Part 1

Introduction

Chapter 1

The Muskrat: A Semiaquatic Rodent

THE MUSKRAT'S COMMON NAME is accounted for by the odor associated with the species during the breeding season. Both sexes have special glands situated beneath the ventral skin near the external genitalia. With the enlargement of these glands, a yellowish, musky-smelling substance is secreted and deposited at stations along the routes of travel of muskrats, and at defecating posts, bases of lodges, and mud bars. Stevens and Erickson (1942) concluded that the musk oil contained a mixture of cyclopentadecanol and cycloheptadecanol and corresponding odoriferous ketones. The scent retains its properties sufficiently long after exposure to air to serve effectively as an advertising medium — up to several days in intensities readily detected by the human nose and possibly for weeks under circumstances favoring retention. Grinnell, Dixon, and Linsdale (1937, p. 744) noted that dried glands kept their odor indefinitely.

THE MUSKRAT IN THE WATER

The coat of the grown muskrat may be considered waterproof under ordinary conditions. It consists of dense and silky underfur and coarser, longer, and peculiarly glossy guard hairs. The long, laterally compressed tail is rudder-like. Hind feet are modified for swimming by fringes of stiff hairs, as well as by a side-twist of the ankle joints. The much smaller fore feet are suitable for rather skillful manipulation. Ears are small and almost hidden in the fur. Eyes are also small and may protrude noticeably. Nostrils, lips, and tongue are adapted for underwater activities, and the animals have conspicuous incisor teeth with which to gnaw and transport submerged materials.

Mizelle (1935), after reviewing some of the controversial statements in the literature concerning the muskrat's manner of swimming, wrote of his experiments with presumably *O. z. rivalicius* in a concrete pool. His animal was clearly visible in every phase of swimming on and below the surface of the water. In neither surface nor submerged swimming did it use its fore feet, but held them motionless under chin with palms inward. (Iowa individuals, however, have been observed using the fore feet in leisurely swimming.) In surface swimming, Mizelle observed the animal propelling itself forward with alternate strokes of the hind feet. The propelling movement came chiefly from the ankle joint, but to a slight degree from the knee. Movement of the femur was imperceptible. On the forward stroke, the foot folded to facilitate its return to a forward position. Practically no undulation of the body was noted, nor was the tail used in the surface swimming, it being trailed in a straight line. In turning, the animal altered the strokes on one side or the other. The fore feet were used to assist in submergence. The estimated speed for surface swimming was one to three miles per hour, which is about the speed shown by undisturbed animals in the wild.

The strokes of the hind feet in submerged swimming were as in surface swimming except that they were made in a nearly horizontal plane instead of vertically. The tail was used vigorously as a scull at all times when the animal was under water, making lateral strokes toward the feet in the backward motion. When the muskrat was stimulated, its tail strokes became faster than the combined rates of both hind feet; but, in ordinary swimming, the tail strokes equalled the foot strokes, tending to make the animal's course a straight line. The animal turned on its course underwater in the same manner as in surface swimming.

Muskrats are capable of surprisingly swift lunges under water, as in pursuit of fishes, during fights, or when suddenly alarmed. During some fights, participants may pop out of the water with about the speed of big fishes striking at flies.

Readers interested in the anatomical basis of the muskrat's swimming movements may find detailed accounts in recent German papers. Müller (1952–53) wrote mainly about the skeleton of the animal as a whole, including some descriptions and illustrations of movements of extremities, whereas Eble (1955) devoted his corresponding paper to musculature in relation to movements of extremities.

Surface swims by muskrats living in regular residence seldom exceed a quarter of a mile, and such long swims are usually to be witnessed on the part of shore-dwelling muskrats swimming out on a lake or open marsh to feed. When swimming in rough water, the muskrats are apt to swim submerged, coming to the surface from time to time for air.

Our Iowa experiments with fur-refuges on state-owned marshes trapped by the public have shown that the setting of traps at the refuge boundaries may effectually "suck out" the muskrats for a distance of somewhat less than 200 yards into the refuge, provided that there were near the boundaries lodges or other resting places to attract swimmers. At the same time, the population living 200 yards or deeper in the refuge seemed to be generally unaffected by the intensity of the trapping effort outside. The fact that this depopulation of the outer zone of a refuge occurred either during the open water of late fall or in early winter after freezing over of the entire surface of the marsh is indicative of the freedom enjoyed by northern muskrats in their under-ice movements.

