Chapter 13

The Muskrats of North America Other Than *Ondatra zibethicus zibethicus*

THE FIFTEEN RECOGNIZED FORMS of muskrats having North American ranges outside of the range of *O. z. zibethicus* show many differences as to population status, habitats, and geographical distribution. Of these other muskrats, *O. z. cinnamominus* — the subspecies with which, next to *zibethicus,* I have had the most experience — can be notable for its low densities over tremendous areas of the arid and semiarid Great Plains; it may hardly be represented at all for stretches of hundreds of miles, yet seldom does it fail nominally to hold essentially its regular range, and it often reaches typical muskrat abundance in suitable marsh or stream habitats.

Westward from the range of *cinnamominus* extend the ranges of the evidently closely related *mergens, occipitalis,* and *osoyoosensis.* The one of these having the smallest range, *occipitalis,* shows some behavior differences, whereas the widely distributed *osoyoosensis* is probably as versatile with respect to habitats and climate as any muskrat subspecies, including *zibethicus.*

It is true that *zibethicus* in northern Ontario and *osoyoosensis* at high altitudes in western United States illustrate muskrat adaptability to long cold winters and marginal habitats as well as do any of what may be called the true northern muskrats — *obscurus, aquilonius, albus, zalophus,* and *spatulatus.* Nevertheless, much may still be learned from this latter group about what constitutes habitability of northern muskrat range and what muskrats can there endure in the way of edge-of-range phenomena.

The subspecies *macrodon, rivalicius, ripensis, bernardi, goldmani,* and *pallidus* are all natives of warm climates and all have restricted geographic ranges. Parts of some of the ranges, however — such as

those of *rivalicius* and *macrodon* — may have at times among the highest densities of muskrats to be found in the world. It is conceivable that in certain years *rivalicius* in its comparatively small range along the Gulf Coast may outnumber *zibethicus,* although the latter occupies a range in North America equal in size to about half of the United States. Boundaries of ranges are very definite in some cases or marked by wide zones of intergradation in others. There may or may not be manifestations of special habitat niches or of barriers. Often it is not apparent just what determines the edge of a subspecific range, especially where two ranges overlap.

THE GREAT PLAINS MUSKRAT, cinnamominus

I think of Medicine Lake, in the northeastern corner of Montana, as rather exemplifying some of the muskrat habitats seen in the northern high plains during a personal inspection of waterfowl and muskrat marshes in 1934. The status of this lake varies with the years from that of a great marsh to an open water lake, with marshy tracts confined to shallow bays and outlying waters. Across the International Boundary into southern Saskatchewan lie many similar bodies, of all sizes and all degrees of suitability for muskrats, from cracked-mud bottoms encrusted with salts to the best of bulrush and cattail marshes and, on to the other extreme, foodless open water lakes. The marshes continue northward but soon take on an aspen-fringed appearance. In the wheat-growing areas are thousands of these potholes, most of them less than four acres in area, and usually with an open water center and a thick rim of emergent vegetation.

From the standpoint of the muskrats, the chief drawback of the potholes is the likelihood of their drying up in late summer. If the exposure from drying be neither excessive nor prolonged, the muskrat occupants may take care of themselves fairly well, but in the event of a real drought, they suffer great mortality. By late summer of the drought of 1934, almost the only remaining good habitats that I saw in southern Saskatchewan and southwestern Manitoba were the Qu'Apelle River marshes. The latter showed much lushness in the midst of the dry countryside. Information on winter conditions was given me by Jack Leader, a resident old-timer, and it was clear that a place like this may be strategic in the survival of muskrats for repopulating surrounding areas after cataclysmic weather emergencies.

Soper (1946), in his paper on the mammals of the northern Great Plains, wrote that the subspecies *cinnamominus* ranges

> well north of the International Boundary from about Red River, in the east, west to southern Alberta. In addition to the Great Plains proper, it also occurs on Turtle and Wood Mountains and Cypress Hills; also, it is thought to be this form that occupies Moose Mountain. The animals are well distributed over the territory at large, often occurring commonly in streams, lakes and sloughs even on the high, arid plains of the Missouri watershed.

Specimens taken early in the century from Touchwood Hills, perhaps about fifty miles northwest of Regina, Saskatchewan, were considered by Hall (1938) to be nearer *albus* than to any of the three adjacent subspecies, *spatulatus, osoyoosensis,* or *cinnamominus.*

I suspect that there is a wide zone of intergrading between *cinnamominus* and *albus,* the Hudson Bay muskrat, in southern Manitoba and Saskatchewan. When I worked in Manitoba in 1948, I was informed by personnel of the Game and Fisheries Branch that the Whitewater Lake area in the southwestern part of the province was the source of most of the recognizable *cinnamominus* taken by the fur trade. The Assiniboine River is the sort of place in which *cinnamominus* could be expected to occur, but the animals I saw, alive or dead, in the delta marshes south of Lake Manitoba, not far to the north, looked like *albus,* as did those of the Netley marshes south of Lake Winnipeg.

A wide variety of fair to excellent habitats may be seen over different parts of North Dakota, except for the badlands and other dissected semiarid terrain lying mainly south and west of the Missouri River. In the north central part lie the Lower Souris marshes, once inadvisedly drained for agricultural use, later restored through a series of dams to some approximation of their originally splendid condition for wildlife (Henry, 1939). Their 1948 appearance, when I inspected them in company with C. J. Henry, M. C. Hammond, and Edward Wellein of the U.S. Fish and Wildlife Service, varied from open, windswept bodies of water to solid blocks of cattails, from natural-type marshlands to those intersected by ditches, embankments, and artificial islands. To quote from Henry's paper:

> From the pioneers we learn that the Souris (or Mouse) River Valley once was one of the most productive wildlife nurseries in the country. Waterfowl, especially, were very abundant, and from a distance their flights often resembled huge clouds of smoke. . . . Sometimes in summer evenings the marsh noises made normal conversation almost impossible among farmers living at the edge of the valley.

Lac aux Mortes, about 80 miles east and southward, was the site of an interesting study of muskrats by Dr. James W. Johnston, Jr., formerly of the North Dakota State University. He observed (unpublished memorandum, 1947) an apparent correlation between large size of resident muskrats and exceptionally thriving stands of cattails, bulrushes, reeds, and like marshy emergents.

From eastern North Dakota, some good muskrat range extends down into South Dakota via the James River Valley. There are also irregularly distributed muskrat marshes in the general area northwest, west, and southwest of Aberdeen, to within 10 to 25 miles of the Missouri River, but these become fewer in central South Dakota, where the terrain away from streams takes on a flat and monotonous aspect.

The Sand Lake National Wildlife Refuge, of about 11,000 acres of open water and marsh, was the site of muskrat studies carried on, 1943–45, by Aldous (1946, 1947). When I last saw this place, in company with Watson E. Beed in 1938, it had a relatively small proportion in marsh, and as I remember it from my early years as a South Dakota resident, it was typical "Jim River" bottomland. The river itself, running south and southeast past Huron and Mitchell, to enter the Missouri River east of Yankton, had stretches of fair to good sluggish-stream habitat for muskrats, but the artificial impoundments at Sand Lake really were responsible for the high local muskrat densities there. Beed, in a letter of July 9, 1942, explained that

> The drought [of the thirties] had eliminated almost all muskrats. With the return of water they increased until in the spring of 1941 there were 200 lodges confined almost entirely to the James River channel. Muskrats taken during the 1941 season were under size, parasitized and their pelts were of very poor quality. In April, water came down the James River and flooded 8000 acres of marsh to an average depth of three feet. This marsh area was maintained during the entire summer and winter by inflow from the north. A lodge count early in January, 1942, showed 4000 scattered over the entire marsh. Due to poor trapping conditions only 3000 muskrats were taken during the 1942 open season. These rats were taken March 1 to 20 and were of excellent quality, nearly all grading as "sealers."

According to Dr. Wilfred D. Crabb, River Basin Studies, U.S. Fish and Wildlife Service, muskrats barely exist along the main stream of the Missouri River between the mouths of the Cheyenne and Cannonball rivers in north central South Dakota and south central North Dakota (conversation, July 22, 1948). The recorded Indian catch for this approximately 150-mile stretch had averaged less than a muskrat per mile, and the muskrats living there were localized in oxbows, small marshes, and the mouths of creeks. The stream here is heavily silt-laden and subject to great fluctuations, cutting away old mud bars and building up new ones; its banks vary from steep cut faces to those of low willow and cottonwood-grown flood plains and islands.

Crabb and his associates reported no muskrats from the Belle Fourche irrigation impoundment of northwestern South Dakota and very few along 113 miles of irrigation streams in the vicinity, but scarcity of muskrats in many irrigation developments is often due to repressive measures taken against them. Muskrats were scarce about the Fort Peck Reservoir in northeastern Montana, which at least would not seem due to remoteness from muskrat-occupied habitat. Crabb referred to the muskrats as being numerous along the Milk and Musselshell rivers, the former joining the Missouri River below the Fort Peck Dam and the latter entering the reservoir near its upper end.

The description by Jellison, Kohls, Butler, and Weaver (1942) of

an 80-mile stretch of the Musselshell River applies to other streams of similar type in central and south central Montana:

> Each year during the fall and early winter months part of this river is frequently not a flowing stream, but is represented by a series of ponds of semistagnant water. These ponds are separated by low, dry gravel bars. . . . When revisited in February [1940] a good stream was flowing and much of the river was covered with ice.
>
> Large cottonwood trees, willow thickets, and a variety of shrubs grow along the banks, the cottonwoods and willows being the principal winter food of the local beavers, which were fairly numerous. No beaver houses were seen as the animals in this area live largely in bank burrows. There were numerous caches of cut willows and cottonwood limbs as well as beaver dams. Muskrats . . . were abundant in the smaller streams and in marshes tributary or adjacent to the river, but were not common in the river itself.

These authors' photographs of the main channel of the Musselshell River, taken in late November, reveal little of wintering habitat that would attract muskrats. While the muskrats would not be averse to helping themselves to the tender willow twigs of the beaver caches, it is easy to see how they might be forced into dangerous outside activities in cold weather and why they would not congregate in the main channels as long as they had better quarters available.

Personal experience, beginning in 1924, along the Cheyenne River and some of its Haakon County tributaries in west central South Dakota, provides a background for appraising year-round habitability of steppe streams for muskrats. The Cheyenne River itself—alternately swept by flash floods and drying to silt-choked channels and residual pools and riffles—had practically no muskrats at times when those animals were passably abundant in such attractive local niches as did exist. The main stream served as an avenue of travel for muskrats, however, both during the spring dispersal and to some extent during late summer and early fall population adjustments.

The situation at Plum Creek, a tributary of the Cheyenne River, in 1924–25, illustrates the vicissitudes to which "West River" muskrats are subject during relatively favorable years. Late fall, 1924, had been a time of population adjustments between shrunken pools. The muskrat-occupied pools averaged about two and a half feet in depth at the center and had a water surface possibly averaging about 1,500 square feet. Such pools were short of readily available food, and the animals fed rather indiscriminately on vegetation of the surrounding land until freeze-up. Trapping yielded about one muskrat per pool, although six were caught in one elongated pool of about 100 yards in length. My December catch of 149 pelts showed major strife wounds in all stages of healing. A few animals were coming out in subzero weather to feed on the wolfberry *(Symphoricarpos)* stems that they could find in the snow, but, by New Year's, outside activity had ceased.

Notes taken while I was trapping afforded an index to the mortal-

ity suffered by muskrats wintering in these pools. A reconnaissance of two creeks before the opening of the trapping season indicated that the fall muskrat population was about the same on each. Only one creek was trapped and, from this, all known trappers took slightly over 160 muskrats from about six miles of stream bed, or probably close to 95 per cent of the total population. Despite the severity of this trapping along one creek, the earliest spring signs appeared to be no heavier along the creek that was not trapped, which suggests near-annihilative losses of the untrapped population.

Mrs. Grace Fairchild, who, from 1902 to the mid-fifties, lived on a ranch through which Plum Creek runs, first noticed muskrats on the creek about 1909. She recalled that many were traveling cross-country during the drought summer of 1911 as the water disappeared from Plum Creek. Only a little water then remained in the vicinity of the Fairchild ranch except in a few puddles of a neighboring creek and behind a large earthen dam. Normal water levels came back in 1912, but muskrats did not again become numerous until 1924, the year of my trapping and the year of greatest muskrat abundance in the memory of the local people. Later, I observed that the muskrat populations for 1925, 1928, and 1930 were fairly well distributed, though much less dense than in 1924. The drought of 1931 did not completely dry up the creek pools; but, by 1932, the pools had further diminished; and, by 1933, muskrats were barely represented. A vestigial population was present in the spring of 1934, but drought depopulated the creek of muskrats before June and July rains refilled some of the pools. By late summer, 1934, what seemed to have been a single muskrat occupied a dam pond three miles away, and muskrats were said to have been living in one other dam pond — a distant one, which was not personally visited. No sign of muskrats was detected along the Plum Creek water course in 1935, despite temporarily favorable environmental conditions. The last year of extreme drought was 1936, and this all but annihilated the muskrats of the whole "West River Country" of South Dakota. A very few muskrats had reappeared locally by the fall of 1938, but stream and dam pools remained essentially unoccupied for several years.

By 1946, muskrats were present in widely scattered places, usually in the choicest habitats available. I did not inspect Plum Creek in 1948, but similar streams in the western Dakotas then showed evidences of slowly recovering populations — at perhaps a tenth of the 1924 level. A late summer drought in 1949 seemed once again to eliminate the creek-dwelling muskrats, though some still persisted in neighborhood dam ponds. There were a few muskrats around in 1954, the last year that I saw Plum Creek.

The creeks of badlands and sagebrush semidesert vary tremendously in their attractiveness and habitability for muskrats. Most of them have neither permanence of water nor food to provide more than submarginal habitat. North Dakota's big program of building

earthen dams across formerly dry gullies has resulted in many small impoundments that became well-grown to emergent marsh vegetation and occupied by muskrats. I saw similarly splendid marshlike artificial impoundments, with muskrats in them, in northeastern Wyoming in 1948. Scattered about in northeastern Wyoming, southeastern Montana, and the western Dakotas were natural watercourses with marshlike pools — some rather isolated about the headwaters of creeks and seldom connected by running water — others representing merely deeper or more sluggish stretches of intermittent streams. Of these pools, those most likely to harbor muskrats had water between eighteen inches and four feet in depth and were bordered by dense growths of cattails, bulrushes, arrow heads, and other food-rich plants.

The Yellowstone River of eastern Montana has, like the Musselshell, limited muskrat habitat in its main channel, but numbers of the animals live (or could live) in oxbows, about eddies fringed by willows or emergent marshy vegetation, and about the miscellaneous pools, seepages, and irrigation flowages in the valley. Some of the best muskrat habitat and signs seen along the Yellowstone River in 1948 were downstream from Billings, where the clear-greenish, swifter waters of the upper tributaries began to take on more and more of a silted, sluggish appearance.

It is anything but clear just where a dividing line between the ranges of *cinnamominus* and *osoyoosensis* might be drawn east of the Rockies. The upper reaches of the Yellowstone River surely have *osoyoosensis,* and I think that that is the muskrat of Rock Creek and mountain stream tributaries at and west of Red Lodge, south central Montana. Yet, I examined a dead animal found beside a small impoundment up on the tableland about five miles northeast of Red Lodge and another dead one beside another impoundment and desert-like creek a few miles farther east, and both of these looked just like the ones I once handled in western South Dakota. The zone of intergradation is probably wide in many places, and the best I can do at present is to suggest that *cinnamominus*-like muskrats may be expected in the lower-altitude streams and marshes eastward from Great Falls and Billings, Montana, eastward from the Big Horn Mountains, and through most of the southeastern quarter of Wyoming. The gorges of Clark Fork east of Yellowstone Park would seem a most effective barrier between *cinnamominus* downstream and *osoyoosensis* upstream. To my eyes, they looked impassable for muskrats, and their surrounding mountainous country would hardly permit muskrats to travel overland.

The subspecies of that isolated mountain range, the Black Hills of western South Dakota and northeastern Wyoming, is probably *cinnamominus.* All animals I have seen within 200 miles east of the Black Hills looked like typical examples.

Central Wyoming has streams that are typical of badlands and sagebrush desert, along with some impoundments having rushes and other

emergent vegetation. East of the Big Horn Mountains are localized irrigation flows and seepages, many of which are entirely habitable for muskrats, and still farther eastward are sluggish streams that have muskrats in the more attractive places. From Newcastle, Wyoming, to Custer, South Dakota, there are a few meadow streams having some muskrat habitat. Near Custer itself are some artificial lakes with considerable growths of submerged vegetation and marshy shores. These had muskrats in 1949, as did also sluggish stretches of small mountain or foothill streams. The little foothill streams along the east side of the Black Hills were extensively willow-grown and occupied by fair numbers of muskrats, but seemingly fewer in 1949 than in the years 1923–28, when I knew this country better.

