

Chapter 14

The Muskrat Over the World

THE CHIEF PURPOSE of this chapter is to generalize on the biogeography of *Ondatra zibethicus*, in its constituent subspecies, over its native and acquired range. Its range by now includes most wetland areas of the northern hemisphere.

THE MUSKRAT IN ITS RACIALLY NEW RANGE IN EURASIA

There are many accounts of the introduction and initial spread of the muskrat in Europe, of which one of the best and most accessible for American readers is Storer's (1937). (See also Mohr, 1933.) Prince Colleredo-Mannsfeld released five animals (two males and three females) at Dobrisch, southwest of Prague, in 1905. By 1914, the whole of Bohemia had been colonized, and the population of muskrats in that country was estimated at two million. The spread of the species had been at the rate of four to thirty kilometers yearly. "For more than one and one half decades," as Mohr wrote, "the muskrat, starting out from Bohemia, has been a middle-European calamity." Storer explained that, under the more rigid economic limits of life and sustenance for central European peoples, the interpolation of any new element arouses concern. As early as 1912, the potentialities of the muskrat for harm had been publicized. Damage was principally through burrowing in canal banks, railroad grades, and earthen dams, though some could occur through raiding of gardens and fish ponds.

To me, the various references to the muskrat's piscivorous habits (see Ahrens 1921, as well as the two papers by Mohr and Storer and the bibliographies of Mohr and Storer), with implications of shortages of muskrat foods, may explain certain observed phenomena:

higher densities of the muskrats at the periphery of the expanding range and scarcity of animals in parts that had been colonized earlier. From what I have read and what I have seen of northwestern Europe, I would suspect that central European muskrat habitats may have a rather low supporting capacity, at least as concerns the choicer types of food. At the time Storer prepared his manuscript, muskrats in Bohemia were "believed to have reached an equilibrium as to numbers."

I should not expect the muskrat to thrive in the rugged Balkan region, though there would seem to be localities in which the species might live if it reached them. Hoffmann (1952) mentioned its occurrence in the cool waters of high mountains of Germany, and he showed its range extending into Yugoslavia and at least to the northern boundary of Bulgaria. Muskrats apparently straggled into Switzerland from Alsace, and from 1942 through 1957, many thousands were reported killed (Hoffmann, 1958, p. 109). Muskrats were still being caught in fish traps in the Vierwaldstätter See of Switzerland, originating, according to Hoffmann, from escapes from muskrat farms legally closed in 1929.

The following quotations from Bourdelle (1939) illustrate the situation in France.

The relative ease with which breeding stock could be procured, the prospect initially of rearing them in captivity, and the remarkable fecundity of these animals were the factors which encouraged many to undertake the raising of *Ondatra*. Numerous centers of propagation were established, but serious difficulties were quickly encountered. Whereas the nutria bred well when closely confined, the muskrat, on the contrary, showed little inclination to live under the same conditions, and did not reproduce well in captivity. To satisfy the biological requirements of this ungovernable rodent it was necessary to give it semifreedom. . . . Still more easily than the nutria, and in far greater numbers, the muskrat escaped from the parks where it was propagated and invaded the neighboring regions. . . . From this time on the importation and breeding of muskrats in France was rigidly forbidden, and an active campaign was organized against the wild populations by trapping and by the use of virus.

What the French refer to as "virus," used against the muskrats (Chappelier, 1933), is the bacterium, *Salmonella typhimurium*.

In northern France there have been four areas of infestation (Chappelier, 1948): (1) the north area in the region of the Somme, (2) the northeast area, Ardennes, (3) the east area in the region of Belfort near the Rhine, and (4) the west area in the region of Normandy, occupying four river basins and extending almost to the English Channel. Within these areas, the distribution of muskrats may or may not be continuous, depending both upon natural facilities for dispersal and upon numbers and sites of introduction.

The spread of the muskrat into Holland from northern Belgium, 1941-52, is well shown by a series of maps in a report by van Koersveld (1953). That the species was continuing to gain ground throughout the forties and into the fifties despite intensive campaigning is illustrated by the following figures. From 1941-46, the number of

animals taken was reported as 23; in 1947, 74; in 1948, 164; in 1949, 537; in 1950, 337; in 1951, 569; and in 1952, 659. The size of the area occupied by muskrats was about 10 square kilometers in 1946, 30 in 1947, 70 in 1948, 500 in 1949, 650 in 1950, 750 in 1951, and 1,000 in 1952.