Trappers have reported muskrats lying submerged beneath thin ice, expelling bubbles into the water and, after intervals, drawing the bubbles in again, or lying with bubbles at the ends of their noses, alternately drawing in and letting out. I, too, have seen muskrats behaving in this way, whatever may be the explanation. The general supposition is that the expired bubble becomes oxygenated through contact with the water, and ready for reuse by the muskrat in the space of minutes, but consideration of the physical properties of gases and the few parts per million oxygen content of most natural water makes it appear most doubtful that a muskrat can get sufficient oxygen from the procedure really to benefit therefrom — except insofar as the breathing out and in may make for more efficient utilization of the oxygen already in the bubble. Or, muskrats swimming under the ice may have access to large quantities of oxygen-containing bubbles. Atmospheric air may lie between water and ice, entering through cracks caused by buckling of the ice or somehow filling in as water recedes from below. (But it should not be assumed that all bubbles under the ice contain air or oxygen from any source, for, in many cases, it is apparent that they do not.)

In underwater travels under the ice, muskrats make occasional stops at feed houses and push-ups, as well as at bubble patches, but they certainly are adapted for prolonged diving. Koppanyi and Dooley (1929), experimenting in the laboratory with reflexes inhibiting respiration in muskrats on the point of recovery from anesthesia, found that submergence apnea would result whenever the nostrils were brought in contact with the water. Manipulation of the position of the head also induced apnea. Both submergence and postural apnea were accompanied by rises in blood pressure and slowing of the heart rate.

Respiration in diving mammals has been studied particularly by Irving (1938a; 1939b; 1939). Seals, beavers, and muskrats can withstand submergence about five times as long as can land mammals. Their respiratory adjustments, though mammalian in type, are extreme and manifested, for one thing, by insensitivity to carbon dioxide. The failure of carbon dioxide as a respiratory stimulus in divers implies that it is not effective in activating the quick internal responses that mammals generally make to escape asphyxia during apnea. The respiratory adjustments of the divers do resemble those of land mammals except that the divers adjust with quantitatively greater effectiveness. When breathing of a mammal is arrested, the blood flow through the muscles decreases while increasing through the brain.

One of Irving's experimental subjects was a 600-gram muskrat (probably a subadult of *O. z. macrodon*), which endured submergence for 12 minutes in the laboratory. It, like other divers experimented with, relaxed muscular activity. Muscular relaxation is in itself an adjustment to avoid wasting the oxygen supply in useless struggles. In contrast with the violent struggling of a land mammal when forcibly immersed in water or prevented in any way from breathing, the muskrat accepted the situation with equanimity and waited with muscles relaxed for several minutes. It then deliberately explored means for escape, and, as in the case of other divers, did not begin violent struggling until 5 to 10 minutes had elapsed.

But diving ability in a mammal is not solely a matter of passive oxygen conservation, for a submerged diver may be quite active. A most interesting adaptation of muskrats and other diving mammals is their apparent faculty for running up an "oxygen debt," for "borrowing" oxygen from tissues outside the lungs.

Muskrats have been observed to dive longer than the 12-minute period of forced submergence of Irving's animal. Smith (1938) cited examples of two dives timed by W. A. Gibbs for a muskrat caught alive in a fish trap. It first remained down for 17 minutes, then surfaced and, becoming alarmed, dived again almost immediately, staying under for 10 minutes. It refused to dive again. Throughout the observations, the animal was in plain sight of Mr. Gibbs and could not have obtained air except while on the surface.