For that matter, the muskrat populations of the northern Great Plains were patently below the supporting capacities of their existing habitats throughout nearly all of the areas visited in 1948 and 1949. This is reflected by recent data on fur harvests. In North Dakota, for example, the reported muskrat catches were 178,518 for the season of 1943–44; 215,797 for 1944–45; 324,809 for 1945–46; 161,811 for 1946–47; 50,067 for 1947–48; no open season in 1948–49; and 112,440 for 1949–50 (Hargrave, 1950b).

In eastern Montana, a pronounced decline of muskrats was apparent by 1946, this appearing to be less notable about artificial impoundments than along the poorer habitats afforded by natural streams. The evidence, at least through 1949, suggests a continuing subnormal population and the operation of the hemorrhagic disease or tularemia, or both diseases, as well as climatic emergencies. Robert F. Cooney, of the Montana Fish and Game Commission, made inquiries for me concerning the situation. Although Deputy Game Warden E. M. Krost knew of no muskrats dying of disease in the extreme northeast corner of the state (letter to Cooney, September 11, 1946), H. C. Friede, stationed in the counties to the west including those through which much of the Milk River drains, found considerable evidence of disease loss. A dead muskrat examined by Friede had a spotted liver and enlarged "glands in the neck and under the legs" (letter to Cooney of September 4, 1946).

Many of the streams of the western, northwestern, and northern fringes of the Sand Hill country of southwestern South Daokta and northwestern Nebraska have steep shale banks, very muddy water, and almost no attractive habitats for muskrats. Westward extends the sagebrush desert of eastern Wyoming. To the north of the Sand Hills lie the South Dakota Badlands. The larger streams of southwestern South Dakota — such as the Cheyenne and White rivers — are, essentially like any large streams of the northern Great Plains, of very limited habitability for muskrats. This may also be said of the Niobrara River and its larger tributaries running through much of the Sand Hills in Nebraska and of the Platte River to the south of the main Sand Hill formations. But what may be called the real Sand Hill creeks — as these occur south and southeast of Hot Springs — often have cattail

or other marshy growths in sluggish places. There are also roadside ditches well grown to marsh vegetation. Marshes and sloughs of the South Dakota Sand Hills are abundantly scattered in the general vicinity of Martin, which has some of the best muskrat habitat in the state.

The approximately 25,000 square miles of Sand Hills in Nebraska do not have lakes and marshes distributed with any great uniformity throughout. Two major wet areas of value to the muskrats exist where stream drainage is poor. One of these lies south of Valentine and southwest of Ainsworth and the other mostly east of Alliance. They are about 75 miles apart. These wet areas are literally dotted in places with larger or smaller bodies of water surrounded by hilly and level expanses of sand stabilized, such as it is, by grassland flora.

(Appendix J relates especially to Dr. J. Henry Sather's muskrat study in the Nebraska Sand Hills.)

Wakeeney, in northwestern Kansas, is a type locality for *cinnamominus,* and Black (1938) considered this subspecies to be of state-wide distribution except in the southeast corner, which is occupied by *zibethicus.* Cockrum (1952) referred to the muskrat as being much more common in the eastern, more humid, half of the state. It builds lodges in suitable marshy habitats. Of *cinnamominus* in Colorado, Cary (1911) wrote:

> On the plains scores of muskrat houses may often be seen on a single marsh or lake. This is especially noticeable at Barr and other points in the lake region northeast of Denver. Although muskrats are present in most of the streams on the plains, their numbers are small compared with those inhabiting lakes and marshes. They are very troublesome in irrigated regions as they are continually burrowing in the banks of ditches and reservoirs, often causing serious leaks.

Cary mentioned a specimen of *cinnamominus:* "a female which contained eight small fetuses, taken . . . in a small snow-fed lake at 9,500 feet, near Ward, Boulder County, June 8, 1893." This locality is in north central Colorado and represents what would seem to be extreme edge-of-range habitat for the so-called mountain subspecies, *osoyoosensis* itself. The occurrence there of *cinnamominus* demonstrates that the Great Plains subspecies has a wide range of habitat tolerance, also.

Blair (1939) wrote that *cinnamominus* was distributed over most of Oklahoma from the Cherokee Prairie biotic district westward, undoubtedly including the Oklahoma Panhandle. Of the southeast corner of the state (which is about 200 miles north of the known range of *rivalicius* in either Louisiana or Texas), Dr. F. M. Baumgartner wrote (letter, September 21, 1950):

> Of particular interest is the fact that [citing Duck and Fletcher, 1945] no muskrat pelts were sold in southeastern Oklahoma in the biotic districts known as the Oak-Pine Forest Type, Loblolly Pine Forest Type and the Cypress Bottoms Type. Lawrence B. Semple, Superintendent of Game, has

informed me that there are apparently no muskrats at all in this area roughly one hundred miles in diameter.

Glass (1952) described the changes in muskrat habitats that followed the years of virgin forests and grasslands. The soil then retained water from the brief and violent spring and summer rains and released it slowly through springs and seeps. At the time of the great land rushes, there were not only springs but even marshy and swampy spots. The plowing and planting of the homesteaders resulted in rapid surface run-off, decreased water storage, drying of springs, and stream flow becoming intermittent. Then, the tragic "dust bowl" conditions stimulated a big program of water conservation.

The work carried on by Glass is of interest not only as relating to *cinnamominus* living in a part of its range having water only in places but also to a region that the subspecies might find – for reasons as yet unappraisable – less and less habitable toward the south. Edge-of-range effects are suggested, for one thing, by the low densities existing in what Glass has described as superior habitats for his study area. Appendix K quotes certain parts of his paper in detail.

THE WESTERN MUSKRATS, mergens and occipitalis

Grinnell, Dixon, and Linsdale (1937, p. 730) showed that the natural distribution of *mergens* in northern California was confined to an area near the northeast edge and lying mostly less than 50 miles inside of the state line. This is in the Great Basin part of California, eastward from the Sierra Nevada Divide, and the altitudes of occurrence given were from 4,000 to 6,200 feet.

Storer (1937) wrote about the puzzling gaps in the distribution of the muskrat in northern California. If *mergens* could have reached the Pit River drainage from its native range at Eagle Lake (a distance of no more than 15 miles), it would have been in a position to have reached the Sacramento-San Joaquin basin, thus to colonize most of California. Through escapes from a fur farm in the Fall River Valley (connected by creeks and canals with the Pit River drainage), a muskrat stock of mixed origin finally did become established in a tremendous new but previously muskrat-vacant range.

Twining and Hensley (1943) reviewed the status of muskrats in California. They visited nearly every area in the state that was populated by muskrats. From their introductory paragraphs:

> It appears obvious that in prehistoric times they inhabited the shores of the great Lake Lahontan which once washed the eastern base of the Sierra Nevada and with the disappearance of that Lake the muskrats were left to continue their existence in any rivers or sinks that offered suitable habitat.

With respect to the more recent status of muskrats in the newly colonized range of northern California, Dr. A. Starker Leopold of the University of California wrote of "the rapid spread and increase of the muskrat in the Central Valley" in a letter dated March 30, 1948.

Then, Ben Glading, of the California Division of Game and Fish, wrote (letter, November 27, 1950) that:

> Muskrats have spread to practically all of the suitable habitat in the Sacramento Valley but as yet have not spread to all parts of the San Joaquin; however, they are on the increase there, and it is expected that in a few years the entire central valley area will be well populated.

(However, this population does not consist of *mergens* but of what Twining and Hensley called a great "hodge-podge of types" occupying range that one might almost regard as "rightful" *mergens* range.)

Hall's (1946, p. 565) map of the distribution of muskrats in Nevada depicts the native range of *mergens* as divided into two parts. One of these is in west central Nevada (as well as adjacent California), in the Reno–Carson City–Fallon triangle and surrounding wetlands. Hall's map shows *mergens* range along the Humboldt River and connecting the main western part with a big block in north central Nevada, south of the Snake River drainage. Concerning the muskrats of southern Idaho and presumably northern Nevada, Davis (1935, pp. 329–30) wrote:

> Specimens from the Snake River Valley are intergrades between *osoyoosensis,* the race occurring typically in the northern portion of the state [Idaho], and *mergens,* a race occupying the Great Basin. . . . Other specimens which I have examined from southern Idaho are light in color like *mergens*. . . . The subspecific name *osoyoosensis,* rather than *mergens,* is here applied arbitrarily to the specimens from the Snake River area, merely for the sake of convenience.

Ruby Lake, at the altitude of 6,000 feet in the Ruby Mountains of northeast Nevada, is near the eastern edge of the range of *mergens.* Borell and Ellis (1934) described the area comprising muskrat habitat:

> The region in general is arid and the winter climate is severe. Snow and freezing temperatures prevail from October to March and heavy frost may occur, even at the lowest altitudes, during any month of the year. . . . Snow remains on the north-facing slopes of the higher peaks until late in the summer, and some may persist throughout the year. This snow supplies water for the creeks that flow out of the larger canyons. Some of the streams flow throughout the year; others dry up during the summer. The water from these streams is used mainly to irrigate ranches about the base of the mountains. The water that does not evaporate or soak into the ground escapes into Franklin and Ruby lakes on the east slope and into the Humboldt River on the west slope. In addition to the creeks there are a large number of springs, which arise at the base of the mountains. . . . Several of these are found along the west shore of Ruby Lake. Among the higher peaks of the range are a few small lakes. . . . Ruby Lake is . . . about sixteen miles long and from one to four miles wide. The water in the lake is practically fresh, although there is no visible outlet. It is fed by numerous springs, most of which are on the west side. Most of the lake freezes over during the winter, but the springs, as well as the streams which originate from them, remain open and keep parts of the lake from freezing.

These authors wrote concerning *mergens:*

Ruby Lake presents conditions ideal for habitation by muskrats. Since the lake is in reality a large tule [*Scirpus acutus*] marsh, interspersed by numerous areas of open water, the conditions existing in the middle of the lake are as favorable to muskrats as were those along the shore. Muskrats were quite numerous over the entire marsh but were being rapidly reduced by intensive trapping. During the first part of August, 1928, two or three pairs of muskrats were inhabiting Favre Lake at an altitude of 9600 feet, which is the lowest one of Three Lakes. At Favre Lake the muskrats lived entirely in holes in the bank; there were no houses on the lake. Muskrat trails ran back from the edge of the lake through the tall grass into the willow thickets, where gnawed limbs and cut twigs of willow saplings were found. There was little growing vegetation in the lake.

At Ruby Lake, muskrats lived in holes in the banks and also in houses which were located among the tules in shallow water, rather than out in the open water. . . .

Muskrats often were seen abroad in the late afternoon, especially during the winter. On December 21, 1927, at four P.M., eight muskrats were swimming about in an open lagoon. One of these entered a hole in a bank, from which it emerged again in great haste, closely pursued by another rat. On several occasions muskrats were seen walking about on top of the ice. At one place a muskrat trail led three hundred yards through soft snow from one lagoon to another.

Hall (1946, p. 565) quoted a letter of December 27, 1940, from G. H. Hansen to L. T. Turner, Jr.: "Mr. Dill indicates . . . that the rats in Ruby Lake are carrying tularemia."

The Washington distribution of *occipitalis* is given by Dalquest (1948, p. 363) as, "The southwestern corner of the state, extending north to Aberdeen (V. B. S.) and east to Cathlamet (V. B. S.)." (The V. B. S. initials are those of Dr. Victor B. Scheffer, of the U.S. Fish and Wildlife Service, who indicated in a letter of September 22, 1949, that the eastern boundary must extend a considerable distance east of Cathlamet, which is on the Columbia River only about 30 miles from the Pacific Ocean.)

From Scheffer's letter:

The northern boundary of its range is the Chehalis River, Washington. . . . [Concerning the] eastern boundary of its range in Washington . . . I can see no natural barriers in its way until one reaches the Cascade Range. . . .

With regard to the habitats of the two races [*occipitalis* and *osoyoosensis*] in western Washington, I think that they are similar. I have tramped over a good deal of the Puget Sound Trough. Certainly the *osoyoosensis* range in western Washington is more like *occipitalis* range than it is like the *osoyoosensis* range in eastern Washington.

Stanley G. Jewett wrote (letter, September 17, 1949) that "*occipitalis* of the west coast is . . . common along the Columbia River from the Cascades to the coast, throughout the Willamette Valley, and along the immediate coast to salt water from Astoria through Tillamook, Lincoln, Lane . . . and Coos" counties.

The Oregon coast muskrat, *occipitalis,* would then appear to have a range approximately 250 miles long and 90 miles wide. Within this range, Wesley M. Batterson, of the Oregon State Game Commission, has done a great deal of field work and summarized his observations in a letter dated November 26, 1949:

> Types of country occupied are marsh areas, sloughs, small creeks and streams, drainage ditches in fields, tideland marshes and . . . the edges of the bays within a short distance of the ocean. Muskrats are seldom found in the mountain streams, but are found in some of the higher mountain lakes which afford sufficient plants for a food supply. Most of the sloughs near the ocean have a small colony of muskrats, from ten to thirty.

In another letter (December 5, 1949), Batterson elaborated on the habits of *occipitalis:*

> Even though the muskrats have an abundance of cattails, tules and other suitable vegetation they . . . build no lodges. At times they do pile up a floating raft of tules or cattails which they use to climb out of the water and feed on, but these are not lodges . . . and they build these only occasionally in large lakes. . . . Washing away of floating materials I am sure has no connection as we have many lakes with an abundance of cattails and tules where the lodge could be well anchored or built in protected places.

A great muskrat-vacant area originally lay south and southeast of the range of *occipitalis,* with many splendid and extensive marshy habitats awaiting colonization. One of these was Tule Lake, in northern California; another, just east of the Cascades in southern Oregon, not very far from the California state line, was Upper Klamath Lake. According to Twining and Hensley (1943), Tule Lake was stocked in 1930 with twenty-two pairs of muskrats purchased from Michigan, and the pelts of the Tule Lake muskrats are exceptionally choice. Jewett (letter, September 17, 1949) wrote that during the twenties

> a company of fur farmers started a muskrat farm at Aspen Lake along the west side of Upper Klamath Lake. . . . Before they were well started a spring flood washed out their inclosures and the rats escaped into the main body of Upper Klamath Lake. In a few years they increased greatly over the entire Klamath Basin, to and including Tule Lake and Lower Klamath in California.

Once the muskrats took over these favorable but previously isolated habitats of south central Oregon, they naturally spread into many places. Heustis (1938) reported muskrats in Crater Lake National Park in 1937: "In all [three] cases these animals were found a considerable distance from a body of water of any appreciable size. . . . It is suggested . . . that the specimens seen in the park are immigrants from the Upper Klamath Lake," which lies about twenty-five miles south of the park.

THE ROCKY MOUNTAIN MUSKRAT, osoyoosensis

Bailey (1931, pp. 207–8) wrote of *osoyoosensis:* "The Rocky Mountain muskrat, a large dark form, occupies the San Juan and Rio Grande valleys of northern New Mexico. . . . There are specimens from Farmington, Costilla River, Rinconada, and Albuquerque, which agree perfectly with others from the mountain region of Colorado and northwestward to southern British Columbia." In northeastern New Mexico, Hill (1942) found no signs of muskrats above 7,800 feet, though Bailey (his page 217) had referred to a muskrat sitting on the edge of a beaver lodge of a pond in the upper part of the Costilla River in the Culebra Mountains at an altitude of 9,400 feet. Cary (1911) reported *osoyoosensis* in most of the streams of central and western Colorado below 9,000 feet, but found them common only in the marshes and lakes of the intermountain parks.

Despite the local abundances of muskrats to be found in southwestern Colorado, much of eastern Utah does not afford livable habitat for any of the subspecies. This is the desert country traversed by the canyon-bound Colorado and Green rivers. Durrant (1952, pp. 358–59) wrote that almost "nothing is known with reference to animals from the eastern part of Utah — Colorado River drainage — nor of animals from the central part of the state."

In the summer of 1949, I spent considerable time studying the muskrat populations of mountain and desert regions in southwestern Wyoming, northern Utah, southern Idaho, and southern Oregon. This work was largely centered about Great Salt Lake, with the invaluable help and company of Dr. Jessop B. Low of the U.S. Fish and Wildlife Service. The marshes bordering the east side of Great Salt Lake — especially the Bear River and Ogden Bay (Weber River) marshes — are among the most life-rich places on earth. These are given more extensive treatment in Appendix L.