Dr. F. W. Braestrup, of the Museum of Zoology at the University of Copenhagen, wrote (letter, March 6, 1951) that the muskrat has not spread to Denmark and that the Danes "have very strict regulations forbidding any import of live muskrats on any pretext whatsoever." I heard of no reports of muskrats in Denmark while visiting there in the spring and summer of 1959.

To quote from Storer (1937):

The entrance of the muskrat into Germany was a natural consequence of the spread from Bohemia. There are no sharp biological barriers and the waterways crossing international boundaries afforded every opportunity for spread of muskrats. Ulbrich's (1930) chart shows clearly that the increase of territory occupied was a natural spread. By the time control measures were instituted in Bavaria the species already occupied a wide extent of waterways. . . . It now seems impossible that the countries of central Europe can ever hope actually to rid their lands of the muskrat. The species will not only hold much of the territory already occupied, but may continue to spread and, in time, to occupy most of continental Europe suitable for its existence.

In connection with their campaigns, the Germans did a substantial amount of work on the biology of the muskrat, and Ulbrich's (1930) book has been especially useful to me in my own investigations. Later, Hoffmann (1952; 1958) summarized the German findings, especially the data acquired after Ulbrich's publication.

Ulbrich emphasized foxes and polecats (*Mustela putorius*) as enemies of the muskrat in central Europe. The habits he described for the polecat were rather minklike, and polecats used muskrat burrows as dens. Many instances were noted of house cats preying upon young muskrats that came to shore, also of predation by raptorial birds. The latter included small or weak owls — 11 of 57 pellets of *Asio* spp. contained remains of young muskrats.

The muskrat was first introduced in the British Isles in the middle and late twenties as a fur-farm animal. Then, as in France, some escaped to establish themselves as free-living muskrats. Within a few years, there were five centers of infestation (three in England, one in Scotland, and one in the Irish Free State). The rapidity with which the animals spread and the lessons provided by central European experience resulted in effective action, and the species was extirpated from England and Scotland in about five years (1932–37), at the respective costs of \$28.29 and \$52.43 per muskrat taken (Storer, 1937).

Of the best English habitats, Warwich (1940) wrote:

Shrawardine Pool, near Shrewsbury, where Musk-rats were originally enclosed in the autumn of 1929, has low banks, consequently few land burrows were made, and the animals lived mostly in houses. The increased population after the breeding season of 1930 so cut the dense growth of *Typha* that by the

end of 1931 the pool was a clear sheet of water. . . . The Severn [which flows close by] is a very suitable river for Musk-rats, as, although its banks are rather bare and do not support much rank vegetation, there is an abundance of aquatic plants in the river itself. The banks are high, in many place overhung with willows, and of a tough boulder clay, which becomes sandy below Shrewsbury. . . . After the first escapes from Shrawardine in 1930–31, a dense population was established on the adjacent ponds and ditches.

The catches, from June, 1932, to December, 1933, varied up to 147 per square mile and averaged around 35 per mile within a radius of about two miles of the point of introduction, on land lying near the Severn.

While the Germans and other peoples of central and western Europe regarded the value of muskrat pelts as little compensation for the damage the species did there, the Finns and Russians intentionally spread the muskrat, as a wild fur-bearer, over a large area of their northern lakes and marshes. From the German summary of Lavrov (1936), I would judge that, in the more thickly peopled parts of western Russia, the muskrat may do damage as in central Europe, though to a less serious degree.

Dr. Lauri Siivonen, of the Game Research Institute, Helsinki, Finland, sent me a list and notes on the contents of sixteen Russian publications on the muskrat of which he knew (letter and enclosures of March 1, 1947). The subject matter covered principally the ecology, introductions, food habits, enemies, parasites, and fur values of the species. N. P. Lavrov (or Lawrow, according to the German spelling) has carried on a great deal of the Russian investigations of muskrat biology, and I have had access to several of his papers and a book (1957). Dr. Teodor Juszkievicz, of the Polish Veterinary Research Institute, Pulawy, Poland, was very helpful in translating for me "key" passages from Lavrov's book. Another account of muskrats in the U.S.S.R. that I found especially informative was in Artimo's (1949) comprehensive paper on the muskrat in Finland, which Dr. Thomas A. Hippaka of Iowa State University translated for me, along with other material, from the original Finnish.