On several occasions, I have surprised transient muskrats in pools or streams where they had no access to existing burrows, and I have forced them (generally by touching them with a pole) to continue diving until they were exhausted enough to capture alive. A typical instance relates to a newly mature male encountered April 19, 1944, at the edge of a small oxbow pool. At my approach, it dived, reappearing in approximately 10 minutes over the spot where it had dived. I stood in the middle of the pool for a good half hour, forcing it to dive as soon as I could, each time that it came to the surface. It would lie, partly concealed, under the dead leaves on the bottom and, about a half minute before surfacing, would expel a stream of bubbles. It finally seemed unable to continue diving, though very willing to attack as it was shoved to land and held with a pole for marking.

Other muskrats may show more versatility in their efforts to escape capture. They may succeed in doing so, as through quickly digging a short, shallow burrow, and coming up under the sod of the bank above the surface of the water. A good digger working in soil of the right consistency may almost make the mud squirt through the water and may be lost from sight in a few seconds. Unquestionably, such an accomplishment has survival value for individuals pioneering in strange waters.

While submerged, the muskrat may not only be adept at digging and gnawing when having a soft medium to work with, but it may also put on some of its best displays of prowess in winter, as it cuts through frozen material. Its incisor teeth protrude ahead of the cheeks in a way most serviceable for underwater work and for cutting away of rootstocks of cattails, bulrushes, and reeds at the frostline under the ice. It may cut through thick lake ice from beneath (though usually choosing the thinner places or openings of cracks) or, likewise from beneath, cut away the ice of a frozen plunge hole in an unused lodge. Some of the most spectacular rehabilitation of long-frozen lodges is forced, as when a heavy winter rain or thaw floods the nearly dry tunnels in which the muskrats had previously been living under the ice somewhat away from the lodges.

Another way in which the muskrat may show adaptation for its aquatic way of life is in its respiratory tolerance for foul air inside of lodges during cold-climate winters. Over nearly all of North America where winters are sufficiently cold to seal a marsh with ice for two or three months at a stretch, muskrats may be found living in their familiar dwelling lodges in chambers having about as little fresh air as one might imagine. These lodges are not of uniformly tight construction, but the chambers of hundreds examined in early and midwinter were, to my eyes, virtually air tight above the water line. Ice-shells lining the lodge chambers may be built up to a thickness of two to four inches through splashing or contact with wet bodies. While it need not be assumed that such shells provide a perfect seal, they certainly can leave few places through which air may be expected to pass very rapidly. Some of the lodge chambers, furthermore, may reek of hydrogen sulfide or other decomposition products, yet, there in the chambers, with unfrozen water at their feet, the muskrats characteristically huddle. They may huddle together, even up to a dozen or more, doubtless all but filling a chamber at times. Now and then, an animal may dive in the plunge hole and swim off under the ice or sit or float by itself in one of the small feed houses or in the opening of the ice under a push-up or in an air space under a ridge of pressure-buckled ice; but field observations clearly show that the dwelling lodges, ice-lined or not, are the main day and night retreats of muskrat populations occupying the central parts of marshes as long as the water level remains well up in the plunge holes.

Huenecke, Erickson, and Marshall (1958) took air samples at weekly or biweekly intervals from individual muskrat lodges on eight Minnesota marshes, November, 1949, through March, 1950. For a total of 245 samples, the . . .

. . . only gas found to accumulate to any extent in muskrat houses in winter was carbon dioxide . . . .

When the carbon dioxide accumulations were plotted by dates, there was a gradual build-up from less than 0.5 per cent in early November to a high of 5–7 per cent in early February, followed by a sharp decline to less than 0.5 per cent by mid-March. The accumulation may be related to the external snow cover and the formation of an icy shell 1½ inches thick on the inside of the walls of the houses. . . .

The oxygen content of the air inside muskrat houses was inversely related to the carbon dioxide content. This balance is probably due to the respiratory activities of the muskrats occupying the houses. . . .

This investigation showed that, under the conditions that existed during the winter of 1949–50, no gas accumulations in muskrat houses were found that would have been lethal to muskrats. . . . No correlations were found between carbon dioxide concentrations and atmospheric temperature or precipitation.

THE MUSKRAT OUT OF THE WATER

The muskrat is awkward on land or on the surface of ice. In its own way, nevertheless, it can cover ground, walking or bounding. Differing rates of cross-country movements have been recorded during the Iowa investigations, but the following may be a fairly typical example: One thin old male, a late January wanderer, which I trailed in the snow without its awareness, covered 2,800 yards in about a half day, with several rests enroute.