Southeast of Great Salt Lake lies fresh water Utah Lake. When inspected on July 15, 1949, it was said to have been at maximum level. Dead stands of hardstem bulrush could be seen out for about a quarter mile from the northwest side. These hardstem stands, Low told me, were once full of muskrats, but the live bulrushes were reduced to a margin seldom more than 30 yards in width, and the muskrats were reduced with them. Wave action was relatively light because of the usual calmness of the air.

During dry periods, this lake goes down, both as a result of natural lowering of the water levels and pumping for irrigation. Generally, the lake becomes more productive of muskrats in the course of droughts, as the water recedes slowly enough so that emergent vegetation can grow in the successively new shallows. The bulrushes may cover the shallows for as far as a half mile into the lake. Although a sample of about a half mile of shore was looked over without seeing current muskrat signs, a sluggish canal bordering the

lake and leading to a pumping station did have a fair population of muskrats.

Utah Lake is connected with Great Salt Lake by the Jordan River, which runs through an area of mud flats, open water, and marshes north of Salt Lake City. Most of this area looked rather poor for muskrats, with the stands of bulrush and cattail chiefly occurring next to stream channels. The best marsh I saw in this part of Utah was about a 10-mile stretch of emergent vegetation on the silted bed of the Jordan River.

Three main foci of muskrat abundance then occur along the eastern shore of Great Salt Lake: about the deltas of the Bear, Weber, and Jordan rivers. These deltas and impounded waters have few minks and still fewer coyotes, but a certain amount of predation upon muskrats very probably takes place during periods of vulnerability through the agency of the abundant California gulls *(Larus californicus)*. California gulls are aggressive, and as they are known for their depredations upon young or sick water birds (they may disembowel large ducks sickening from botulism), I should expect them to attack handicapped muskrats if they had inviting opportunities.

West of Brigham, waters of irrigation origin as well as from springs produce some fairly extensive marshes, such as those of the Public Shooting Grounds along Salt Creek, to the north of Bear River. When I visited the Public Shooting Grounds, many of the artificial lakes and sloughs were merely shrinking bodies of open water or dry alkaline bottoms. The deeper waters had much *Chara* and some *Potamageton* and *Ruppia* but almost no emergent vegetation. Few muskrats lived in them except in places where the banks were steep and near the water, as in the vicinity of dikes. The ditches flowing out of these impoundments, however, had green vegetation, both submerged and emergent, and fair populations of muskrats.

Low told me that warm (in the sense of not freezing in winter) springs occur for about 40 miles along the edge of the mountainous promontory extending into Great Salt Lake from the north, and these may be full of muskrats. Two examples of springs were inspected on July 13, 1949. One spring came out at the base of a typical dry hillside, and the water flowed off cross-country for about three-quarters of a mile; its margin was grown to heavy stands of *Scirpus olneyi*, which spread out in places but usually maintained the form of a narrow belt. The second spring was larger, watering a belt of *S. olneyi* perhaps 100 yards wide and up to two miles in length. Muskrat signs were to be seen about both examples, and Low said that one of the heaviest concentrations of muskrats he had ever observed was along one of these spring-watered strips of *S. olneyi*.

Between the spring-strips and Great Salt Lake may be little muskrat habitat, and the springs may be likened to a series of oases. They are not so far apart that muskrats may not be expected to cross intervening desert from one to the other on occasion, especially at times

when great numbers of animals may literally overflow from the Bear River marshes. Sulphur Creek, emptying into Bear River near the delta, is a major avenue of travel for muskrats in spring. Individual trappers are said to take hundreds here during some dispersals upstream from the Refuge.

Stray muskrats do reach and establish themselves in remarkable places in this desert region. Despite the inhospitableness of the briny waters of Great Salt Lake for vertebrate life, Dr. S. D. Durrant told me of collecting a muskrat swimming in a spring on Antelope Island, in the southeastern part of the lake. At the place where the muskrat had probably crossed from the mainland four or five miles away, the lake bottom was mostly exposed but with stretches of concentrated salt water seven or eight inches deep. Durrant also showed me in the Museum of the University of Utah a skin of a muskrat collected in 1941 from tiny Egg Island, off the northern tip of Antelope Island, by C. N. Greenhalgh, who was at that time banding gulls. If this muskrat had come from the mainland to the east, it would have crossed a minimum of about eight miles of salt water; if from the south, it would have crossed over to Antelope Island, then traveled up to about 15 miles of the length of that island before crossing to Egg Island.

Antelope Island does have springs of fresh and brackish water and dense growths of *Scirpus paludosus,* and it lies close enough to the mouths of rivers so that muskrats or even terrestrial mammals might occasionally be transported from the mainland on logs or other flood debris. Readers interested in exploring further the possibilities of mammals reaching and becoming established on islands in Great Salt Lake may well consult Marshall (1940).

The Locomotive Springs are several big springs lying close together and separated collectively by about 15 miles from the nearest water except Great Salt Lake. They come out of the ground in a flat desert, and their flow crosses a few miles more of desert to enter the extreme northern tip of the lake. Marshy growths, notably *S. olneyi,* were seen in mid-July, 1949, extending to the south toward the lake for about two miles.

Dikes built during the years of CCC camps profoundly modified the marsh habitats locally. Above the dikes, which run long distances through the marshes and around the heads of the springs, the emergent vegetation had largely disappeared by 1949, whereas, below them, splendid-looking growths had insufficient water for muskrats. Fair to excellent growths of emergents existed about some of the spring flows above the diked impoundments, but the acreages of marshy emergents above were not nearly so great as those below the dikes.

Much open water occurs in winter (the steam can be seen for miles), in the spring flows, and even in the lower marshes, freezing varies greatly. Generally, there is water under the ice at all times, fresh from the springs. The muskrats of the open-water impoundments are all

but confined to the dikes; in the marshes below, muskrats may be either abundant or scarce. The main environmental difficulty here would seem to lie in shortage of water at critical periods. Old-timers maintain that they caught thousands of muskrats annually from Locomotive Springs before the diking, compared with hundreds since then. Whether or not this is an exaggeration, it is very probable that the marshes were damaged rather than improved for muskrats by the diking.

The Locomotive Springs are surrounded by typical northern Utah desert, and when a big environmental crisis is underway and large numbers of muskrats evicted, there can be a tremendous amount of vulnerable wandering. Coyotes were fairly numerous, and Low had found conspicuous representations of muskrat remains in their scats at times. This is quite to be expected, for muskrats must occasionally travel about on dry land by hundreds. In addition, cattle pastured about the springs in winter are said to trample and flatten the lodges.

One other factor is in the muskrat equation at Locomotive Springs: tularemia. Quortrup and Sudheimer (1942) reported this disease in the muskrats on the Bear River Delta, and Quortrup later wrote (letter, July 14, 1944) that "the losses here were noted during the hot summer months only. . . . [The] disease is very prevalent in this area. . . . It may interest you that the winter following the summer losses noted here, there was no appreciable reduction of the muskrat population." At Locomotive Springs, the outstanding vectors must be the abundant and ferociously pestiferous tabanid flies (Jellison, 1950b). Low told me that when the CCC boys worked there years ago, about 20 contracted tularemia nearly simultaneously, and at the time of our visit in 1949, dead jackrabbits *(Lepus californicus deserticola)* were strewn all over the desert immediately surrounding the water, their remains being undisturbed except for decay. These rabbits could not have died through human agency, for ours was the only sign of human visitors laid down for months at least. Those swarming tabanids loaded with tularemia made the place one of singular menace, and hardly any local mammals that would be about during hours of fly activity could escape being bitten. I do not know what tabanid-muskrat relations might be, but even were the muskrats almost entirely nocturnal, they still should suffer bites now and then, and with so much tularemia apparently in the vicinity, might well be exposed to it in other ways.

No one seems to know of muskrats ever having been planted at Locomotive Springs, and it looks as if they arrived there naturally. Springs other than the above occur north of Great Salt Lake, and they are visible as green spots for long distances. Two were seen within 20 or 30 miles of Locomotive Springs, of which one was looked at and found to have no muskrat signs. Great Salt Lake itself had caked brine beaches, and the only clear-water spring seen there during the trip had a salt content of about 13 per cent.

In the extreme northwestern part of Utah were many streams that started in mountains but dried up in the desert. One of these was looked over carefully and found to have beaver workings but no muskrat signs. To the north, the tributaries of the Raft River had muskrats. Stretches that I saw were mostly of steep-banked small streams in sagebrush desert, but higher up in the foothills were some willow-grown places of sorts that might have had either beavers or muskrats.

The streams of west central Wyoming are typical of badlands and sagebrush desert, but some impounded waters had bulrushes and other emergent vegetation when visited in 1949. A large tributary of the Big Horn River near Shoshoni had recently been in flood when seen on July 13, yet most of the stretch looked at had no surface water except for some of whitish color remaining in shallow pools of the silted bed. It appeared about as uninhabitable for muskrats as a stream could be. In general, I saw few places where muskrats might live away from dam reservoirs. The Wind River Canyon between Shoshoni and Thermopolis was full of very muddy, very rough water, and I doubted that muskrats could even travel through. North of the Wind River Canyon, the stream smoothed out and ran through country in which a few muskrats might have lived.

One of the most interesting places was a tract of about an acre of cattail in a pond formed by a warm spring at the northern outskirts of Thermopolis. It reeked of sulfides, and the spring flows were barren of cattails, but to the sides were heavy growths of vegetation and some muskrat signs. Fringing willow thickets along the Big Horn River between Thermopolis and Greybull and cattail seepages in the irrigated lowlands afforded some muskrat habitat. In the hills were gullies with heavy localized growths of cattails, mostly merely damp but of sorts that would have some attraction for muskrats during wet seasons. A fair-sized alkaline lake had scattered patches of bulrushes and cattails, an abundance of carp, but no muskrat signs.

Gray's Lake, in southeastern Idaho, was in 1949 the site of an intensive muskrat investigation by Roger M. Williams, of the University of Idaho (Williams, 1950; Reeves and Williams, 1956), and I spent a few days with him there in early July. This is a big bulrush and cattail marsh lying at an altitude of 6,386 feet and used as a reservoir for irrigation water. Its normal marshy area covered about 32 square miles, and the surrounding lowlands fully as much more. At the time of my visit, following unusual spring rains, its water level was the highest in the memory of the people living about its edges. About 10 per cent of the marsh had open water full of pondweeds and bladderwort, and this was mostly in the south end; the rest was covered by an almost solid stand of emergent vegetation growing in about two feet of water — tracts of hardstem bulrush stretching away for miles, in almost unbroken stands except for strips of cattail. Williams had observed that the muskrats preferred bulrushes to cattails, the latter being mostly narrow-leaved. The muskrat population was rather low.

Williams seldom found lodges with young nearer than 100 yards of each other.

Old-timers said that they had known of die-offs of muskrats in the past for which tularemia was believed responsible. One trapper had nearly died of tularemia evidently contracted from a muskrat.

Williams wrote (letter, January 18, 1950) that the water level of the marsh dropped possibly 18 inches in the weeks following my visit in early July. "It reached its lowest level [for 1949] in late August or early September, but there was still plenty of water for muskrat habitation" in the observational areas. Rain and snow water later in the year "raised the level more than a foot above what it was at its lowest point."

In another letter (December 17, 1949), Williams wrote of the data obtained from 176 muskrats taken as specimens in the fall of 1949. These were close-trapped to give a cross-section of a population of a comparatively small area. Of the 176 muskrats, 16 were adult females, and of these, one had not conceived in 1949, 5 had placental scars indicating one litter each for 1949, and 10, two litters each. The mean litter size shown by the placental scars was 7.04, compared with the mean of 6.97 young found in 35 litters examined during the breeding season in lodge nests. The average adult female had conceived 11 young, whereas a ratio of 8.75 juveniles to each adult female was found in the sample trapped. At Dingle Swamp, 55 miles away, the mean conceived per breeding female was 19 and the mortality rate of the young was 47 per cent from birth to their first fall (Reeves and Williams, 1956).

The natural outlet flowing northward from Gray's Lake was, when seen in July, a shallow stream 40 to 50 feet across, with fringing growths of sedge and grass and much yellow water lily and some emergent vegetation in places. It flowed through a heavily pastured valley in sagebrush desert. Muskrat densities were not high at this place, but some animals were present. The irrigation diversion, a rather swiftly flowing ditch stream about 15 to 20 feet wide and a couple of feet deep, led off through more sagebrush desert.

*The marsh edge varied considerably in affording possible burrow*ing sites for muskrats away from the flowages. The whole east side had shallow water grading off into wet meadow, but in places along the western and southwestern edges, muskrats could dig bank burrows without much trouble. Beavers were so abundant as to be a nuisance — plugging ditches — in lowland willow tracts, and some muskrats were associated with these beavers.

Between Gray's Lake and Bear Lake (the north half of which lies in the southeastern tip of Idaho and the rest in Utah) were other extensive marshlands, consisting mainly of large tracts of hardstem bulrushes with variable amounts of open water. One marsh of several hundred acres, looked over from shore and surrounding hills, was found to have muskrats in low densities, as at Gray's Lake. The im-

mense flats north of Bear Lake at Montpelier looked like a great seepage area having alternate patches of grassy meadow and stands of bulrushes or cattails; for most parts, the water looked too shallow to winter many muskrats. Nearer Bear Lake, the marshy stands became more and more extensive, stretching away mile after mile for nearly the width of a wide valley. Bear Lake, itself, a large body of open water, had a fringe of bulrushes about 100 yards in width along its northwest shore, and a single, weed-grown muskrat lodge was seen from the road.

The Snake River makes a roughly semicircular loop from south of Yellowstone Park westward and southwestward through southern Idaho, then northwestward and northward along the Oregon-Idaho boundary. The main stream, all across Idaho, is "western-type," often cutting between steep bluffs or canyons or meandering through silted valleys. Above irrigation impoundments in southeastern Idaho, it was full of water up to the fringing willow growths of its divided channels in early July, 1949. In south central Idaho, dams had widened the river to form Lake Walcott (having attractive bulrush fringes in places) and the big American Falls Reservoir. South of Hagerman, in the Thousand Springs area, springs came out of rock faces for miles along the river, and the river here had very substantial bulrush fringes with muskrat signs. Downstream toward the Oregon line, Snake River became increasingly unattractive for muskrats as its course led through canyons and desert. The real muskrat habitat of the Snake River Valley in southern Idaho is in the tributary streams and irrigation waters, where the animals may be very abundant locally.

The Malheur Lake area of southeastern Oregon has been noted since presettlement days for its abundance of marsh life, especially muskrats and water birds. The flat land having extensive marshes near its center comprises about 600 square miles, at an elevation of 4,100 to 4,200 feet and surrounded by mountains of 8,000 to 9,400 feet. Geographically, the marshes and watercourses leading into them are isolated in a desert, though tributaries of the Malheur River (which joins the Snake River at the Idaho boundary) approach it from the east.

As muskrat habitat, the Malheur River, as I saw it, was nothing special. It was creeklike in size in most places where irrigation waters had been drawn off, and its best stretches from the standpoint of muskrats had willow and bulrush fringes. Some bulrush-filled pools occurred at the bases of springs or where the ground was wet from irrigation seepage. Whether this stream provided much of a connection between the muskrats of Malheur Lake and vicinity and those of the Snake River Valley was not clear. Bailey (1936, p. 215) referred specimens from the Malheur Valley to *osoyoosensis* rather than "to *mergens* of Nevada, while those south of the Malheur Valley are perhaps nearer to the pale *mergens,* although not typical. For the present purposes, all of the specimens examined from east of the Cascades in

Oregon can be treated under the single form *osoyoosensis.*" Davis (1935, pp. 329–30) considered specimens from the Snake River Valley in southern Idaho to be "intergrades between *osoyoosensis* . . . and *mergens.* . . . Other specimens which I have examined from southern Idaho are light in color like *mergens.*"

The last week of July, 1949, was spent on or about the Malheur National Wildlife Refuge in company with Dr. Ray C. Erickson of the U.S. Fish and Wildlife Service.

The approach to Malheur Lake was one of miles of dusty sagebrush-covered dry lake bottom surrounded by steep hills. On the outskirts of the wet area were occasional shallow or partly dry ponds. Malheur Lake and neighboring Harney Lake were but remnants, without outlets, of a lake that once covered the vast flat lands. The Silvies River entering Malheur Lake from the north and the Blitzen River from the south were practically the only sources of water for months or even years at a time in the dry climate prevailing. Irrigation demands reduced the flow from Silvies River, although in years of heavy snowfall this river contributes more water to Malheur Lake than does the Blitzen River, which arises from melting snowbanks of the Steens Mountains to the south.