The introductions best known to Artimo were in areas neighboring Finland, especially Solovetsk Island. There are over 400 lakes on this island, most of which have a very rich plant life, and the muskrats soon populated all of the lakes. From 1927 to 1955, 160,000 muskrats were introduced in the Soviet Union (Lavrov, 1957). According to a 1941 publication by S. P. Naumov and N. P. Lavrov cited by Artimo, trapping was initiated in 1935, with a catch of 5,000; in 1939, the catch was 300,000. Hoffmann (1958) gave a 1956 figure of three million.

Lavrov's (1955a; 1957) distributional maps and one reproduced in Hoffmann (1958, p. 125) show a vast region of the central U.S.S.R. as occupied by the muskrat, extending east from the Urals to the Lena drainage in eastern Siberia, and from Outer Mongolia north toward the Arctic Circle — a region greater in size than all of Europe. In addition, there is a large region extending from Finland east to the

Urals, and many scattered localities in the southwestern U.S.S.R., especially north and northeast of the Black Sea and in some of the headwaters of tributaries leading north to the Ob River, within a relatively few hundred miles of India. I learned (through Mrs. Olga Garner's translation of the Russian text for me) that Lavrov (1955a) considered the area lying south of the present main range of the muskrat in central Asia to be unfit for the species and that it cannot be expected to occur there. The muskrat-less area referred to is principally that lying between 40 and 50 degrees of latitude and between 80 and 120 degrees of longitude. On the other hand, Lavrov's (1957, p. 184) curve plotting increase of the Russian muskrats from 1937 through 1955 conforms in a rough way to a lower asymptote of a Pearl-Verhulst-Reed logistic curve, with the 1955 population suggesting the beginning of a steep climb; it could be that the upper asymptote is still far off and at a level that would be hazardous to predict.

From Artimo's English summary, it may be seen that the muskrat was, beginning in 1922, transplanted to at least 216 places in Finland, from Hankoniemi in the south to Inari in the north. By 1931, possibly a fourth of the south half of Finland was occupied range for the species; by 1937, the spread had included possibly two-thirds of the south half, plus areas in the north half, nearly up to the northern tip of the country; by 1948, practically all of the south half of Finland was occupied, as well as what seemed to be the habitable environment of the north half.

The species is shown in Artimo's paper as occupying the Åland Archipelago of southwestern Finland. Introduced on Åland, itself, in 1926, the muskrat has apparently spread over thousands of the smaller islands by natural means. Muskrat populations, however, have not thrived on the sea islands to the extent that they have on the inland waters of southern Finland. From what I have seen of Finnish archipelagoes, I should not rate much of this type of habitat very high from the standpoint of the muskrats — possibly about the same as our Quetico-Superior region.

Artimo showed that the muskrat had by 1948 lost some of the range in northern Finland that it had occupied in 1937. The Finns were considering trying the introduction of *zalophus*, *spatulatus*, *albus*, *aquilonius*, and *obscurus* into the places in Lapland that seemed too uncongenial for *zibethicus* or other of the more southernly subspecies or strains thereof. But, it is understandable why the muskrat should build up dense populations locally and be virtually unrepresented in the open-water, food-poor lakes and ponds and the "north woods" terrain characterizing much of Finland. The heaps of muskrat-opened mollusk shells on the rocks of lakes, the water lily pads, the fringing Cyperaceae of open waters, the wooded backgrounds bespeak ecological counterparts of, let it be repeated, the Quetico-Superior region.

Artimo wrote that "North Finland is less productive than South Finland and East Finland less productive than West Finland. The

best cultivated districts are also the best muskrat areas." The hydrographic district of Kokemäenjoki in southwestern Finland includes some of the most productive habitat, its yield being "considerably larger than in the greater part of the country." In visiting (spring of 1959) some of the best muskrat-producing wetlands of southwest Finland, I was especially aware of the great local differences in habitats. The muskrats were living in places and at about the same densities that I would expect for comparable North American habitats, but in general, I thought that the accommodation capacity of Finnish wetlands for muskrats must be rather low.

