in the Whiteshell area were usually rather substantial and the fur of excellent quality – the so-called "rice rats," famous in the fur trade. Actually, there was not much habitat to be rated as first class, but much was fair to good.

The Lake of the Woods country of the southwest corner of northern Ontario was intermediate in appearance between that seen in the Whiteshell Park and what I remember of that south of James Bay. Among other things, the streams looked at, except for the occasional rapid, had quieter waters than in the James Bay region, with more marsh vegetation growing about their margins. The extremely indented east shore of Lake of the Woods in view from the highway had innumerable bays and corners more or less grown to cattail, sweet flag, wild rice, sedge, reed, and bulrush. Despite long stretches of inhospitable, wave-beaten rocks and beaches, there was living room for many muskrats in the aggregate. Sluggish, interlake streams had both emergent and submerged vegetation growing in likely places. North of Sioux Narrows were splendid marshlike expanses between lakes, which surely must typify others in the many ramifications of the waters of Lake of the Woods. Beaver-flooded creeks afforded additional muskrat habitat. Water levels at most places where emergent marsh vegetation dominated looked at least passable for wintering muskrats as of late August, 1948, and certainly many places should have provided first-class wintering grounds.

Enroute from Sioux Narrows to Rainy River, Ontario, small bodies of water were seen, some of them suited to muskrats. The terrain became flatter southward and westward to the International Boundary, and streams were brown colored and boggy, having considerable bordering vegetation of willows and occasional cattail clumps. The western and southwestern sides of Lake of the Woods were not personally visited, but Dr. Kenneth D. Carlander, who once carried on fisheries research on that lake, described the west side for me as being bordered by great amounts of floating bog and the south side as a shallow wave-beaten beach without emergent vegetation.

Across the Minnesota line southward from Rainy River, Ontario, I looked over during the same trip representative tracts of swamp, bog, and stretches of roadside ditches. The latter were quite well occupied by muskrats. As wintering habitat, the ditches here did not look especially favorable: the water was seldom over one and one-half feet deep, and the best vegetation was no more than scattered growths of sweet flag, cattail, and pond plants. In several ditches on the "Big Bog" between Waskish and the ranger station of Pine Island, the flow varied from trickles to a couple of feet in depth. Muskrat signs could be seen especially about the pools behind beaver dams.

Away from the grid-pattern of ditches (dredged decades ago throughout the immense, mainly tamarack, swamp lying north and east of the Red Lakes) were occasional places having the appearance of good muskrat marshes. Some were big gravel pits, with deep open water grading off into cattail-grown shallows, and these had expected populations of muskrats. One small gravel pit having some cattails over the water had a freshly dug small burrow, evidently of a single muskrat. Other gravel pits had good cattail growths but no water. A forestry road and ditch embankment had served as a barrier to a past fire, and on the north side was a typical tamarack, spruce, and white cedar swamp, while the fire-swept south side was dominated by cattails growing under the dead poles.

A tiny flow of water coming out of an isolated cattail stand of about a quarter-acre in the midst of a swamp had muskrat and mink signs about it. The cattails were in shallow water but in the sort of place where some muskrats might winter if they had the protection of plenty of snow. Kermit Peterson, the Refuge Patrolman of the Minnesota Department of Conservation, had indeed known them to winter in such places, living in snow nests under the cattails.

As a background for my late summer observations of 1948 about northeastern Upper Red Lake and the Tamarack River, I had hunted and trapped there throughout the fall and winter of 1920–21. In addition, on-the-ground discussions with Peterson, who accompanied me during the 1948 visit to this area, were most helpful, as was information received in correspondence from Taylor W. Huston, then Supervisor of Game of the Minnesota Department of Conservation.

The eastern half of Upper Red Lake had along the north shore a much thicker growth of reeds and rushes (up to a couple of hundred yards in width) in 1948 than in 1920. These emergents were attractive to muskrats – and some muskrats were there – during the warmer months, but the bottom was of hard sand and the water so very shallow that I do not see how the animals would stand any real chance of surviving a winter in this shore zone proper, even with great snowdrifts over the reed clumps. I recall that, by the end of the winter of 1920–21, the bare lake ice had thickened to a depth of between four and five feet.