John C. Scharff, the Malheur Refuge superintendent, told me that there had been many muskrats in the Blitzen Valley during the early forties, but later they all but disappeared. Only a few signs were seen along the creeklike Blitzen River at the time of my visit, but larger numbers lived in some of the shallow, food-rich marshes lying off to the side. South of Frenchglen, the river took on more and more of the appearance of a swift mountain stream.

Malheur Lake's main body of water was perhaps 10 miles in length when Erickson and I worked over a representative part of it. What I saw consisted of large acreages of rather shallow marsh dominated by hardstem bulrush and a large *Juncus,* which occurred in clumps and in more or less solid stands. The wettest parts that we looked over by wading and by canoe had from a few inches to a foot and a half of water. Much of the emergent growth had been heavily cut by muskrats the previous year, but the cutting had served mostly to clear away the top growths and did not appear to have injured the 1949 stand. Current muskrat densities were estimated at possibly a family group per one to two acres.

A shallower bulrush marsh in which muskrats had been badly drought-exposed in other years was in process of going dry again, with the driest part of the summer being ahead. A notorious "botulism flat" had fringing growths of bulrush clumps and some muskrat lodges, but the muskrats remaining here were largely concentrated along a wet channel — which also had prospects of going completely dry in the weeks to come. Ditches along dikes were partly dry, and the usual sign of muskrat adjustments between the dry and the wetter parts was evident. In places, heavily used muskrat trails ran for

hundreds of yards from dry or drying marsh into wetter areas, yet at the same time, it could be seen that occupants of other parts were confining their detectable activities to established territories.

Muskrat movements of impressive magnitude have been witnessed. Bailey (1936, p. 217) wrote that most of the muskrats left Malheur Lake in the winter of 1914–15 and scattered for miles over the sagebrush. "They were poor and possibly diseased, but more probably starving, as their regular food supply had been destroyed by unusually high water that summer. . . . Many thousands were estimated as killed outside of the lake, and as many more died that were not recovered. The next summer the writer saw their carcasses in the sagebrush over the valley and the animals were scarce in the lake." Stanley G. Jewett (letter, September 17, 1949) observed in the early spring of 1917 a big movement of muskrats traveling over the snow-covered desert to the east of Malheur Lake. "During a two day trip . . . I saw evidence of where not less than 20 were killed by coyotes and rough-legged hawks."

Scharff described some of the mass movements taking place across the desert. One winter in the mid-thirties, school children at Crane clubbed large numbers of muskrats along a travel route about 10 miles from the lake, making more money at this, it is said, than their teachers were receiving in salaries. He thought that this migration was a result of overpopulation rather than of drought or perceptible food shortage. Wanderers have also been seen during more ordinary years scattered all over the desert west of Refuge Headquarters, three or more miles away from water.

Some idea of the productivity of Malheur Lake for muskrats may be gained from the vertebrate remains to be seen about the middens of an old Indian campground near a big spring at the present Refuge Headquarters. Bones of ungulates and large birds are abundantly mixed with the broken arrowheads and stone utensils, but what one really notices are the literally countless skulls of muskrats.

There is reason to think that the hemorrhagic disease may have some importance in the population dynamics of the Malheur area muskrats. Dr. M. P. Chapman, of Oregon State College, sent me (letter and enclosures, April 2, 1947) necroscopies on two muskrats that had been sent to him in February from Malheur Lake. The lesions described were similar to those often observed in Iowa victims. In submitting the specimens to Chapman, Scharff had written:

> During the last month or six weeks there has been a considerable "die-off" of muskrats on Malheur Lake. . . . At first this "die-off" was noticed only over a small area but later it seems to have spread to most of the rat inhabited waters. As many as 14 dead rats have been found in one house.

Scharff and other refuge personnel at Malheur told me that trappers there regard digging into lodges by coyotes as indicative of dead muskrats within. This digging may occur on a considerable scale dur-

ing years of known disease losses, and some of the local residents even asserted that a coyote would not dig into lodges unless it were after dead muskrats.

Buena Vista marsh, one of numerous marshes within the refuge south of Malheur Lake, was the site of a suspected die-off, and Erickson and I worked it by canoe. It had a good water level and well-dispersed islands and clumps of cattail, bulrush, and burreed but very few muskrats. About 1942, the muskrat population had been very heavy but had since declined to the extent that neither the shore zone nor some solid blocks of the best-looking emergent vegetation showed recent muskrat signs. While a few tracts of about six to eight acres had possibly a family group per acre, there was over most of the marsh (including parts having 1949 spring lodges) no fresh or recent signs, as of late July, except of what seemed to be scattered subadults.

The decline of the muskrats was ascribed by the public to an abundance of minks, but I do not see how that could have been. Wintering conditions had been favorable, and in summer, muskrats lived in lodges that minks should rarely have gotten out to. Along the shore, mink as well as muskrat signs were conspicuously absent at the time of my visit. Minks were frequenting to some extent — much less than I had been prepared to expect — the more accessible small islands, where they were preying rather severely upon nesting water birds. On the principal island having mink signs, we examined about 100 scats from winter or early spring, of which 3 scats contained muskrat remains. The staple prey consisted of mice. None of about 168 later scats contained muskrat remains; the food items were mostly avian (blackbird and some waterfowl), with some mice and invertebrates.

No one knew of disease losses among the Buena Vista muskrats, but the population symptoms were those of a continuing epizootic. In the case of dense stands of wet vegetation not penetrated by canoe, the view from a high rimrock nearby revealed a decided lack of lodges, of muskrat openings or trails, or of anything indicative of the species. Some of the parts of the marsh that were muskrat-vacant in July had been well used in the spring.

Harney Lake receives water at times from Silver Creek (rising in the Blue Mountains to the north) and from Malheur Lake, which lies about 15 miles to the northeast. When Erickson and I visited Harney Lake in late July, 1949, it had some springs with marshy vegetation but was otherwise a salt-flat desert surrounded by miles of sagebrush. We walked out to a series of springs — surrounded chiefly by alkali bulrush clumps, the largest about four acres in area — about a mile from the nearest recent shoreline. Here, at the largest bulrush clump, we found an old dead muskrat, bones intact.

Ex post facto "reading of sign" indicated that this same lone animal had lived in a small lodge built of the 1949 growth of vegetation and, before then, in another small and flattened lodge dating back at least to the fall of 1948. Erickson had seen the drying body in

much fresher condition in June, and we judged that it had probably died early in that month from old age. As wintering habitat, the bulrush clumps with their spring water looked quite good. Erickson said that the springs remain wet and that snow collects over the bulrushes, so that an animal living here should be able to reach rootstocks without difficulty. The place was diligently hunted over by coyotes, but the muskrat had taken care of itself in this restricted niche for about a year.

Scharff told me that, in 1942, when the water had been higher in Harney Lake, he had seen 20 to 30 lodges in the bulrush clumps. Maximum depths of water in the bulrushes (not counting the depths of the springs) had been about a foot and a half in recent years. It may be significant that this isolated colony was noted during a year of high muskrat populations in the Malheur area.

Other isolated wet valleys lie to the west and southwest of Malheur and Harney lakes and the Blitzen Valley, and some of these afford excellent habitat for muskrats. The animals have been introduced at Summer Lake, about 90 miles WSW of Malheur Lake. They occur in the Warner Valley lakes and marshes about 50 miles southwest of Malheur Lake, though local residents are not in agreement as to whether muskrats were there at the time of settlement or were introduced. Other suitable places in south central Oregon are still muskrat-vacant and for obvious reasons, with 40 to 50 miles of desert separating isolated watersheds.

In Washington, Dalquest (1948, pp. 362–63) depicted the range of *osoyoosensis* as including all of the state except that occupied by *occipitalis* in the southwestern part and the crests of the Cascade Mountains. To quote from his pages 361–62:

> In the extensive marshes along Lake Washington, King County [east of Seattle], muskrats are abundant. They occupy sluggish water, often water polluted by garbage and sewage. In these marshes, banks suitable for the construction of burrows are absent and houses are made of cattail stalks and leaves. . . .
>
> Near Richmond Beach, Snohomish County, muskrats took up residence in a small tidal pool along Puget Sound. The nearest fresh water stream large enough to support a muskrat was two miles away. Two muskrats were trapped here. Investigation of a tidal pool a mile to the north disclosed unmistakable muskrat signs. Traps set in the culvert connecting the pool with Puget Sound at high tide took several specimens. Study showed that the muskrats were not living in the pool but among the large boulders forming the breakwater for the Great Northern Railroad, along the sound itself. They were feeding on marine mussels (*Mytilus*). These mussels lived in the salt water of the sound, not in the tidal pool.
>
> At Peavine Pass, Blakely Island, in the San Juan Islands, muskrats were living in the swift tidal current and deep, marine waters. Several were seen in late afternoon. All were swimming parallel to the shore about 50 feet out. Here also they fed on *Mytilus*, but their homes were not discovered. . . .
>
> In the interior of Blakely Island a colony of muskrats was discovered living in a marsh of about one acre. In the rainy season the ground of the marsh was covered with less than one inch of water. Residents said that in the dry season springs kept the ground moist. Muskrats were living in burrows whose

entrances descended at a 45-degree angle and were filled with water. The ground about some occupied burrows was dry, the only water visible being in the burrow itself. A variety of marsh vegetation provided food.

Minks *(Mustela vison energumenos)* may be abundant over some of the muskrat range of the northwest Pacific states, some trappers taking, according to Dalquest, as many as 100 in a winter. From Dalquest's pages 200–201:

> In the San Juan Islands minks have forsaken the shoreline and roam over the uplands, feeding on the abundant, feral domestic rabbits. . . . Along Puget Sound, minks spend part of their time on the beaches, feeding on dead fish and other marine animal life. These animals, however, seem to live along the rivers and streams flowing into the sound. Along the ocean coast, some minks seem to live exclusively in the marine shoreline habitat. . . . The muskrat forms an important item of diet near the larger lakes and streams. Muskrats trapped near Seattle were often attacked by minks.

Dr. Ian McTaggart Cowan, of the University of British Columbia, told me in conversation, March 9, 1949, that *osoyoosensis* occurs right down to the seashore in British Columbia. Later, he wrote (letter, March 16, 1951) that "it is abundant on the delta of the Frazer River in the vicinity of Vancouver, but north of this on the coast, it is of only sporadic occurrence."

The many glacial waters of eastern Washington, northern Idaho, and southeastern British Columbia present various grades of muskrat habitats. I traveled over part of the region in 1938, inspecting in particular the Palouse country of Washington and the vicinities of the Pend Oreille and Coeur d'Alene lakes of northern Idaho. There was muskrat habitat, along with muskrats, in bays and seepages grown to emergent marsh vegetation, in the quieter streams of forest and farmland, in potholes and beaver ponds and backwaters of rivers. There, too, as elsewhere, wave-beaten rocky lake shores and rapids-filled canyons were largely muskrat-vacant.

Farther north, in the Kootenay National Park of British Columbia, Munro and Cowan (1944) reported muskrats in expected types of habitats. I would judge, however, that the area is more suited to beavers than to muskrats, though the presence and activities of the beavers surely must make some of the smaller streams more habitable for muskrats than would otherwise be the case. This park, which lies just inside of the British Columbia boundary about eighty miles west of Calgary, Alberta, and about an equal distance southeast of Jasper National Park, may be close to the northern edge of the range of *osoyoosensis.* Soper (1947) wrote that muskrats from Jasper Park and north are undoubtedly referable to *spatulatus.*

It may well be that genuine *osoyoosensis* extends much farther north in British Columbia than in Alberta – possibly northward from its known range in the Columbia River Valley far up into the Cariboo Parklands. The lakes and marshes of this area are known as waterfowl

breeding grounds, as is illustrated by many papers by J. A. Munro, and they have muskrats. This author (1945) described the

> territory . . . [lying between the 51st and 53rd parallels] as one of shallow east and west valleys from which grasslands and aspen-covered slopes ascend to forested ridges. One of the notable features is the multitude of water areas of varied extent . . . from small, shallow ponds and sloughs to deep, usually narrow lakes up to 12 miles and more in length.

Also:

> the lakes are not connected with the main drainage systems and hence not subject to flooding so that the water level is fairly well stabilized during the course of any one season. None of the marshes is of great extent; they vary in size from a few acres to 100 acres or more. Some are in the form of a series of discontinuous shoreward strips between open areas of boulders or soft bog. Others encircle the circumference of small lakes or ponds. . . . [Still others] cover relatively large areas in which open water is restricted to a few narrow channels. Certain small lakes in narrow valleys have their main areas of marsh at the outlets.

The disease complex in muskrat populations of western United States may be most involved, and with tularemia, hemorrhagic disease, and fungus diseases dominating local situations, one might wonder to what extent they may depress or keep depressed the numbers of muskrats over significant areas. (See Appendix M for a résumé of disease studies centering upon Montana muskrats.)

Over much of Montana where good, naturally formed marshes are scarce, I saw during the late forties many cattail-grown irrigation seepages that furnished fair ecological equivalents of natural marshes. Those were seen from main highways in many parts of the state. Some particularly fine marshes originating from irrigation seepage — two or three acres in size, or larger — were noted, together with those of presumably natural origin, between Missoula and Flathead Lake. South of Flathead Lake were the Nine-Pipe marshes, having obviously excellent muskrat habitat in places. Jellison told me of a trapper who took about 1,000 muskrats per year from these, mainly seepage, marshes and sloughs.

Toward the mountain foothills, typical small streams were bordered by dense growths of willows, sufficient both to catch drifting snow (thus affording protection against the deep freezing of the ground and water so detrimental to wintering muskrats) and to attract beavers. Waters impounded by beaver dams were not always grown over by cattails and bulrushes, but those having marshlike aspects were almost certain to have muskrats unless the animals happened to be generally scarce. Sometimes, large acreages of creek lowlands were flooded by complex series of beaver dams, which resulted in extensive willow thickets being interspersed by plant growths of marshes and meadows and by open or debris-filled pools. The pools were from an acre or two up to perhaps 40 acres or more in size. In these ecological

blends of meadow, marsh, bog, and willow swamp, with clear streams trickling through, the muskrats naturally stood some chance of finding suitable living quarters, whether with the beavers or away from them.

No precise figures as to population densities of muskrats in the waters of foothill "beaver meadows" are at hand. The view of local trappers and ranchers seemed to be that muskrats seldom became as abundant there as along the streams of lower altitudes. Drying of snow-fed flows in winter surely must have affected the habitability of considerable areas of foothill country for the muskrats, despite the beaver impoundments.

Field work in the Flathead area of northwestern Montana was centered in 1948 about two localities. One locality included the valley of the Clearwater River north of Seeley Lake, along the west side of the large wilderness or roadless area of the Flathead National Forest. Inez Lake, at slightly over 4,000 feet, was one of a string of five narrow lakes connected by the Clearwater River. It was a trout and perch lake with deep, clear water and little vegetation, but the muskrats were about as abundant along its shores in early July as they usually were along the shores of open-water prairie lakes – perhaps the equivalent of a family group about every 500 to 800 yards. At the north end of the lake, where the river came in, were rather extensive border zones of yellow water lily, pond weeds, bulrushes, and fringing willow growths. Here, both beaver and muskrat signs were evident, especially in the food-rich places. The river between lakes was shallow and had many willow-grown bars and banks, much driftwood litter and many old beaver dams. Muskrat signs suggested (on the basis of known fall catches from Iowa streams of similar size and appearance) populations of around 40 to 60 per linear mile. George W. Roskie, a veteran resident outdoorsman (retired forester and Boy Scout executive) regarded the parts of lake and river that I inspected as being fairly typical for the lake chain. He said that muskrats occurred in numbers in suitable places all along the stream.

The second locality worked over was the east side and the south end of Flathead Lake, a large (about 7 by 35 miles), deep (over 100 yards maximum depth), oligotrophic lake having an altitude of about 3,000 feet. It had a waveswept cobble beach, with a water level artificially lowered by about 10 feet in late winter. Those stretches of lake shore that were looked over were so unsuitable for muskrats as to arouse questions if the animals could live there at all and, if so, how. Dr. Gordon B. Castle, Director of the Biological Station of Montana State University at Yellow Bay, made available the facilities of the Station during a four-day stay, and the Station personnel discussed with me the ecological problems that resident muskrats would be up against.