The muskrat's main problem, in the event of prolonged activity away from unfrozen water, is not so much in getting around as in staying alive. As a species, it is sensitive to freezing cold. Gerstell (1942, pp. 58–59) experimentally deprived six captive *O. z. zibethicus* of food and and water until death. Two animals, which were subjected to a temperature of zero degrees Fahrenheit with a constant artificial wind of 5.8 miles per hour, survived approximately 40 hours and lost an average of 13.2 per cent of their starting weights, whereas two animals not exposed to the wind lived over 90 hours, with an average loss of 20.7 per cent. The other two, kept in still air at temperatures of 36 to 48 degrees, died after an average of 200 hours, after losing an average of 30.0 per cent of their starting weights.

An abundance of field data exists on the condition of winter-wandering muskrats in Iowa, South Dakota, and northward. The first part of a muskrat's anatomy to freeze is the tail, and this may freeze solidly to within a few inches of the body without necessarily lethal consequences to the victim. The animal then chews away the frozen flesh, after which the bare tail vertebrae tend to be lost. Trappers' catches from Iowa marshes show variable numbers of adult muskrats having such stub tails. In advanced cases of freezing, still-living muskrats may be seen with eyes and toes frozen.

No field data of which I know adequately demonstrate the lengths of time that muskrats may live when exposed to given temperatures. I do know that ill-situated individuals may wander in snow or on top of the ice for a period of days at air temperatures of around 10 to 15 degrees Fahrenheit, yet suffer little more than frost-bitten tail tips, if that much, provided that they keep well nourished and avoid violence. It should be made plain that even ill-situated muskrats need not always be fully exposed to the wind and cold of a winter day. They may seek shelter in snow drifts and ice ridges or improvise nests in which to spend a few hours in weedy or rushy growths, corn shocks, and culverts, or enter badger or woodchuck holes or the root-tangles of trees.

Outside the water, a strong, full-sized muskrat, using fore feet and teeth, can penetrate a markedly resistant medium. It is not equipped to displace tremendous quantities of hard-frozen marsh bottom in quest of food, but it can utilize frozen food in concentrations — rootstocks of a cattail *(Typha)* or bulrush *(Scirpus)* clump if not too inaccessible, or a cache of ear-corn (*Zea Mays*) or tubers of duck potato *(Sagittaria)*. In north-central waters that are very shallow at freeze-up, the last places having living fishes (such as the bullheads, *Ameirus)* may be the channels and entrances of muskrat habitations. When the water in these freezes, it may be packed with fishes for hungry muskrats to gnaw on, the frozen fish and encompassing icy matrix together.

During winter crises, Iowa muskrats remaining in dry marshes or stream-beds spend most of their time underground in burrows kept plugged with mud. The mud plugs quickly freeze in cold weather. When an animal living within the burrow emerges to forage outside — as it generally must under such circumstances unless it has duck potatoes or corn stored inside — it has to gnaw its way out. Gnawing out of frozen burrows and lodges is done so much at will by vigorous muskrats that I can hardly conceive of muskrats being imprisoned therein to the extent of starving. They may starve but not because of inability to get out of their living quarters.

Once they find themselves outside of and separated from living quarters by frozen barriers, they may not be able to get back inside, and may die outside, only a few feet from the shelter of a subsurface retreat. Sometimes they seem unaware of the exact location of channels or chambers concealed by the ice, or they may be unable to do the necessary work while exposed to outside cold. I also think that a muskrat has far less inherent ability to gnaw downward than upward through frozen material.

On occasion, a muskrat, upon returning to its burrow after outside foraging, may find the passageway plugged from within by another occupant, and the plug frozen and indistinguishable as an entrance site. One such "locked out" individual was observed as it sat beside a small hole it had cut in a crack over the tunnel leading to its lodge. It still had 12 to 15 cubic inches of frozen mud to remove before it could enter, and it was already too lethargic from cold to keep working steadily.