A long stretch of lake shore, itself lacking in any kind of emergent marsh vegetation, did have a used muskrat retreat at the mouth of a brook. Although the channel leading through the ice ridge to the lake was only about two feet wide and had a flow only about five inches deep, a pool had formed between ice ridge and where the stream came out of the woods. This pool was 15 to 25 feet wide, about 60 feet long, and up to five or six feet in depth, with margins grown to cattails. It was the sort of niche where perhaps two or three muskrats might winter comfortably and where more might conceivably get by. It had fair muskrat signs, as did also the flowing brook upstream.

Muskrats were also noted at two other short natural streams and

a ditch along the northeastern shore of Upper Red Lake. The ditch, near the lake, was wider and deeper than most of those in the Big Bog and had considerable marsh vegetation growing at its sides. The smaller of the two natural streams was brooklike, mostly shallow with occasional pools and considerable marsh vegetation. It was not good muskrat habitat but it doubtless could winter a few. The larger stream had a sluggish water channel about three feet wide, with masses of submerged and some emergent marsh vegetation; and a combination of peaty soil and deep snow (about five feet had accumulated on the level during the winter of 1920–21) should protect some of the food accessible to muskrats from freezing. All three of the above places had fair muskrat signs in late summer, 1948, the most being seen about the larger of the natural streams, very possibly of more muskrats than really could be accommodated. Twelve of 16 mink scats examined from Big Bog muskrat habitats contained muskrat remains, which is indicative of a high degree of vulnerability for the time of year. Several land-active, presumably transient muskrats also were seen in different places.

Varying stands of cattails — sometimes quite extensive — dominated the flora between the south edge of the Big Bog and the hardwoods-grown sand ridge and the lake shore lying north of the lake. These, however, tended to be so dry or nearly dry that they could have been of little ordinary use for muskrats. In late summer, 1948, they had few if any muskrats living in them, though, with a rise in water level of the lake, they could have afforded superb muskrat habitat.

By far the outstanding place for muskrats within a large area was the Tamarack River, and this seemed even more true in 1948 than in 1920, when it had been the best seen in weeks of fur-cruising in Beltrami and Koochiching counties. For one thing, profound ecological changes favoring muskrats had taken place in the mid-stretches of the river during the 28-year interval. Furthermore, the 1948 population status of muskrats in north central Minnesota was judged to have been decidedly higher in relation to habitats than it had been for years; and on the Tamarack River, the muskrat population probably approached the accommodation capacity of that stream and environs for the species. I would say that the 1920 fall population of the river had averaged from 60 to 80 per linear mile for about the 10 miles nearest the mouth. The 1948 densities appeared to have been as high, with a promise of being able to rise (though not necessarily to be maintained) still higher during a good muskrat year. Farther upstream, the river became narrow, shallow, and rocky, losing itself as brooklets threading bog and swamp.

In analysis, the superior muskrat environment of the Tamarack River differed little from that of numerous inter-lake streams of the Pre-Cambrian Shield east of Lake of the Woods and northwest into Manitoba. At its mouth, the river was nearly 100 yards wide, sluggish and deep, having wide margins grown to sedge, cattail, reed, sweet flag, wild rice, yellow water lily, and submerged plants. Upstream a

few hundred yards, it had narrowed to about 50 yards, was still sluggish and deep, and with the same vegetational types. About two miles upstream from the mouth, the river had started to widen again, meanwhile becoming shallow enough so that the bottom could be touched with a canoe paddle, and the margins had locally dense stands of cattail, reed, and redtop grass. All this was in 1948 as it had been in 1920; but in the course of the next few miles, what had been in 1920 a marshy stream with a fringe of hardwoods in the midst of a belt of tamarack and spruce swamp had in 1948 the appearance of stream intersecting a marshy reed and redtop savannah up to three-quarters of a mile or more in width. Only remnants (mostly dead stubs) of the stream-side hardwoods were to be seen in 1948.