Dr. Philip L. Wright of the Station's staff, through inquiries of year-round residents, established that muskrats were seen from time to time along the lake shore, but rarely except in spring. One had been

observed trying to winter in a boathouse, which it had partly filled with miscellaneous debris. Away from the lake, several places were seen where muskrats lived or had lived. A beaver pool in the woods about 50 yards from the lake had had a muskrat (seen by students) earlier in the summer, though no signs remained by mid-July. An open pasture type of slough of about six acres had many old sunken muskrat burrows, as well as some in current use. The evidence indicated about three breeding territories, including one in a lodge built on a rock pile out in the water. This slough was appraised as being short of food, like many midwest pasture sloughs having little emergent vegetation. Wright spoke of there being many sloughs like this one scattered through woods and meadows between the lake and the mountains to the east.

The highest, really good, extensive muskrat habitat observed, with substantial numbers of muskrats resident, was at Lower Red Rock Lake, about 3,500 acres, at 6,800 feet, 40 miles west of Yellowstone National Park. It had in 1948 about 6 feet of water in the deeper parts, which were mainly of open water except for bulrush *(Scirpus occidentalis)* islands. The shallows — especially those grading off into meadow around the edges — were dominated by the sedge, *Carex rostrata*. Dr. Ward M. Sharp, in describing the winter status of the muskrats, said that the muskrat lodges are then distributed both in the bulrush islands and in the sedges of the shallows. The winters are long and cold, and the muskrats here are doubtless confronted with obstacles to survival much as are the muskrats living at lower altitudes a thousand miles to the north.

A small sample of the sedge margin was looked over in mid-July, 1948. A mink den with four or five active young was found, and in its vicinity were two recognized breeding territories of muskrats. The muskrats at existing densities seemed quite secure, as no muskrat remains were seen in a collection of about 300 mink scats, the contents of which were mostly of avian material. In one of the above muskrat territories, a litter of muskrats of about three and one-half weeks was being kept under a boat only about ten feet from the mink den.

Good stream-dwelling populations of muskrats were noted in suitable habitats of the Red Rock Creek and the Beaverhead River into which the Red Rock lakes drain. (The Beaverhead River is one of the streams along which beavers and muskrats were reported by Jellison, Kohls, Butler, and Weaver (1942) as dying of tularemia in the spring of 1940.) These streams at altitudes of 4,500 feet, or higher, had many of the features of good muskrat habitats of the lowlands, especially willow-hung eddies, oxbows, and old beaver pools. Exposed sand or mud bars were often packed by muskrat trails and sitting and feeding places, and scattered about was the plant litter characteristic of the activities of high densities of muskrats. Smaller creeks and irrigation flows had many muskrats. One typical 150-yard stretch examined in 1948 had the equivalent of two territories. Local stands of cattail

furnished attractive muskrat environment, and the animals occurred abundantly in meandering waters choked with bittercress.

Hegben Lake, lying just west of Yellowstone National Park and north of the Idaho-Montana boundary, had considerable marsh area, sluggish streams, willow parkland, and fair numbers of muskrats.

The Gallatin River, at the northwestern tip of Yellowstone Park, had muskrats even in some of its higher source waters. Here, streams angled off through wide, grassy valleys, where a few beaver pools and quiet eddies fringed by sedges could be seen. Downstream, where the river had quite swift water running through a deep channel, muskrats were restricted to the less turbulent stretches having mossy or grassy banks.

Because they are protected from human exploitation or persecution, the muskrats of Yellowstone National Park should represent one of the most "natural" high altitude populations of the species to be found in the United States. Their status in the Park has therefore been a matter of exceptional interest from the standpoint of the investigations. Although pressure of time in mid-July, 1948, permitted my inspection of muskrat habitats only in the northern third of the Park, David de L. Condon, Chief Park Naturalist, contributed a very useful summary of his observations on distribution and numbers over the Park area as a whole. The statements immediately following are based upon an interview with Condon and personal notes taken shortly afterward in the field.

The highest altitude at which Condon observed muskrats was at 9,400 to 9,500 feet, at Mariposa Lake on Two Ocean Plateau, in the southeast corner of the Park. Some glacial ponds near Mammoth in the northwest corner have muskrats, but the altitude there is only 6,200 feet. Muskrats occur at about 7,800 feet all along the Yellowstone River between the Grand Canyon and Yellowstone Lake, in quiet waters where the river meanders and has much vegetation. Alum, Trout, and Sour creeks, tributaries of the Yellowstone in Hayden Valley, have generally more attractive vegetation for muskrats than do the Firehole and Gibbon rivers on the other side of a plateau; and the muskrats, while present on both sides of the plateau, are more abundant on the ecologically better side. Some of the willow parks bordering small streams have many muskrat lodges in fall.

In 1949, I looked over the southern part of the Park and the approaches from the south, including Jackson Lake. Here, there are marshy places or quiet waters with muskrats, but the good habitat is very limited. Beaver pools near Moose, Wyoming, had some muskrats; and, from what Dr. O. J. Murie told me of wintering conditions, the species should be able to maintain itself in such niches. Muskrat signs were also to be seen about some of the oxbows of the upper Snake River, but the main channel was too swift to be attractive. Yellowstone Lake, as seen from its west and northwest shores, offered few attractions for muskrats. Its altitude of 7,731 feet, its 100-mile shore line, and

approximately 139 square miles of surface area gave me somewhat the impression of a large lake in the Pre-Cambrian Shield of the Canadian North.

Dr. Adolph Murie, in studying food habits and prey relations of coyotes in Yellowstone National Park, observed (1940, pp. 124-25) that:

> Muskrats are not very numerous but are generally distributed along the water courses and ponds. During the fall and spring they are especially vulnerable to coyote attack when they wander out over the snow. Should a muskrat be discovered by a coyote when journeying on land, its chances of escape are, of course, slight. Journeys of more than 100 yards on the ice were noted. . . . Coyotes have been found to investigate a network of tunnels along a stream but it seems probable that muskrats are generally captured accidentally, for it would hardly be profitable for the coyote to spend a great deal of time hunting them.

This sort of behavior on the part of muskrats in winter is so indicative of individual insecurity that one may suspect that either the food situation was bad or that numerous transients were moving. If the animals tracking up the snow were truly wanderers, they might represent either or both the drifters from habitats occupied in summer but untenable in winter or the harassed surplusage of overpopulation — overpopulation in the sense of there being too many muskrats for the habitat even though numercial densities may not have been high. While Murie wrote further that "Coyote pressure upon muskrats does not appear to be great," and while the probability is that the elimination by coyotes of essentially doomed surplusages had little or no net effect on population levels maintained by the muskrats, his finding of remains of 98 muskrats in 5,086 coyote scats might mean quite a pronounced vulnerability of muskrats, considering their relative scarcity.

In short, it would be strange if, in muskrat environment as marginal as most of that of the Park, winter did not ordinarily bring about lethal crises. Repeated pruning back in winter of the ranges expanded in summer would seem to be the big natural regulator of numbers, with a fairly secure population nucleus left here and there to perpetuate the process.

One of the superior muskrat habitats in the Park is the Lamar River valley. Trumpeter Lake in this valley has muskrats the year around, and these are a probable source of the muskrats that occasionally reach the high and inhospitable Beartooth Plateau, lying northeast of the Park. (See Appendix N for discussion of special study of muskrat movements and distribution centered on and about the Beartooth Plateau.)

At the higher altitudes where muskrats were found, where the streams became rockier, swifter, more intermittent in flow with change of seasons, and more lacking in vegetation of the sorts eaten by muskrats, the muskrats tended to be restricted to beaver ponds.

The close association of muskrats with beavers in many parts of the mountainous Northwest is readily understandable. Where streams are fed by melting ice and snow and dry up in winter, there is often virtually no place except in water impounded by beavers in which muskrats could winter. Individual beaver ponds may or may not have nutritious vegetation available for muskrats under the ice. If not too high, some beaver ponds take on marshlike aspects, with variable stands of cattails, bulrushes, water lilies, and other well-known muskrat foods. An example seen next to East Rosebud Creek, at about 6,500 feet, had in early July, 1948, no fresh beaver signs, but one of its two old beaver lodges had been taken over by a family group of muskrats. The pond was about one-half acre in area, with maximum depths of four feet and much water one and one-half to two feet deep. Heavy growths of yellow water lily, besides good herbaceous swamp growth (no cattails nor bulrushes) and thickets of willows, were growing in or near the water.

At altitudes exceeding about 8,000 feet in south central Montana, such few muskrats as were able to maintain themselves in stream habitats fed on much the same kinds of foods that the beavers ate — among other things, upon the terminal branches of willows and aspens cut down and dragged to the ponds by the beavers. Moreover, the muskrats lived in both the lodges and bank burrows of beavers, including some occupied by beavers at the time. And muskrats living in the beaver colonies after freeze-up would have for their own feeding some of the food stored by beavers for winter use — sometimes available in huge piles under the ice.

The highest habitat so far observed that appeared to be occupied on a year-round basis by muskrats was a beaver pool in the Big Horn Mountains of north central Wyoming at an altitude of approximately 10,000 feet. At lower levels in the Big Horns, the beaver ponds were also the main habitats of muskrats. These included extensive flats of willow parklands as well as little trickling headwaters dammed in numerous places to create a series of ponds.

A possible indirect role of disease in the population fortunes of the mountain-stream muskrats should here be brought out. In the spring of 1946, both forks of Rock Creek and some neighboring tributaries were all but depopulated of beavers, evidently through the agency of tularemia. Apart from the deaths of muskrats from tularemia itself, the loss of beavers could well reduce very decidedly the amount of livable habitat that the muskrats might have. Except for beaver floodings so old that they have become truly marshlike, with natural growths of cattails and Cyperaceae, the usual beaver impoundments of mountain streams in the above locality have little food suitable for wintering muskrats after the beavers no longer bring it in from outside.

Winter food shortage certainly must be a foremost limiting factor for muskrats in south central Montana far below the altitudes of the

mountains. Residents of Red Lodge have described muskrat trails in the snow about the willow parks and old beaver pools upstream along Rock Creek, at about 5,600 feet. In here, a strong flow of water continues in the main channels of the stream throughout the winter, and early snows usually prevent the boggy parts from freezing deeply. Bernt Egenes, of Red Lodge, who one winter trapped 45 muskrats from a place nearby, noticed that they were much smaller than the muskrats with which he had been familiar as a central Iowa trapper years before; the largest specimens of his Red Lodge catch were graded medium size by the fur buyer. But if these muskrats happened to have been *cinnamominus,* or intergrades therewith, their smaller size need not be ascribed wholly to difficult environmental conditions.

A few data on what may be classed as lone muskrat pioneers in mountain-stream habitats west of Red Lodge should be worth presenting. One animal lived throughout most of the summer of 1935 (it had left by late August) under a wagon bridge across a canyon brook at about 6,000 feet; the nearest place where muskrats were found to be living during close inspections in six later summers was in a series of beaver pools over a mile downstream. Another animal appeared about a half mile farther upstream in 1949, though there were not any in maintained residence for at least three miles downstream, or along the entire length of this particular brook valley. All of the old beaver pools were by then washed out, dry, and weed-grown, having signs of neither beavers nor muskrats. Summer and fall wandering of muskrats up and down this stony brook might be expected from time to time, but, without the beavers, the stream seemed to lose all the habitability it ever did have for muskrats.

Another muskrat pioneer — a big animal — moved about late May, 1948, into a spring-fed beaver pool to the side of the West Fork of Rock Creek, at an altitude something less than 9,000 feet; it was still around by late July, living in the main set of beaver burrows with the beavers and feeding chiefly on beaver-carried vegetation. This particular pool was 20 to 25 yards wide, from 8 to 21 inches deep, and with a considerable area of sedge meadow around it. Adjoining it was a 20 by 65-yard pool with a maximum water depth of about one and one-half feet, impounded by a very old but still functional beaver dam about 80 yards long, and surrounded by sedge meadow having an area roughly twice that of the open water. Between the latter pool and the creek lay about a half acre of willow and cutgrass swamp and old beaver pools. No muskrats were known to be living farther upstream (though they had occurred at least six miles farther up in 1939), nor were other sites of residence known for nearly seven miles downstream — which meant one known muskrat along the entire 20-mile stretch of the West Fork of Rock Creek. In 1949, I could find no muskrat signs along the West Fork.

The comparable 20 miles of the South Fork of Rock Creek had many more muskrats than the West Fork in the summer of 1948,

but it, too, was seemingly devoid of the species in 1949, despite better looking environmental conditions than in 1948. The highest point known to have been occupied by muskrats here at any time was at an altitude of about 8,500 feet. In 1948, an apparent family group lived in an old beaver lodge in the midst of about four acres of beaver-flooded creek valley. Downstream were several other places where muskrats lived, notably in a wide area of beaver floodings above the junction of the West Fork and South Fork. The South Fork has the wider valley along much of its course and consequently many more places of superior attractiveness to beavers and muskrats alike.

THE EASTERN CANADIAN MUSKRATS, obscurus and aquilonius

I have been unable to find in the literature more than fragmentary information on the Newfoundland muskrat, *obscurus,* but learned much from correspondence with H. W. Walters, of the Newfoundland Department of Natural Resources, and Austin W. Cameron, of the National Museum of Canada.

Walters (letter, April 11, 1949) wrote that the

> marsh areas in Newfoundland suitable for muskrat are small and it is only on rare occasions that one would see a muskrat house. Generally they burrow within the banks of ponds or small lakes. From personal observation I would say that their food consists of various types of grasses and weeds and I believe the leaves and roots [of the yellow waterlily]. . . . Short lengths of the yellow waterlily root can always be found stored near the burrows of muskrats.

Cameron very generously undertook to record for me any observations he might make on *obscurus* in connection with a field program he had planned in Newfoundland for the summer of 1949, and, along with a letter of September 24, 1949, he sent me the following notes:

> The Newfoundland muskrat (*Ondatra obscura*) is a rather small, dark insular species differing from continental forms in a number of morphological characters. Local furriers contend that pelts of this species are of less value for fur purposes, due to the thinness of the skin.
>
> This species is widely distributed over the island, occurring in ponds, streams, and in the bays of the larger lakes. The greatest concentrations are to be found on the Avalon Peninsula and in the river valleys along the west coast. Much of the interior consists of barrens or semi-barrens dotted with numerous rocky, largely unvegetated ponds and lakes. Here a few muskrats manage to subsist on the scanty vegetation.

(Appendix O contains Cameron's notes as to the localities in which he found *obscurus.*)

Jean Duguay, of the Department of Fish and Game, outlined for me the distribution of *aquilonius* in the Province of Quebec (letter and enclosure of April 1, 1949). The forty-eighth parallel is the approximate dividing line between that subspecies and *zibethicus* to the south, but both subspecies occur in places on either side of this line.

On a detailed map, it can be seen that, in western Quebec, this line follows roughly the height of land between the Hudson Bay and St. Lawrence drainages. Probably there is a big area of intergrading south and southeast of James Bay: "The trappers divide the aquilonius in different types. They call it Lake St. John type, Mistassini type, Abititi type. . . . One thing is sure: the more you go north the less you meet zibethicus."

Anderson (1934), after writing of *zibethicus* being "found around both sides of the southern end of James Bay, ranging from thence southeast to the St. Lawrence," described the recorded range of *aquilonius* as from the Strait of Belle Isle (between Newfoundland and Labrador, at about the fifty-second parallel) to Fort Chimo, which lies south of Ungava Bay above the fifty-eighth parallel. "There is still a wide area from James Bay to Chimo and the northeast end of the gulf of St. Lawrence where the muskrat is known to occur but no scientific specimens are yet available."

It is rather clear from present information that the main range of *aquilonius* extends northwestward from the Gulf of St. Lawrence to the vicinity of the fifty-fifth parallel.

I know of two records of extreme northern occurrence of *aquilonius* in Quebec. Dr. O. J. Murie told me in 1949 of having collected a specimen in 1915 at the Nostapoka River, along the east coast of Hudson Bay. This place is between the fifty-sixth and fifty-seventh parallels, beyond the timber, characterized by many little clear lakes in granitic hills. Concerning the northernmost record in the Carnegie Museum, J. Kenneth Doutt wrote (letter, April 14, 1949):

> The specimen was obtained at the mouth of the Kikkerteluk River which is between Great Whale River and Port Harrison on the east coast of Hudson Bay at approximately a point where the 58th parallel crosses. . . .
>
> I got the specimen from an Eskimo boy on July 28, 1945. . . . From him I was led to believe that muskrats were not abundant, but were not uncommon at that point.

The sparseness of *aquilonius* populations over Quebec is illustrated by a statement in Duguay's letter to the effect that, despite the much larger geographic range of *aquilonius,* it comprises on the average only about 30 per cent of the muskrats caught for fur in the province. And, included in the range of *aquilonius* is a famous muskrat-producing area about Lake Mistassini, lying in the James Bay (Rupert River) drainage but nearly half way between James Bay and the mouth of the St. Lawrence River. The Lake Mistassini "rice rats" are considered by the fur trade as among the choicest in Canada.