Artimo found that the muskrats had done considerable leveling off in Finland between 1940 and 1945. He indicated that too few observations had been made over too short a time to permit very definite conclusions as to "cyclic" behavior of the species in Finland. The gross fluctuations of North American muskrats (see Elton and Nicholson, 1942) and the Finnish muskrats do not, however, agree very well chronologically. This might be in part explainable in terms of weather conditions, as the winters of 1939-42, which coincided with a "high" phase of the "10-year cycle" in central North America, were in Finland exceptionally severe. The meaning of the gross fluctuations of muskrats can surely be as badly obscured by climatic emergencies in Finland as they can be in North America. The same also applies to the U.S.S.R. (Lavrov, 1955b — see the newly available Canadian translation).

Artimo discussed biotopes occupied by muskrats in Finland and the quantitative investigations of the species carried on in the Kokemäenjoki district, 1946-48. On the basis of his results and known fur catches, he figured that "the catch of muskrats in our country in peak-years may possibly amount to 250,000." The maximum catch of 240,000, made in the spring of 1947, is approximately the same as his calculated maximum and far below the predictions of some earlier workers on Finnish muskrats. According to Hippaka's translation notes, Artimo indicated in the Finnish text that the attainment of peak catches of even 250,000 would require better management than had been practiced up to the date of the writing. Actually, I did not see during my visit what kind of management short of expensive, large-scale manipulation of biotopes could stand much chance of greatly increasing the Finnish muskrat populations. It should be pointed out, however, that according to Hoffmann (1958, p. 117), the Finnish catches for two years exceeded the 1947 figure of 240,000: 262,000 for 1950 and over 600,000 for 1955, the latter catch following a closed season in 1954. In 1956, the catch was down to about 212,000; in 1957, to about 128,000.

In his English summary, Artimo reported that the "most important enemies of the muskrat in Finland are the fox, the dog, and the birds of prey. The fish traps levy an annual tax of about 10,000 muskrats from the muskrat population of the country."

Little information is available on disease in Finnish muskrats,

though animals have been found dead at times (Lampio, 1946). Lampio, who had done much work on diseases of Finnish game, spent some time with me in late spring, 1952, in connection with an extensive survey he was making of wildlife research in the United States; and after inspecting the sites of recurrent die-offs at Little Wall and Goose lakes (Chapters 8 and 9) he volunteered the comment that disease could well be a more important factor in Finnish muskrat populations than had been recognized. What the possibilities are cannot yet be appraised, but on the occasion of my 1959 visit to southwestern Finland, I saw some evidence of mortality that could have been due to disease, and the Russians have many records of tularemia in their muskrat populations (Tcherkasski, 1951).

A question that keeps recurring to me is: Do the Finns really have predator-prey relationships on their muskrat marshes that differ greatly from those studied long and intensively on the Iowa observational areas?

What, for example, is the basis for the emphasis that the Finns place upon repression of predatory enemies of the muskrats as a management measure (Artimo, 1949, 1952; Brander, 1951)? Specifically, just what is behind Brander's (1951) designation of canids as, next to man, the most serious enemies of muskrats because of their tendency to attack muskrats through the latter's biologically weakest point, winter habitations? In Finland, as in northern United States and Canada, the quality of habitations varies with location and construction material; similar types of freezing and water fluctuations occur, and I see no reason to believe that wintering security or lack of security should differ in comparable parts of the Old and New Worlds. Admittedly, I have no first-hand knowledge of canids and other predators or scavengers exploiting muskrats in Finland, but the Iowa areas have often yielded data that looked much like what the Finns described, yet which, in detailed analysis, proved to reflect something very much different from simple predation by foxes and minks upon a favorite prey animal. I have in mind the case history after case history of epizootics of the hemorrhagic disease in which responses of flesh eaters could have been so easily misinterpreted. Scent-hunting predators may be adept at smelling dead muskrats lying inside of habitations, and when these dead are dug out, eaten, and remains scattered, the signs certainly can resemble those of predation. Other faulty appraisals rather frequently arise through the propensity of sick muskrats to spend their last days or hours on top of the ice, wandering around or burrowing into the sides of lodges. When a predator takes one of these, the resulting sign is that of a direct and bloody kill that may not be further diagnosed unless one obtains enough of the carcass to reveal identifiable lesions.