Farther upstream, the river had in 1948 much greater marshy growths — typically thick fringes of reed, cattail, sweet flag, and sedge, and back toward the redtop, wild rice. I did not visit the upper reaches in 1948 but remember clearly, from 1920, many shallow water burrows in frozen mud having the signs of poorly situated muskrats and muskrat tracks in the snow about air holes over rocky brooks.

So far as the observed 1920–21 wintering conditions for muskrats in the Big Bog area were concerned, the pools between three and four feet deep in the ditches and creeks did not freeze to the bottom under the thick covering of snow. The Tamarack River, three miles upstream from its mouth, had little or no ice under snowdrifts several feet in height that were piled about certain curves where the slow current ran close to the bank, and at almost any place over the main channel the snow-covered ice was less than three feet in thickness. As late as February, after months during which air temperatures had dropped to between 20 and possibly 50 degrees below zero Fahrenheit virtually every night, snowdrift tunnels used by muskrats (and minks) could be traced to open water. Ice-glazed chambers and sitting and feeding places could be found either on the river bank or the ice shelf next to the open current under drifts. The snow tunnels and chambers were similar to those typically existing along less ice-bound streams of northern Iowa and eastern South Dakota. Food debris was also similar, consisting mostly of fish remains. Two muskrats were discovered in the Tamarack River drifts after having been partly eaten by minks in late winter, and these, when skinned for examination, were sufficiently lean to give me the impression that the muskrat population was not getting along very well.

The Red Lakes drain westward into the Red Lake River, which joins the north-flowing Red River near Grand Forks, North Dakota. As I remember the Red Lake River from having traveled it by canoe three times in late summer and early fall, 1920, the best muskrat habitat was in the Indian reservation, west of the outlet of Lower Red Lake, where the channel was bordered by wide growths of reed, cattail, and wild rice. Muskrat signs did not then seem to be as plentiful as expected, but the Indians had been trapping them for food at least as early as September.

Thief River, a tributary of the Red Lake River and one of the low-gradient streams in the former bed of glacial Lake Aggassiz, was visited in late summer, 1920, two years after completion of the artificial draining of Thief Lake. Thief River was in effect but an elongated, woods-bordered slough, filled near its mouth with backwaters from Red Lake River and finally ending in diminishing puddles in its then exposed stream bed. It was of interest to me chiefly because of the astounding concentrations of small fishes, which could be expected to furnish a source of food available to muskrats under the ice in an otherwise food-poor, mud-margined habitat.

The large, peaty marshes, Thief Lake and Mud Lake, were among the famous waterfowl- and muskrat-producing areas of early settlement days in northwestern Minnesota. They lie near the edge of a zone where prairie and hardwood forest grade off into mixed forest and conifers to the east. Following their drainage for agricultural purposes in the second decade of the present century, the "reclaimed farmlands" of their bottoms were abandoned by bankrupt homeseekers. In midsummer, 1934, after a long drought, I saw Mud Lake as a desolation of burnt or smouldering peat grown up to little except farm weeds. By 1937, when flood waters came again, public agencies had acquired both lakes and surrounding lands and had dammed the outlets, so that by 1941 the lakes together had around 50,000 acres in water and marshes with substantially restored productivity for marsh-dwelling animal life.

Southward from the Red Lakes (which with over 280,000 acres constitute the largest body of water exclusively within the boundaries of Minnesota) extends a complicated system of woodland lakes and marshes and interconnecting waters. Lake Winnibigoshish, Leech Lake, Mille Lacs Lake, and other of the larger lakes are as inhospitable for muskrats along their open water stretches as large lakes usually are, and even many of the smaller have an essentially "northern" appearance, on the whole short of muskrat food plants except for bulrush fringes and such vegetation. But, interspersed with these are also some fine marshes. Southward from Mille Lacs Lake, the wetlands take on more and more of the aspect of those of the glaciated prairies of southwestern Minnesota, northwestern Iowa, and the eastern Dakotas; and like the prairie marshes in late summer and fall of 1948, they appeared to be much underpopulated by muskrats, despite their frequently excellent condition for the species.