THE HUDSON BAY MUSKRAT, albus

In the summer of 1948, I had opportunities to inspect representative parts of the eastern range of *albus,* largely through the cooperation of the Hudson's Bay Company and the Manitoba government. In

addition to transportation and facilities furnished by these agencies, D. E. Denmark (Manager of the Company's fur preserves) and G. W. Malaher (Director of the government's Game and Fisheries Branch) gave me access to many years of records on the management and fur yields of celebrated muskrat-producing areas of southern and central Manitoba and east central Saskatchewan. In wilderness regions, the usual investigative procedure was to look over wetlands from aircraft, then cover them by canoe. The main reliance in gathering data was placed upon firsthand "reading of sign" and questioning of competent observers familiar with local situations. Between trips with personnel of the Hudson's Bay Company and the Manitoba government, I headquartered at the Delta (Manitoba) Waterfowl Research Station at the invitation of the Station Director, H. A. Hochbaum.

The eastern edge of the range of *albus* may be imperfectly traced. Anderson (1934) wrote of it being "found on part of the west coast of Hudson Bay, at least as far south as York Factory, but is not definitely known to occur as far east as James Bay coast." Near York Factory, in northeastern Manitoba, is a tract of Barren Grounds comprising the edge of muskrat range.

Among the other troubles to which muskrats of the Barren Grounds are said to be subject is the eating of their lodges by caribou, which apparently can well clean up the plant material within their reach above the ice. The significance to the muskrats of this molestation is not clear from information at hand. The species, nevertheless, does exist hundreds of miles to the northwest and north of York Factory, though in here the range of *albus* should be grading off into that of *spatulatus*. John S. Tener, of the Canadian Wildlife Service, sent me a record (letter, February 22, 1955) of a muskrat having been "shot in a pond at Eskimo Point, Keewatin District, N.W.T., in September, 1952."

Clarke (1940) wrote concerning his investigation of the Thelon Game Sanctuary, which lies in the Northwest Territories almost due north of the Province of Saskatchewan and west of the north part of Hudson Bay:

> According to Mr. A. J. Knox, muskrats [which could be *albus*, or intergrades with *spatulatus*] are found regularly in the ponds on Crystal Island, Artillery Lake, at the extreme edge of timber, and he once found a wanderer at Ptarmigan Lake. In the eastern end of Great Slave Lake there are few marshes suitable for large numbers of rats, and there is only one record.

Southward from the Barren Grounds near York Factory, the terrain becomes more typical of the timbered rocky formations of the Pre-Cambrian Shield. Some of the country south of James Bay (which I remember from a canoe trip in 1921) had lakes with shores that were more precipitous than the lakes of the Whiteshell area of southeastern Manitoba. There was also more about northern Ontario south of James Bay that reminded me of the near-timberline woods, waters, and

rocks in the western mountains and, conversely (if this be not taken too literally), more about southeastern Manitoba to be likened to the lower slopes and valleys of the mountains. The undersized muskrats reported trapped in the high altitude streams east of the Beartooth Plateau of south central Montana and from the Barren Grounds at York Factory would strengthen these analogies. Still, the Pre-Cambrian Shield about James Bay is known to have fine muskrat country yielding the choice "rice rats." These muskrat-producing areas – whether in the actual ranges of *albus, zibethicus,* or *aquilonius* or intergrades thereof – have bays grown with emergent vegetation, including almost pure stands of wild rice.

In southeastern Manitoba, Soper (1946) believed, lacking museum specimens, that the muskrats possessed chiefly the characteristics of *albus,* perhaps showing intergradations with *zibethicus* in the extreme southeast corner. Examples of living and dead animals that I saw in the Netley marshes south of Lake Winnipeg in 1948 certainly agreed with *albus* in size, if not in coloration. Toward the southwestern part of its range, *albus* seems to come close to or to intergrade with *cinnamominus* in the vicinity of Touchwood Hills, northwest of Regina, Saskatchewan (Hall, 1938).

Of its general range, Anderson (1937) wrote that the Hudson Bay "muskrat is found in waters draining into Hudson Bay from the west and which arise in northern Manitoba, northern Saskatchewan, and Keewatin District north to the limit of trees." Preble (1908) considered specimens from Athabaska and Great Slave lakes to be "somewhat intermediate between [*spatulatus* and *hudsonius (=albus)*] and might without impropriety be referred to *hudsonius.*"

Beginning at the middle of Lake Manitoba and extending 500 miles northward and 700 miles northwestward is a triangle of wilderness wetlands, largely of bogs and shallow limestone lakes and marshes. The view from the air varied in 1948 from that of tremendous expanses of willow and scraggly tamarack bog, with an occasional pond or a low ridge of spruce-covered limestone, to equally extensive, interconnected open water separated by crooked and narrow fringes of shore vegetation. In August of that year, the water level in many places was still two or three feet above normal, as a consequence of spring floods. Dr. J. A. McLeod of the University of Manitoba said that many of the lakelike areas then to be seen were nothing more than mud flats in late summer of ordinary years. This is a country of moose and woodland caribou, of breeding waterfowl, and of muskrats, too; but the last found good environment only locally. Indeed, in the vastness of this triangle, the really attractive muskrat marshes may be likened to islands in the waters and bogs.

Looked over only from the air in 1948 were innumerable – generally small – marshes along the west side of Lake Winnipegosis. These had alternating strips of water and vegetation, and irregular "feather-edge" shores. Many had open centers surrounded by bulrush

rings; others had scattered bulrush clumps. (I had seen some of these, or at any rate some like them, at the height of the drought in 1934, and, even then, a surprisingly large number had remained in attractive condition for marsh-dwelling life.)

A celebrated muskrat marsh, Plummer's Island, was mainly open bog dominated by strips and clumps of coarse grasses, but there were also substantial bulrush growths in places. This lease of 21,145 acres (A. G. Cunningham, letter and enclosure, June 2 and 4, 1938) had 40 lodges in the fall of 1933; 1,554 in 1934; 4,053 in 1935; 4,793 in 1936; and 4,361 in 1937. The spring catches following the falls having more than 4,000 lodges fell off from 10,891 muskrats in 1936 to 8,426 in 1937 and 5,055 in 1938. I do not have any information as to the mechanism of the decline. Fur managers with whom I talked at The Pas in 1948 felt that the muskrat habitat on this lease had greatly deteriorated because of high water.

The east half of the Hudson's Bay Company's Steeprock lease, near Dawson Bay of the northwest end of Lake Winnipegosis, was worked by canoe and on foot. This was the site of Butler's (1940) study of muskrat foods, in which he calculated that the existing stands of marsh vegetation could have furnished sufficient food for an average of 15 muskrats per acre. Between then and 1948, the emergent vegetation had evidently deteriorated somewhat, though it had not been subject to the excessive flooding prevalent over much of the region.

Management of the muskrats through manipulation of water levels has been singularly effective. An anonymous article (1943) reported that the 1,400-acre marsh on the Steeprock River had once been

> famous for muskrats. The drought years around 1930, combined with heavy trapping, reduced the muskrats to nearly the vanishing point. In 1934 the marsh with its surrounding area, comprising a total area of 4,830 acres, was leased . . . and a control dam . . . below the marsh, was completed. . . . Water levels were raised and have since been kept at the desired level.
>
> Muskrats were protected from trapping for nearly three years. Under protection and with the right depth of water, their increase was rapid.
>
> The raising of water levels increased the acreage of marsh suitable for muskrats. In the newly flooded sections, it was some time before muskrat food grew, but there is now much more than before. Care is taken to reduce water levels in spring to allow the growth of vegetation. As it grows, the water level is raised until the best level for winter is reached. . . .
>
> Trapping during the last seven years [1937–43] has produced 20,144 muskrats, an average of 2,878 per year. Before development and with uncontrolled trapping, 100 muskrats was an average crop.

(See also Appendix P.)

During my 1948 visit, I looked over parts of about a 20-mile stretch of the west shore of Dawson Bay of Lake Winnipegosis near the road between Mafeking and The Pas. The visible shore for many miles was irregular in outline, marshes and "feather-edges" alternating with rocky banks rising up one and one-half to three feet above the mid-

August high water level. Side marshes, connected by channels with the lake, had fair to good stands of bulrushes, and there were some muskrats about these. Wintering conditions could have been expected to be difficult for the muskrats except in the very best of the marshes adjacent to the lake and near the wide-channelled, sluggish mouths of streams entering the lake.

Among the once-good muskrat marshes west of The Pas that I saw in 1948 were Saskeram and Pasquia lakes. Pasquia Lake was inspected by canoe and on foot, and the following description applies more or less to a great many of the flooded marshlands of the region. In early August, 1948, the water was two or three feet above the normal level, and it had been three to four feet higher earlier in the year. Stalks and fruiting bodies of dead cattails protruded from the deeper parts — drowned tracts of a half square mile or more extending out in places, with practically all of the still-living cattails growing next to shore. On the other hand, great areas of former haylands were then grown up to river bulrushes and sedges. Muskrats were extremely scarce on the main bodies of water. They were present at low densities along the shore, which, though rocky, had flooded willow growths of varying thickness. Some of these willow growths extended for many yards into the marsh waters; others grew on both sides of rocky shore reefs; and in these muskrats lived at densities of the equivalent of about a breeding pair per quarter of a mile. Young were found in a low nest on the base of a tipped-over willow. It was apparent that essentially the entire muskrat population had taken refuge in the willows all summer up to that time. An adjacent marsh had island-like clumps of willows in extensive growths of river bulrushes. Here the muskrats were still living in the willows at the time of the visit, though beginning to forage out in the bulrushes.

A local concentration of muskrats was observed along The Pas River, a sluggish stream about 40 yards wide cutting through the flooded marshlands. Muskrats of all sizes were seen actively swimming in the fringing willow growths, and these muskrats were using very shallow, but in some cases very complex, systems of burrows in the low banks. Several muskrats had earlier established themselves in the yard about some flooded Indian cabins. They had renovated a small haystack, hollowing out and heaping vegetation over one side to make a lodge of it, besides building nests on a woodpile, on the floor of one of the cabins, and on top of a hay rake. Stretches of river bank were treeless, grown only to weedy herbaceous vegetation, and the shallow burrows here were thinly roofed over with cut plant materials. The muskrat densities of this stream ran about the equivalent of one pair and their season's young per 100 yards. Trappers' catches during fall "salvage trapping" in 1948 were reported as poor (memo, November 18, A. C. McMillan to Malaher): As of that date, four of six trappers had been checked in and these had a total of 150 muskrats, classified as 51 adults to 99 young.

The Thomas Lamb lease of 54,120 acres — also not far from The Pas — was truly a pioneering venture in northern muskrat management. A. G. Cunningham (letter and enclosure, June 2 and 4, 1938) summarized the data on lodge counts and spring catches: 40 lodges in the fall of 1931; 840 in 1932; 4,163 in 1933; 5,633 in 1934; 8,356 in 1935; 4,599 in 1936; and 2,153 in 1937. Plotted on coordinate paper, the 1931–35 figures define a passable lower asymptote and slope of a Verhulst-Pearl-Reed logistic curve. When the decline came, some of the spring catches fell off even more sharply than did the lodge counts, and the fact that the largest spring catch preceded the largest fall lodge count would seem to rule out possible overtrapping as a major cause of the decline. The spring catches were 12,257 for 1934; 23,780 for 1935; 17,792 for 1936; 15,179 for 1937; and 1,739 for 1938. Lamb found dead muskrats with liver lesions ("white spots") on his lease as early as the spring of 1934 and in what would appear to have been considerable numbers in 1938 (letter, A. G. Cunningham, January 11, 1940).

Lamb flew me over his lease at the time of my work in the vicinity of The Pas in August, 1948. It then had a very limited amount of good muskrat marshes, with bulrush, sweet flag, reed, and cattail growths usually occurring over about a third of the surface water. Feeding beds of muskrats were seen at from 50- to 100-yard intervals, but the muskrats seemed to have been living in surrounding willows. Probably most of what formerly had been the best marshes had been reduced to the status of open water lakes, the willow fringes of which harbored about all of the remaining muskrats in their vicinities. The brush-fringed outline of a small river could be distinguished amid the flood waters, and Lamb said that he had caught in some years as high as 400 to 500 muskrats along a six-mile stretch.

A special effort was made in the summer of 1948 to study effects of wind tides from very large lakes. Preliminary observations had been made in the summer of 1934 about the south ends of Lake Manitoba and Lake Winnipeg, where rises in water levels up to several feet sometimes accompanied strong winds from the north.

The south and southwest shores of Lake Manitoba were separated from much of the roughest water by low sandy ridges. Between these ridges and shore growths of vegetation extended a border zone of relatively quiet water having variable, sometimes thick, stands of bulrushes and reeds and with occasional long fringes of willow thickets. One of the best lakeshore habitats for muskrats lay out from the breakwater near the village of Delta. Between the 1948 sand bar and the permanent shore, the water was two to three feet deep (less in ordinary years) and was well-grown to cattails, bulrushes, and reeds. Some lodges and numerous feeding platforms of muskrats were seen, representing two breeding territories in a 150-yard sample examined. Provincial Conservation Officers William Newman and D. J. McIntosh said that some muskrats usually wintered here, though wintering along the lake shore generally would be difficult.

More typical shore (for 1948) had willow growths extending out into shallow water, but enough wave action carried past the sandy reef on which the waves broke to wash sand from the roots of the willows. Muskrat burrows in such places could not be expected to hold their form very well until protected by ice from the washing. But, with snowdrifts in the willows preventing deep freezing and the push of the thickening lake ice being held up by the outlying sand bars, some few animals could doubtless get through a winter on the available foods, including willow roots.

The marshes near Delta, south of Lake Manitoba, were connected with the lake, though sufficiently protected from wind tides by engineering devices to have relatively stable if shallow-water habitat for muskrats. Provincial Conservation Officer C. Batten said that, two years before, the water in most bays had been only about one and one-half feet deep, with emergent vegetation standing exposed on mud bars, and muskrat lodges constructed of mud. Much winter mortality of muskrats had followed. The 1948 water level was decidedly higher but not up to the three-foot depths of the otherwise similar marshes extending off to the east, near Lake Francis. Batten found through regular measurements of the thickness of the ice that the water two and one-half to three feet deep, or even shallower, seldom froze to the bottom in the reedy growths — in part because of insulation by snow but also in part because of the nature of the bottoms. With the advance of winter, the layer of ice almost disappeared under the snow and vegetation at certain of his sampling stations.

During the summers of 1955 and 1956, Olsen (1959) made a special study of the ecology of the muskrat on about 2,500 acres of the Delta marsh. He also presented a paper on effects of high water levels and low breeding populations on reproduction of the local muskrats at the eighteenth Midwest Wildlife Conference (Lansing, Michigan, December 10, 1956), which is excerpted in part in Appendix Q.

The Delta and Lake Francis marshes both had good interspersion of water and emergent vegetation in 1948. For a long time, neither marsh had been very productive of muskrats, however, except during a short period a few years before. According to H. A. Hochbaum, the 1948 muskrat population was greatly reduced over what it had been. The major losses at Delta apparently had been due to winter-killing in shallow habitats; those at Lake Francis, to the hemorrhagic disease. This disease had swept local areas of the Lake Francis marsh in the spring of 1948. During my inspection of the epizootic sites in August, I saw evidence of a continuing, practically annihilative die-off. On other parts of the marsh, the populations were low — estimated at the equivalent of about a breeding pair and associated season's young per five acres — but these seemed well situated.

The Netley marshes south of Lake Winnipeg are broadly the ecological and geographical counterparts of the Delta and Lake Francis marshes south of Lake Manitoba, except insofar as the Netley marshes

are not only influenced far more by wind tides but also by changes in the flow of the Red River, which sends three main and several lesser channels running through the marshland into Lake Winnipeg. The Red River's floods are notorious, particularly in spring, when the melt waters from the south pile up on the Netley ice.

About eight square miles of the Netley marshes between Netley Lake and the southwest corner of Lake Winnipeg were looked over personally in company with Malaher a few days after one of the celebrated wind tides. A rise of nearly four feet was indicated by the fresh water marks seen along the main channel of the Red River, where the north wind had backed up waters seven miles south of the lake. Malaher said that this was about what could be expected from a big wind tide. Ordinarily, big wind tides are said to occur only once or twice a year and to last only a day or two.