Or, are the views of the Finns toward muskrat enemies but a carry-over of the anti-"vermin" traditions that have long been strong in European game management? Or, have the Finns really observed more significant predation upon muskrats than I have?

Brander repeatedly referred to a sensitivity toward disturbance shown by Finnish muskrats that far surpasses anything I ever detected in Iowa, South Dakota, and northern Minnesota — or ever heard of in the course of my travels over other parts of North America, including the Canadian North. He reported serious consequences to muskrats driven out of their lodges by horse traffic over the ice, muskrats becoming sufficiently affrighted to wander when disturbed by hunters, trappers, predatory enemies, or anything breaking into their habitations, and abandonment of lodges even because of noisy human activities in rowboats.

One possibility that comes to my mind is that such sensitive muskrats may have been very ill-situated, compared with the Iowa and South Dakota populations with which I have had the most experience. When I consider the trapping in lodges, the mink intrusions, and the variety of disturbances to which the muskrats of north central United States may readily adjust, I feel that there must be a most special reason for the Finnish muskrats behaving as described. Our north central muskrats may at times engage in movements for not wholly apparent reasons, but I have seldom attributed any of this to disturbance by man, livestock, or predatory mammals, except when the muskrats were suffering from overpopulation tensions, acute food shortage, or drought exposure.

Brander did explain (conversation, May, 1959) that muskrats that had newly colonized an area were the ones displaying the greatest inclinations to move when disturbed. The importance that he ascribed to clams in the diet of the Finnish muskrats further strengthens my view that many of the Finnish waters offer muskrats poor habitat in which only a relatively few muskrats could be expected to live, conceivably whether they may be disturbed or preyed upon by enemies or not.

By the early forties, it was apparent, from articles and editorial comments in *Svensk Jakt*, that the muskrat had become a controversial animal among Swedish outdoorsmen, with opinions sharply differing as to whether introduction of the species into Sweden would result in economic benefits or a new pest problem. Then, the question of whether Sweden should or should not have muskrats became outdated in 1954. Velthuysen (1954) considered that the muskrat would sooner or later come over to Sweden across the Torne River and that it had already been reported as established within the Swedish boundary. Six months later, Liljeström (1954) definitely confirmed this report and added that the species had been established for at least a decade — after illegal introduction into the Torne River Valley. Curry-Lindahl (1955, p. 102) wrote that the muskrat had spread through large parts of Norrbotten (through which the Arctic Circle runs) and also to islands south of Haparanda at the mouth of the Torne River. The 1955 range of the muskrat in Sweden appeared to be well over 150 kilometers in length along and adjacent to the Torne Valley.

The strongest muskrat population that I found in Sweden was in

the lower reaches of the Torne River and neighboring streams. Here, signs could be seen generally distributed about sluggish, vegetation-grown waters within a comparatively short radius — 50 kilometers? — of Haparanda; my estimate for this local population was about 1,000. I was unable to find signs of the species elsewhere in this region during two days (mid-July, 1959) of stopping to investigate likely places along the roadsides, though the species was reported at the Pite River, about 150 kilometers southwest of Haparanda.

As muskrat habitats go, I would rate the best that I saw in the Haparanda area as only fair — similar, again, to those occurring in the Quetico-Superior area of Minnesota and Ontario. The landscape of many places in the lower Torne River is rather lakelike, with oxbows, islands, meadows, and other features in a wide, flat valley; but, unless the abundant growths of *Equisitum* are a staple sustaining food (which can be the case for *E. fluviatile* in northern Canadian waters), I hardly could see how the species could winter at all with no more food than it appeared to have. Yet, by its presence, it proved that it must be able to take care of itself passably well during long, cold winters.

The upper stretches of the Torne River that I saw looked still less hospitable. From the Torne River southward, muskrats spreading from their focus of relative abundance would have a wide zone of inferior or inhospitable environment to pass at the higher levels, across wide stretches of mountain and forest, and I am not sure how well they could spread along the coast, once they got away from the flatlands in the vicinity of Haparanda. Except for the human help that one has reason to suspect that they get illegally, they might well have remained essentially restricted to the waters of the Finnish-Swedish boundary for decades.