The exact boundaries between the range of *zibethicus* and neighboring subspecies in the Red River drainage basin south of Winnipeg are not clear. The animals living in the Netley Marshes south of Lake Winnipeg had the appearance of *albus,* and I would expect this to be the subspecies of the lower Assiniboine River, which joins the Red River at Winnipeg. Soper (1946) defined the range of *cinnamominus* in Canada as from the Red River west to southern Alberta. Bailey (1926) considered *cinnamominus* as the muskrat occupying all of

North Dakota. Although such might have been true early in the century, I doubt that it has been in recent years. If there are not typical members of *zibethicus* living in eastern North Dakota, I would be much surprised if the populations of at least the main Red River valley did not include large numbers of intergrades.

Near the sources of the Red River and the Minnesota River in northeastern South Dakota and adjacent Minnesota are the shallow elongated Lake Traverse and Lake Big Stone, of about 20,000 and 22,400 acres, respectively. These lakes go through all stages from being dry to flooded, and at intermediate stages afford much good muskrat and waterfowl habitat. The Red River, itself, south of Winnipeg, is a medium-small to medium-large stream, ordinarily having a sluggish flow and muddy, tree-fringed banks. It is, however, subject to terrific floods, which may cover a great deal of the valley, sometimes for many weeks. Some of the worst floods are the result of ice jams, as spring-melt waters from the south pour northward into places where more winter-like conditions prevail.

The Ottertail River, one of the headwaters of the Red River rising in west central Minnesota, has about its source a large number of lakes and marshes lying generally east of Fergus Falls. These waters are mostly in hardwood country but grade off to the west into those of prairie types and differ little from those about Detroit Lakes to the north, which are near the headwaters of the Mississippi.

OUTLINE OF THE GEOGRAPHIC RANGE OF THE COMMON OR EASTERN MUSKRAT IN NORTH AMERICA

Because of the very extensive area held by *zibethicus* in North America, it might be of some value here to review the subspecific range as well as present information permits. The fact that some of the boundaries may be occupied by intergrades rather than by representative members of the subspecies — especially in the Canadian north and along the dividing lines between eastern and western United States. — should not introduce undue error. It also should be understood that the outlines of the range of *zibethicus* have been known to change in the past and that they may change again in the future. These changes are not necessarily of minor significance but may involve distances of hundreds of miles, as is illustrated by the apparently recent advance of *zibethicus* westward and northwestward into eastern South Dakota and the southward extension apparent in Mississippi and Alabama.

Starting with the northernmost extreme of its range about James Bay, the subspecies extends southwestward probably through southeastern Manitoba and southward along the eastern boundary of North Dakota. I think that it is the muskrat of eastern South Dakota east of the James River Valley. Along the Nebraska-Iowa boundary, its range may possibly overlap with that of *cinnamominus,* which also may be true along the northern part of the Kansas-Missouri boundary. The southeastern corner of Kansas has *zibethicus,* however, and so

probably has the northeastern corner of Oklahoma. From southwestern Arkansas, the southwestern extreme of the range of *zibethicus* probably angles off southeastward toward Baton Rouge, Louisiana.

In the southeastern Gulf States, the range of *zibethicus* extends south almost to the Gulf of Mexico in Mississippi and Alabama, then runs northeastward from southeastern Alabama through about the middle of Georgia and the Carolinas. In Virginia, *zibethicus* is the muskrat west of the Blue Ridge Mountains. Most of Maryland is in the range of *macrodon,* as is Delaware and southwestern New Jersey; but from Cape May, New Jersey, northward and northeastward to the Gulf of St. Lawrence, *zibethicus* finds its boundaries delimited chiefly by the salt water of the Atlantic Ocean. Then, from the St. Lawrence River in the general vicinity of the forty-eighth parallel, the range of *zibethicus* extends indistinctly and unevenly northwestward to James Bay.