A 15-inch rise that reached some of the irregular peripheries of the west side of the Netley marshes was enough to start some lodges floating across open spaces; it was enough to flood lodges solidly anchored on bottom mud; and it put muskrats on shore and into nests built under the foundations of hunting lodges, on boat landings, and such higher locations. The four-foot rise along the channel of the Red River had completely evicted the occupants of bank burrows, and these muskrats had sat out the high water in the riverbank willows. Doubtless, helpless litters had been drowned, drifting of lodges had brought territorial complications, and other upsets in the lives of the Netley muskrats had resulted from the wind tide. Malaher said that, in some years, great numbers of muskrats were forced by wind tides to move up a sluggish stream, Netley Creek, having its mouth seven and one-half miles south of the lake.

Muskrats were scarce over all but the west shore zone of the eight square miles of the Netley marshes that Malaher and I covered. Only one lodge that looked like headquarters of a functional breeding territory was seen in the extensive islands of reed and bulrush of the central parts, and that lodge was about a half mile from shore. A representative sample of the rush- and sedge-grown west shore had what looked like breeding territories at about 150-yard intervals. These were centered about lodges, as the banks were too low and flat even at normal water levels to invite burrowing. The effective muskrat habitat of the eight square miles totaled about ten miles (map estimate) of this sort of shore zone. Its muskrat population, as estimated prorata, should have been the equivalent of about 120 pairs and their season's young.

McLeod worked with me on the Netley marshes and told of a situation brought on by a freeze-up during a high wind tide. The resulting exposure of the muskrats to bad weather at the height of the wind tide could well have meant mortality, but the stratification of ice and air spaces following withdrawal of water to the lake was not without advantages for those remaining alive. After the relative sta-

bilization of the water by the ice covering on the lake, the muskrats beneath the stratified marsh ice built nests and lodges at different levels and established labyrinths of partly dry, partly wet trails and tunnels, plugged and unplugged holes, and littered vegetation and mud.

Aside from the vicissitudes accompanying violent fluctuations of the water, the muskrats of the Netley marshes may have lost as severely from hemorrhagic disease as from any single factor. Like the Lake Francis muskrats, they had suffered from an epizootic attaining its greatest observed destructiveness during the spring of 1948 and also, from an evidently continuing die-off through the summer. (A single dead animal picked up on the marsh on August 6 had no positively recognized lesions, but possible hemorrhages may have been masked by decomposition.)

Later, McLeod (letter, February 12, 1949) prepared a summary of the recent history of muskrats of the Netley marshes. The area had been subject to extremes of flooding and drying several times within the memory of local residents. By the mid-thirties, the water levels of the marsh, the Red River, and Lake Winnipeg were very low, and in 1940, the marsh

> was almost completely dry except for pools in the low places. . . . The water level began to rise in the autumn of 1941 and . . . [continued rising] with slight but steady increases until August 15, 1944. At this time a terrific storm from the north-west raised the south end of Lake Winnipeg and piled an additional four feet of water into Netley marsh. The water level has remained high and erratic ever since with the first appreciable recession in the fall of 1948.

From McLeod's letter and one from Alex J. Reeve (March 26, 1951), the following muskrat catches may be listed for the Netley Fur Block of about 56,000 acres. After closed seasons in 1942 and 1943, 69,677 were taken in the spring and 25,171 in the fall of 1944; 119,634 in spring and 4,300 in fall, 1945; 24,432 in spring, 1946; 9,870 in spring and 364 in fall, 1947; 1,151 in fall, 1948; 25,896 in spring, 1949; 14,980 in spring, 1950. In addition, Reeve furnished figures on the annual catches from a 640-acre tract of Netley Marsh known as Warner's Ranch: 1943, 306; 1944, 6,197; 1945, 2,954; 1946, 1,013; 1947, 834; 1948, 1,330; 1949, 1,292; 1950, 743.

Continuing the quotation from McLeod's letter:

> In the fall of 1944 muskrat houses were very abundant and there were some signs of destruction of the habitat. . . . [Severe flooding from the Red River occurred in late fall, and] muskrats began migrating out of the marsh in hundreds mainly to the north-west. Dozens were killed crossing the Winnipeg Beach highway a couple of miles to the west and muskrats were abundant in grain stooks and hay coils as far west and north as Lundar about forty miles away. They also became plentiful in sloughs and pot holes over this area where they had previously been scarce. Another large scale migration occurred in the spring of 1945 following an early breakup and severe flooding

of the marsh. At this time muskrats were found as far north on Lake Winnipeg as Hecla Island and they were abundant around cottages at Winnipeg Beach.

McLeod (1950) "estimated that the two migrations involved at least 50,000 muskrats."

In 1948, when I saw it, the main channel of the Red River leading into the Netley marshes from the south was about 200 yards in width, with a variable, generally narrow, fringe of bulrushes and other quiet-water vegetation, as well as overhanging willow thickets. Its banks in August were about four feet above the water. Though scarce in 1948, the bank muskrats were reported to have been fairly abundant in some years.

Netley Creek had variable muskrat habitat. Near its junction with the Red River, its banks were the same height as those of the river, or about four feet above the water level observed in 1948. Within about a mile and a quarter upstream, the creek banks gradually became lower until they disappeared in a wide, reedy marsh. Farther upstream about three miles, where the creek meandered through cultivated lands, its banks were better defined, though cattails, bulrushes, sedges, and reeds still covered much of the channel. The banks between the reedy marsh and the Red River had five recognized muskrat territories or about one per quarter mile. Only two territories were found in the reeds in about an hour of cruising with a canoe. The few muskrats present had selected what were rather clearly the choicer habitats in ordinary terms of food, cover, and water, in addition to refuge from the wind tides.

The largest and richest "muskrat country" in Canada with which I can claim any familiarity comprises the Saskatchewan River delta and adjacent lands and waters – especially those extending both upstream and downstream from The Pas and managed for fur production by the Hudson's Bay Company and the Manitoba government. The Company's Cumberland lease and the government's Summerberry Fur Rehabilitation Block have yielded too much information over too many years to facilitate condensing without losing a great deal of what a serious population student might wish to refer to, so treatment of these two areas is reserved for Appendix R.

THE NORTHWESTERN MUSKRATS, zalophus and spatulatus

The subspecies *zalophus* has a restricted range about the base of the Alaska Peninsula, in the area of Cook Inlet south of the Alaska Range. It is *spatulatus* that is really the muskrat of northwestern North America. As Anderson (1937) wrote, it

> inhabits all suitable streams, ponds, and marshy areas in the Mackenzie River drainage of the Northwest Territories, north to Richards Island [which is just below the seventieth parallel] in the Mackenzie delta and on lower Anderson River [which lies to the east of the Mackenzie delta]. It is not very common in the lakes of the rocky districts bordering the "barren grounds" and the rats

in such areas are more apt to live in holes in banks instead of building houses. The best muskrat areas in the Northwest Territories are in Slave River delta and Mackenzie River delta, but many marshy areas also produce large crops of rats, which form an important part of the fur returns in those districts.

Banff National Park in southwestern Alberta seems close to the southern limit of range of *spatulatus*. Dr. Ian McT. Cowan, who has studied the mammals of National Parks of the Canadian Rockies, found muskrats not much higher than 4,000 feet in Banff Park and not above 3,600 feet in Jasper Park (to the northwest of Banff Park), although beavers were noted as high as 7,000 feet in certain areas (letter, February 11, 1948). A Canadian engineer, Alex Campbell, mentioned in chance conversation in July, 1948, that he had watched a muskrat in close association with a beaver, near Banff, at an altitude of about 4,600 feet.

Henderson (1923) referred to heavy winter losses in muskrats, especially in 1915–16 in the Peace River District. There had been thousands of muskrats present in the fall, but a prolonged hunt in the spring yielded fewer than 100. Cowan wrote me (letter, June 20, 1951) that the "die-off this year has been particularly severe and seems to have extended from British Columbia and the Upper Mackenzie right across the Prairie Provinces to southern Manitoba. . . . I know one trapper here who estimates that the disease took two thousand rats from his anticipated crop."

Soper's (1939, 1941) descriptions of the Wood Buffalo Park (northern Alberta and adjacent Northwest Territories south of Great Slave Lake and west of Lake Athabaska) are of the greatest value in appraising the immense delta of the Peace and Athabaska rivers as muskrat habitat. This delta is reminiscent of that of the Saskatchewan River except for much higher elevation, including low mountains, in its vicinity. Soper referred to the Park as lying "some 270 miles southwest of the nearest Arctic tundra." He (1942) found *spatulatus* commonly distributed throughout the region and of "amazing abundance" in parts, especially in the great marshes. Except on the larger, swift-current streams such as Peace and Slave rivers, the muskrats also abounded in many stream habitats. He gave figures of from 70,000 to 90,000 muskrat skins being traded at Chipewyan alone during a peak year, the majority from the Peace-Athabaska delta. I would also suspect that the activities of the numerous beavers of the Park (Soper, 1937) might provide some habitable environment for muskrats away from the extensive marshlands. At the time of Soper's residence within the Park, 1932–34, he saw evidence of recent expansion of beavers in numerous localities. "Thus, in places where beavers had not been seen for a decade or more, they are now established in ponds and insignificant streams which ordinarily would be ignored by a smaller beaver population."

Dr. W. A. Fuller, who made a special study of muskrats of the Park, described about half an area of roughly 6,000 square miles as

ideal for muskrats. However, he found (letter of September 17, 1947) that the muskrats had

> declined . . . in recent years to an exceedingly low point. The chief causes are probably: 1. Series of dry years with a steadily lowering water table in the marshy area. This was undoubtedly aggravated by excessive forest fires and a serious depletion of the beaver population. [He had written earlier in the letter: "From my own travels this summer there appears to be an abundance of plant material available for food, lodges and cover. There are extensive stands of *Typha latifolia, Scirpus* spp., *Carex* spp., *Potamogeton* spp. and *Nymphoxanthus variegatus,* as well as numerous other grasses and sedges as yet unidentified."] 2. The heavy hunting pressure which probably did not injure the population in "normal years," but which should have been regulated during the period when environmental conditions were unfavorable. [Also from earlier in his letter: "The chief difficulty centres about the Indians who have shown themselves to be notoriously poor conservationists. They are invariably opposed to restrictions of any nature and since they were granted hunting and trapping rights in the park, in lieu of the reservation, their protests in most cases carry a great deal of weight."] 3. Probably cyclic fluctuations. 4. Disappearance of other forms of game used both as food and fur which caused the trapper to devote even more attention to muskrats. There appears to be no evidence that disease or predation have played any significant role.
>
> A year ago conditions were so serious for the natives that they would have accepted any restrictions in the hope of restoring fur. This spring, however, there was excessive flooding of the entire area and sufficient precipitation and inflow from the major rivers to preserve a high water level and the trappers are convinced that in a year or two there will again be an abundance of fur. They are unable, therefore, to see the value of any positive conservation programme.

There is no doubt that Indian hunting of muskrats for food may be, especially in the vicinity of large camps, the severest type of predation and one at times capable of depressive influence on local muskrat populations. I have observed evidence of depleted muskrat populations on Indian lands in both the United States and Canada, and from Preble (1908, p. 191) the following about northwestern muskrats may be quoted:

> At Fort Smith they were common in the marshes to the south of the post, and on the lower part of Slave River and in its delta they were abundant. While crossing Great Slave Lake to Fort Rae I found them inhabiting the islands and shore of the Northern Arm wherever marshy inlets occurred, Trout Lake, 25 miles south of Fort Rae, evidently being a favorite locality. In the immediate vicinity of Fort Rae, though conditions were favorable, I found the animals very rare, doubtless owing to the presence of a large band of Indians then congregated about the post.

Fuller (1951), reporting on his studies in the Athabaska-Peace River delta, discussed the types of shallow or food-poor habitats in which muskrats get along during the warmer but not necessarily during the colder months. However, if "frosts are light and snowfall heavy, even shallow lakes may be so well insulated that they do not

freeze solid and the muskrats may survive in them through most or all of the winter."

East of Great Bear Lake are tracts of Pre-Cambrian that Robert H. Smith, who has done much flying over the area for the U.S. Fish and Wildlife Service, described to me (conversation, August 18, 1948) as being nearly all bare rock and shallow waters without vegetation other than occasional patches of *Carex*. He has seen a few muskrat burrows in the Barren Grounds at least 150 miles northeast of Aklavik. Although the Mackenzie delta opens up about the first of June, the Barrens do not thaw until about a month later. Many of the lakes are so shallow that muskrats could winter only in the deeper lakes. They had sedge growths along shore and coontail in the water, but nothing of the emergent vegetation to be found about typical northern muskrat marshes. Smith had also seen muskrats on the Anderson River, about 150 miles northeast of the Mackenzie delta, and thought that they probably extended in limited numbers all the way across the lakes lying just south of the Beaufort Sea.

Clarke (1944), who spent three months in late summer and early fall, 1942, in field work on reindeer between Aklavik and Burnside River (which is about half way between Aklavik and Hudson Bay), "learned with some surprise of the population of muskrats to be found beyond the limit of trees in tundra ponds, whether fresh or brackish, throughout the unglaciated coastal region . . . which extends east to beyond Horton River [north of Great Bear Lake]. They have certainly increased in recent years."

Porsild (1945) wrote that in

> the untimbered country, to the east of the [Mackenzie] delta, some rats are found in most of the large lakes and in the deep creeks and lakes that are tributary to the Eskimo lakes basin. . . . The northward and eastward range of the species is largely governed by the depth of lakes and the thickness of their ice-cover in winter. Rats, therefore, are not found in all lakes in the barren grounds, but only in those that are deep and enclosed by high banks. Due to the shelter afforded by high banks such lakes generally have an abundant snow cover in winter and the ice, consequently, does not get as thick as on lakes where, due to lack of shelter, no snow accumulates.
>
> The local distribution of the muskrat is also closely tied up with its food supply and only in lakes that have an abundant aquatic vegetation and a depth of over 12 feet of water do rats winter successfully. Such lakes also are relatively rich in other aquatic life. The realistic Mackenzie delta Eskimo, who told the writer that "Lake with plenty of rats got plenty of fish too," was aware of this, if not of the underlying cause.
>
> The food of the muskrat, at least during autumn, winter and spring consists of the fruits, rhizomes and winterbuds of pondweeds (*Potamogeton* spp.), rhizomes and tubers of horsetail *(Equisetum arvense)*, the rhizomes and fruits of water arum *(Calla palustris)*, and duck weed *(Lemna trisulca)*. The roots, rhizomes, stems and fruits of a number of other plants, notably sedges and grasses are, no doubt, eaten as well. The Eskimo, who are keen observers, deny that rats eat fish, but say that rats, when "frozen-up" in their houses, often resort to cannibalism.

The mountainous country west of the Mackenzie delta has muskrats in expected types of places. Murie (1944, p. 228) found them scarce in and about Mt. McKinley National Park, and his descriptions of the terrain remind one of the high altitude habitats in which the species barely maintains itself in western United States.

The Mackenzie River delta is the most northerly important muskrat habitat in North America. Here, strong populations live hundreds of miles north of the places about Hudson Bay where the ranges of both *albus* and *aquilonius* grade off into uninhabitability. The Mackenzie delta muskrats will be further treated in Appendix S.

THE MARYLAND MUSKRAT, macrodon

In early March, 1949, Francis M. Uhler, of the U.S. Fish and Wildlife Service, showed me typical habitats of *macrodon* in eastern Maryland. An example of about six and a half acres of heavily populated marsh dominated by *Scirpus olneyi* had an estimated 25 muskrats per acre. In general appearance, this sample was almost meadow-like, with most of the bottom being covered by very shallow water or exposed except for the muskrat channels. It was subject to but a few inches of tidal flow. I could easily see how cold weather could mean a crisis for the muskrat occupants, and Uhler said that cold snaps freezing about four inches of ice were fairly common, though usually of brief duration. By northern standards, this choice Maryland sample would be, at best, of marginal habitability during cold weather, an important distinction to remember in considering population dynamics of the muskrat in different parts of its geographic range.

The impression that I gained from conversation was that cattails became more important as the range graded off into that of *zibethicus* from New Jersey northward along the Atlantic Coast. Uhler did not regard *Typha latifolia,* that great favorite of north central muskrats, as being anywhere nearly as important to muskrats as *Scirpus olneyi* in Chesapeake tidal marshes.

The effects of ditching for mosquito control on habitats and populations of *macrodon* have been sometimes inconsequential, sometimes ruinous. Viewpoints thereon may be most divergent (see, for example, the symposium by Cottam, Bourn, Bishopp, Williams, and Vogt, 1938). Problems and consequences of action vary with localities as well as with methods. Compared with the Long Island operations described by Taylor (1938), the vegetational changes brought about by ditching may be much greater on Delaware tidewater marshes (Stearns, MacCreary, and Daigh, 1939, 1940; Bourn and Cottam, 1950). (See Appendix T for further treatment of ditching.)