There are several places south of the Pite River where muskrats might get along fairly well if they reached them — extensive wetlands including marshes — and the Pite River is about a third of the way to Jämtland, the center of public agitation to introduce muskrats into central Sweden. Jämtland has some wetlands in which muskrats would find livable habitat, but in my opinion, it is much overrated as muskrat habitat by the enthusiasts. The muskrats could well do better in parts of Jämtland than in the Torne River, but I saw no place in Sweden where they could be expected to thrive as well as on the best North American marshes.

I am reluctant to make predictions as to the future status of muskrats in Sweden, but it would seem reasonable to expect something comparable to the situation in Finland, where the better marshes have good populations and where vast areas of inferior muskrat waters have few if any muskrats. Hornborgasjön — far down in southern Sweden — is the most attractive place from the muskrats' point of view that I saw in any part of Scandinavia.

The drainage of marshes that has taken place in southern Sweden and the concentration of remaining water in open, vegetation-poor

lakes has gone to extremes that I never saw over wide areas in North America. In the Kävlinge River valley of Skåne (where I did most of my field work during a six-month association with Lund University, 1958–59), marsh and lake waters had covered about 29 per cent of the surface 150 years ago, but by now the wet area has been reduced by artificial drainage to 3.4 per cent (Wolf, 1956; cited also in Rodhe, 1958). Rodhe considered this the typical fate of marshy areas in Skåne. Granted that the muskrats sooner or later will reach all waters of the Scandinavian Peninsula that can support the species, I do not see how they would ever become sufficiently numerous there to be either a serious pest or a more than locally important fur resource.

SOME COMPARISONS OF MUSKRATS AND MUSKRAT HABITATS

It may seem surprising how little can be said of the living habits of any subspecies of muskrat anywhere in North America or Europe that cannot be said to some extent of the type subspecies, *zibethicus*, in its native or naturally acquired range.

There are differences. The reputed helplessness of *rivalicicus* under ice (O'Neil, 1949) has no counterpart of which I know among the other subspecies, and some of the western muskrats of restricted geographic range apparently do not build lodges under any conditions. Both *macrodon* and *rivalicicus* attain consistently higher densities in very shallow marshes or in meadow-like habitats than does *zibethicus*, but the latter may occur in great local abundance in similar places, as may also *cinnamominus* and *osoyoosensis*. In general, there is less difference between the habitats of *zibethicus* and *macrodon* in New Jersey coastal marshes than between those of *zibethicus* and *rivalicicus* in Louisiana.

A greater tendency may exist on the part of *macrodon* and *rivalicicus* to increase up to densities destructive of their food supply than on the part of *zibethicus* and other of the more northern subspecies – even though *macrodon* and *rivalicicus* have decidedly smaller litters and have great expanses of some of the most food-rich marshes on earth.

Possibly *zibethicus*, with the rather special storage habits it exhibits on occasion in the Corn Belt and in certain duck potato marshes, may have a trait somewhat peculiar to itself, but genuine storage can occur in muskrat populations living outside of the range of *zibethicus* – in Saskatchewan, for example (Carter, 1922). The Louisiana subspecies seems to fall in a special category with respect to its avoidance of stream habitats, whereas all of the others may be frankly stream dwellers. Of the other subspecies living most nearly like *rivalicicus*, *macrodon* on Maryland streams lives about as any northern muskrat would under like conditions.

Mountain or mountain-like habitats of *zibethicus* in eastern United States, northern Minnesota, and northern Ontario differ little in essentials from those occupied by *albus* and *spatulatus* in parts

of the Canadian wilderness or from those of the real "mountain muskrat," *osoyoosensis*. The latter occupies a good deal of range that is much higher above sea level than any area in North America in which I know that *zibethicus* lives, but that does not prove that *osoyoosensis* has a unique specialization for high altitudes. At the edge of the Rockies, *cinnamominus* may get up just about as high as *osoyoosensis* and so, I think, may *mergens* and *spatulatus*, if comparisons between the subspecies be restricted to comparable latitudes and terrain. In its strongest habitats, *osoyoosensis* is as much of a marsh dweller as any muskrat.