Muskrat populations in Delaware appear to have been seriously affected, in recent years, at least locally, by what is almost certainly the hemorrhagic disease. In a letter of March 24, 1950, Robert A. Beck of the Delaware Game and Fish Commissioners described some of his observations:

We are writing in regard to the severe mortality rate of muskrats of different areas in Delaware.

With the help of the University of Delaware, we have made many experiments on the various carcasses with very little success in determining the disease.

At the beginning of my survey in these areas, in October 1949, I trapped muskrats for experimental purposes. . . . [With five traps] I caught from two to three muskrats daily with very little effort. This indicated the muskrat population to have been normal at that time. However, the number of dead muskrats found increased. By December 1 when the trapper of this same area set his line . . . of sixty-five traps . . . the muskrat population had decreased so badly . . . [that he] caught only six muskrats on the first day of the season.

The only external symptom found on the dead muskrats was a severe bleeding of the anus.

Hardy (1950) has compiled a list of trappers' opinions concerning the great decline of muskrats on the Dorchester County marshes. These opinions are remarkable for their variety and scope and cover the whole distance from inbreeding to environmental changes, ectoparasites to predation and trapping methods. But the following quotations may have special pertinence:

Some trappers contend that a disease struck the muskrats ten or fifteen years ago and has subsequently killed off the young. They state that they have opened the tops of muskrat houses and found from four to nine young muskrats, seemingly from three to four days old, all dead; and for no reason which they can explain except "that dreadful disease." In this connection, trappers have expressed the belief that the reconditioning and reuse of old beds by the muskrats have served to perpetuate the disease. . . .

"There seems to be [Hardy quoting E. Lee Le Compte] an epidemic of some sort on the marsh, for dead animals (muskrats) are to be found in considerable numbers. This is probably partly to blame for the scarcity of the muskrat [as of the mid-thirties]. . . . To date no bodies fresh enough to permit examination have been found, so the nature of the disease is not known."

Hamilton (1943) wrote that *macrodon* is said to occur in the southeastern corner of Pennsylvania. From here southward through Maryland are a couple of large rivers (Susquehanna and Potomac) and their tributaries, as well as other small streams. Years ago (1928–29), I lived in Washington, D. C., and became quite familiar with these streams during field trips and also revisited them in the spring of 1949. They have little muskrat habitat except in certain places. Some streams have fairly rich stands of such food plants as a burreed *(Sparganium americanum)* and water starwort *(Callitriche heterophylla).* Uhler told me that the muskrats feeding on these plants were as fat as those feeding on *Scirpus olneyi.* He thought that the muskrats of the streams were almost certainly *macrodon,* comparable in weights with those of the Chesapeake Bay marshes. Roadside ditches may also have cattail stands, and I remember a canal that had good growths of both emergent and submerged muskrat foods. On the Patuxent Research Refuge of the U.S. Fish and Wildlife Service were impound-

ments having at times, according to Uhler, high concentrations of muskrats living without recourse to marsh types of vegetation.

Uhler showed me one of the few natural ponds in the Washington-Baltimore area. It was a backwater from the western branch of the Patuxent River, of about seven or eight acres and having its center filled with the smartweed, *Polygonum portoricense,* and bordered by cattail clumps and sedge. A tract of about two acres of cattail lay near the junction with the river.

Uhler and Llewellyn (1952) carried on a study of the fur productivity of submarginal farmland on a 1,000-acre tract of the Patuxent Refuge for the three trapping seasons, 1943–46. They took 12 to 40 muskrats per season, a total of 79, of which 65 were taken from marshy lake borders and the others from along the forest-bordered Patuxent River. Cattails, bulrushes, burreeds, and arrowheads were particularly valuable muskrat foods.

Since the acquisition in 1933 of over 8,000 acres of timbered land and marsh for the Blackwater National Wildlife Refuge in Dorchester County, Maryland, the Federal government has carried on a long-term research program to obtain data on the natural history and management of the Maryland muskrat. Over 5,400 acres of the refuge consisted of marshland yielding up to 31,000 muskrat pelts in peak years. Dorchester County, on the Eastern Shore Peninsula, long has been celebrated for its muskrat production, and the well-known W. A. Gibbs marsh was the site not only of some pioneering experiments by the owner but also of some of the preliminary studies by the U.S. Biological Survey (Smith, 1938).

Dr. H. L. Dozier, late director of the U.S. Fur Animal Field Station on the Blackwater Refuge, 1937–49, and his colleagues have published many informative papers on the life history and ecology of *macrodon;* and the supplementary treatment in Appendix U will relate largely to their work.

Down the coast from Maryland, Handley and Patton (1947) gave the range of *macrodon* in Virginia as all counties east of the Blue Ridge Mountains, where it was rated as abundant. Statements applying to Virginia muskrats probably could be extended to cover northern North Carolina, but, somewhere in the western part, the ranges of *macrodon* and *zibethicus* must come together. In the eastern part of North Carolina, the range of *macrodon* fades out into the muskrat-vacant Southeast.

In the mid-thirties, W. A. Gibbs made what appears to have been a highly successful planting of Maryland-raised muskrats in a 3,000-acre, improved marsh in Currituck County, North Carolina (Anon., 1938). This location, in northeastern North Carolina, is well north of the stated southernmost limit of *macrodon's* range. In his letter of January 28, 1949, from which extensive quotations were made with reference to the muskrat-vacant region of the Southeast, William E. Baldwin, Jr., wrote:

The coastal marsh form, *O. z. macrodon,* comes south to midway of the North Carolina coast; perhaps the populations in our impoundments at Pea Island and Mattamuskeet National Wildlife Refuges represent southernmost concentration points for this subspecies, although I know that it extends a few miles farther south of those points.

In Baldwin's opinion, the extreme daily fluctuations in tide and the lack of sustaining habitat are among the major reasons for the absence of muskrats along the Carolina coasts south of the existing range of *macrodon.* The combination of hurricane salt tides followed by fresh water flooding of the streams surely would impose emergency conditions upon muskrats and, when suffered by populations confined to small and scattered tracts of livable habitat, might well be expected to push back the little extensions of range occurring southward during relatively favorable years.

THE LOUISIANA MUSKRAT, rivalicius

O'Neil (1949) showed the northern limit of range of *rivalicius* in Louisiana as running west from north of Lake Pontchartrain past Baton Rouge, then running irregularly northwestward and westward from Baton Rouge, to dip southwestward toward the Texas border at about the latitude of Lake Charles and Sulphur; its maximum width, as thus shown, is about 90 miles, narrowing down to about 30 miles in the southwestern corner of the state. It may be recalled that Lowery (1943) found that muskrats taken from fresh-water lakes were intergrades between *rivalicius* and *zibethicus.*

The southern coastal marshland is fairly continuous from north of Galveston Bay in southeastern Texas eastward nearly to Mobile Bay in southwestern Alabama. At the western edge of *rivalicius* range, the limiting factors look more obvious than at the eastern edge, which approaches the mysterious muskrat-vacant area of the Southeast. Earl Atwood told me (March, 1949) that the range gives out north of Galveston Bay, and this is also shown by Lay and O'Neil's (1942) distributional map. Aransas Refuge, approximately 225 miles southwest of Galveston Bay, has no muskrats but Atwood appraised its habitat as suitable. The intervening coast has few protected bays in which marsh vegetation could develop, and the area southwest of Galveston Bay is semiarid, with mostly intermittent streams, all the way down to the Rio Grande Valley.

Bailey (1905) did not mention *rivalicius* in his biological survey of Texas. Daniel W. Lay wrote (letter, January 6, 1949) that

> Local marsh residents don't remember seeing them prior to about 1914 when a Beaumont rancher put a bounty on them because of the holes they dug in his marsh pasture. However there is no barrier or significant difference in habitat between the Texas and Louisana coastal marshes.

In March, 1949, Lay told me that he thought Bailey must have missed the muskrats along the Texas coast, which were living in places

that would have been difficultly accessible before the years of automobile transportation. Lay has observed evidence of what he thought were ancient "eat-outs" on his regular study areas between Galveston Bay and the Louisiana state line.

The eastern edge of the range is Mobile Bay, Alabama, where muskrat populations have fluctuated greatly and not always with any apparent reason. This is more fully discussed in Appendix V.

Of a total of 70,000 acres of coastal marsh in southeastern Mississippi, Freeman (1945) appraised nearly 48,000 acres as being suitable for muskrats, chiefly on the basis of the presence of *Scirpus olneyi*. He reported that muskrats were found on about 13,500 acres of marsh along the Pascagoula River but that not all of this was good habitat for them. Ecological changes apparently resulting from floods were pronounced, and declines of *S. olneyi* were accompanied by population declines of the muskrats. Trappers' catches of 18,000 to 23,000 per year dropped to averages of about 3,500.

Freeman reported much movement on the part of the coastal marsh muskrats, some of which was patently the result of adjustments following destructive utilization of local stands of *Scirpus olneyi*. The Mississippi animals showed strong tendencies to congregate in favored areas and to leave other areas vacant – the instances specifically recorded took place during the fall, winter, and spring of 1942–43.

Freeman considered the abundant raccoons to be

> the greatest limiting factor in the Pearl River marshes and certain parts of the Pascagoula marshes. Thirty houses examined in the Pearl River marshes had been visited by raccoons the previous night. . . . Evidence of the raccoons digging into muskrat nests had been found at all seasons of the year. . . . One hundred and twenty-nine stomachs [of winter-trapped raccoons] were examined. Ninety-one had remains of muskrat. . . . To get some idea of their predations [during other than the trapping months], droppings were collected in March, May, and October. One hundred and twenty-seven scats were examined – 31, or 24.4% of them had muskrat remains.

Minks and alligators were scarce on Freeman's areas, but the remains of nine muskrats were reported from the stomach of an eight-foot alligator. Muskrat remains were found in an unspecified number of horned owl pellets, but not in a collection of over 100 otter *(Lutra canadensis)* scats from all seasons, though the otter is regarded as a muskrat enemy by trappers. Freeman did not know of any serious disease of muskrats on his study areas. Many dead muskrats had been found in 1933, before Freeman's investigations, 1942–45, but the observers attributed it to poison sprayed in connection with mosquito control measures.

Perhaps I may be reading into Freeman's data some things that are not there, but the "between the lines" picture I see is one in which disease as well as environmental deficiencies and emergencies must be considered.

The main range of the Louisiana muskrat is, appropriately, in

Louisiana, and this state has been the site of so much work on the subspecies that the principal treatment in this book will be reserved for Appendix W. Let it be made clear, however, that *rivalicius* was undoubtedly much less numerous and still more localized in its distribution in Gulf Coast marshes a century ago than it is today. Nobody seemed to notice these muskrats in what later became choice habitat, though Dr. Leslie L. Glasgow, of Louisiana State University, described recent finds of *rivalicius* remains in Indian mounds (letter of March 12, 1956). O'Neil (1949) attributed the extensive growths of *Scirpus olneyi,* upon which the muskrats are so dependent, to the burning of marshes by alligator hunters, beginning in about the second decade of the present century. But even when *rivalicius* populations are at their peak, only a minor fraction of the Louisiana wetlands — comprising as they do nearly a third of the state — is real muskrat marsh. O'Neil (1949) wrote that 80 per cent or more of the normal muskrat catch of 5,000,000 to 6,000,000 is produced on approximately 1,000,000 acres of *olneyi* marshes.

The living habits of *rivalicius* resemble those of *macrodon* particularly in the way that both subspecies attain their highest densities in very shallow marshes or meadows dominated by *Scirpus olneyi.* From my own limited observations, I would say that these two subspecies come as close to being habitual land-dwellers as any that I have observed in North America.

THE SOUTHWESTERN MUSKRATS, ripensis, pallidus, goldmani, and bernardi

Bailey (1905) wrote of the Pecos River muskrat, *ripensis,* which occurs 400 to 500 miles west of the westernmost edge of the range of *rivalicius*: "This small, dull-colored muskrat lives apparently in suitable places along the whole length of the Pecos River and on some of its tributaries, and along the Rio Grande near the mouth of the Pecos."

In late years, however, the population status of *ripensis* has changed a great deal, and Dr. W. B. Davis, of Texas A. and M. College, has expressed a fear that it may even be doomed because of irrigation drawing off the water from its best habitat (conversation, March, 1949).

I have never been in the part of the country referred to but, from correspondence with Davis, Dr. W. Frank Blair of the University of Texas, E. G. Marsh, Daniel W. Lay, and O. F. Etheredge of the Texas Game, Fish, and Oyster Commission, I think that I now have a workable concept of the present situation.

Lay (letter, January 6, 1949) wrote that *ripensis* in Texas

> occurs on the Pecos and Rio Grande rivers from Del Rio to New Mexico and is most numerous in the irrigation canals near El Paso. Although we estimated several years ago that the annual catch around El Paso might be as much as 50,000, I feel sure that the catch has dropped more than half. Irrigation programs have removed all except flood water from the Rio Grande channel at

El Paso, the ditches are cleaned of vegetation regularly, and flash floods are increasingly severe in their damage of streamside habitat on the two rivers and their tributaries.

I am very grateful to Etheredge for the trouble to which he went in investigating for me the status of *ripensis* in the vicinity of Fort Stockton, Texas. He wrote (letter of April 5, 1949) that "it looks like the muskrat populations in this area are definitely decreasing." However, land practices on the San Pedro Ranch in Pecos County were favorable for the maintenance of existing muskrat habitat, so that there should "continue to be at least some muskrats on this ranch. We found no one who would attempt to give us a population figure but it is agreed that there could not be more than 2000 animals in the entire district."

This subspecies probably is subject to fluctuations in much the same way as are the others, and it may well increase again in the years to come, but, as muskrats go, it does not seem to have a very strong hold on existence. A series of adverse years, a prolonged emergency like that afflicting *cinnamominus* of western South Dakota in the thirties, and *ripensis* might be all but gone; with no really big reservoir of animals anywhere, the difference between depletion and extinction during a crisis might not be so great, especially with human water use in an arid climate as a complicating factor.

The subspecies *pallidus, goldmani,* and *bernardi* have not always been clearly distinguished. The genuine *pallidus,* or Arizona muskrat, as nearly as I can judge from the literature, appears to be rather restricted to the Gila River and tributaries in southern and central Arizona and southwestern New Mexico. It would seem that the subspecies referred to by Barnes (1927) in southwestern Utah as *mergens* must have been *goldmani,* and Hall (1946) depicted the range of *goldmani* in Nevada as a little stretch of the Virgin River above Lake Mead in the southeastern corner of that state.

Dr. S. D. Durrant had just completed a study of the mammals of Utah when I visited the University of Utah on July 22, 1949, and from him I learned that *goldmani* seems limited in Utah to the Virgin River drainage upstream from a series of precipitous gorges starting at about the state line in the southwestern corner. He thought that these gorges may be an effective barrier, as downstream from these the range of *bernardi* begins (Durrant, 1952). Still, Hall examined specimens of *goldmani* from downstream sections in Nevada, including one that had characters intermediate between *goldmani* and *bernardi.*

Before the reclamation engineering in southeastern California, the Colorado River muskrat, *bernardi,* was confined to the valley of the lower Colorado River, but "recently," to quote Grinnell, Dixon, and Linsdale (1937, p. 731), "found conditions in one restricted section extremely favorable to its needs, and has thrived accordingly . . . . [The] great expansion in the population . . . has come about as a

result of the metamorphosis of a previously arid desert through man's agency." (For further information, see Appendix X.)

Storer (1937) generalized concerning the muskrat as a species:

> In the arid west it is discontinuous in distribution, by reason of the localization of suitable habitat. It probably reached some of these now isolated waters during a period when aquatic and palustrine habitats were more widespread, in late Pleistocene or postglacial times. With subsequent contraction of habitat, stocks were reduced and isolated, since when limited subspecific differentiation has occurred. Parallel cases are known among amphibians and fishes in the western states.

The subspecies *bernardi* is the only one of which I know positively to occur, free-living, in Mexico, though *ripensis* should surely reach Chihuahua or Coahuila, at least as occasional strays, from its known range along the Rio Grande. In Lower California, Mearns (1907, p. 496) saw what he thought was a muskrat in 1894 near Seven Wells, and the following is from Grinnell, Dixon, and Linsdale (1937, p. 733): "On March 22, 1921, at a point five miles south of Mexicali, Lower California, an observer (D.) saw a large muskrat come to the entrance of its burrow."

Upstream, along the Colorado River, *bernardi* extends into southeastern Nevada up to the Lake Mead area and then eastward into northwestern Arizona. I do not know how far this subspecies goes into Arizona, but I should think that the Grand Canyon would be an effective barrier to movement upstream.