Although *zibethicus* does not get near true deserts in the sense that *osoyoosensis* does — unless it now may in its new range in the U.S.S.R. — it certainly has had racial experience with droughts. For that matter, *cinnamominus* is a drought-tested subspecies if this can be said of any muskrat, not excluding from consideration the minor subspecies of the arid American Southwest.

Brackish-water *macrodon* and *rivalicius* notwithstanding, *osoyoosensis* has as much demonstrated ability as one might expect in a muskrat to live in a seaside or saline habitat. The Pacific Coast or the salt flats east of Great Salt Lake offer their own physiological obstacles to muskrats trying to maintain themselves, and one may think it astounding what the animals can tolerate and stay alive, yet the white-rimmed alkali lakes of the northern high plains must be no more congenial for *cinnamominus* during drought crises. Nor does *zibethicus* display any notable lack of tolerance when living in pollution-foul streams, ponds, and puddles.

At the southern end of its North American range, *zibethicus* is not exposed to winter conditions more severe than those to which *rivalicius* is subject, except insofar as the habitat of *zibethicus* is more marginal in the South than is that of *rivalicius*. At the northern end of its range, *zibethicus* may have to winter under several feet of ice. East-to-west extremes vary from a few inches of ice over *macrodon* marshes to alpine depths in the upper retreats of *osoyoosensis*. It may be that the muskrats of the American Far North do have more in the way of adaptations for wintering than do *zibethicus*, *cinnamominus*, or even *osoyoosensis*, though I know that the air temperature has fallen as low as 58 degrees below zero Fahrenheit in western South Dakota; and eastern Montana and northern Ontario have cold winters, at either high or low altitudes. The Torne River between northern Sweden and Finland surely is not one of the most hospitable of places for muskrats of probable *zibethicus* stock, with its long winters and a cold getting down to the vicinity of 50 below zero Fahrenheit. Lavrov's maps show considerable muskrat range extending north of the Arctic Circle in Siberia as well as in western Russia, and, I suppose that these muskrats of the Soviet Far North must also be largely of *zibethicus* stock. The runty *albus* in the Barrens near York Factory has its own problems of winter survival. Of the range of *spatulatus*, Soper (1941) wrote that in the Wood Buffalo

Park "Ice normally appears to attain a maximum thickness of about 5 or 6 feet, though it has been known to reach seven feet at Great Slave Lake"; and above the Arctic Circle lie deep-freezing waters of the Mackenzie delta, in which life for the same subspecies has its restrictions.

Winter-killing of muskrats in northern wilderness and western high plains has many of the characteristics of the winter-killing studied in detail in Iowa. Whether the period of unendurable exposure or starvation lasted a day or three-quarters of a year, whether brought on by an accumulation of 5 inches of ice or by 5 feet or through extremes in air temperature of 15 degrees above or 50 degrees below zero, or colder, it reflected the state of the food, shelter, and unfrozen water available to the muskrats. Losses from droughts or losses from floods similarly had their community of aspects, whether in a stream running through a sagebrush semidesert in the western Dakotas or in the delta of the Saskatchewan River or in agriculturally lush central Iowa.

In other words, the muskrats, whatever the subspecies, live like other living things, where, when, and if they can, in any way that they can; and this certainly is true even in the South and Southeast where, as yet, marginality of range of *macrodon*, *zibethicus*, and *rivalicius* cannot in all cases be satisfactorily defined.

With recognition that we are concerned with essentially the same animal confronted by specific problems of survival differing according to locality and region, we may see that the status of the species in marginal and submarginal habitats becomes of fully as great interest as its status in optimum habitats. The desirability of learning more about why the muskrat or any other animal may maintain itself in a marginal habitat, and how the marginal grades off into the utterly uninhabitable, may at first glance seem merely of "academic" importance. The implications of marginal habitat may be much greater than that, however, insofar as even superb habitat may become, actually or in effect, marginal or worse in consequence of emergencies or deterioration. The fine differences between what a thin-spread, edge-of-range population can endure and what it cannot endure are not only scientifically informative but also contribute significantly to our practical understanding of populations.