An adult muskrat's powers of withstanding thirst are manifestly superior to those of a young one, but its limits of tolerance in this respect are hard to define. The very last muskrats to be found alive in the powdery peat bottoms of Iowa marshes after months of drought exposure are mainly, sometimes exclusively, adults (Errington, 1939a; 1943; Errington and Scott, 1945), so proving that these can keep alive for a protracted time on what moisture they get from dew and plant juices — that is, if they stay in holes or otherwise conserve the water in their bodies during hot weather. Nor are young animals, despite their much higher mortality rates during drought, without resistance to drought conditions. A food-rich bulrush of the Cheever Lake series in northern Iowa was dry from spring through the fall of 1940, yet its muskrat population of mid-November consisted of its three original pairs from spring and their nine successfully-reared young. At times of more acute emergencies, as on Utah and Oregon deserts, individual muskrats may stay alive long enough to travel up to 10 miles or more away from anything that might be called habitable muskrat environment. Flooding of coastal marshes by undrinkable, wind-driven salt water may result in spectacular losses of muskrats (Arthur, 1931, p. 338; Smith, 1938; Dozier, 1947a). Of these authors, Smith reported *O. z. macrodon* dying in two or three days after becoming marooned on high spots by salt water.

Against man, large birds of prey, dogs, coyotes, and medium to large sizes of flesh eaters rather generally, a muskrat surprised away from water may be in a hopeless situation unless it finds refuge in protective cover. The less powerful foxes and minks may easily kill the smaller-sized muskrats that they can seize on land, though the larger muskrats may be able to take care of themselves in the event of attacks. Much depends on the psychological attitude of an adult or subadult muskrat that is being overtaken or confronted by a mink on land or ice. If the muskrat becomes panicky and tries to escape by running, the mink may have little trouble making a kill; if the muskrat carries the fight to the mink, it stands a far better chance of defending itself. If it backs into a hole or finds some other advantageous position in which it need not present much except teeth to an adversary, a muskrat may be too formidable for a mink to care to attack. It may not have the comparatively limitless stamina, the hard-muscled toughness, and the tenacity of life that the mink has, and it rarely shows anything of a mink's faculty for directed attack; but its bite is not slow in delivery and, bite for bite, may lay open as much flesh as the bite of a mink.

Habitual transients among land-active muskrats may be further beset by a sort of occupational hazard in the form of the wounds of intraspecific strife. That muskrats can die of wounds received from their own kind is, or should be, common knowledge to anyone who might examine large numbers of those dying about the peripheries of dense or friction-ridden populations. That muskrats can continue living while severely cut up also is, or should be, common knowledge to observant trappers or outdoorsmen having much to do with the species (Seton, 1929, vol. 4, p. 597; Errington, 1939a; 1943, pp. 916–21).

Selected examples of muskrats bearing strife wounds might include a drought-evicted adult female collected in September while journeying across the higher land between two marshes. It had two very severe wounds on the abdomen, just below the sternum, and these wounds and parts of liver and intestines were crawling masses of fly larvae. The animal was vigorous and making progress toward healing the wounds, though I felt at the time that it probably would have died from them. A second fall-wandering adult female had a severe, nearly healed, wound below the sternum and a wound in the region of a kidney through which putrid-smelling intestinal contents had penetrated. Whatever may have been its prospects for recovering, it was far from helpless when collected. Another fall transient of undetermined age and sex was seen sitting on a lake shore, resting on its elbows; one fore leg had been so mangled that it was barely hanging on; the other fore leg also had been bitten into uselessness; a two-inch gash opened the abdomen; and there were numerous fresh and healing cuts about head, neck, and hind quarters.

During the fur trapping months, many of the muskrats wandering about the countryside are those having wrung off feet to escape from steel traps. While the mortality rate of such animals is undoubtedly high (Arthur, 1931, pp. 354–55; Errington, 1943, pp. 885–86), recovery from trap injuries is by no means unusual. Warwick (1940) reported that about 10 per cent of the muskrats taken during the extermination campaign in the British Isles had previously wrung out of traps, to recover in good flesh and with cleanly healed wounds.

As long as living conditions for local muskrats are fairly good, the general run of individuals bearing severe wounds comprise doomed transients, cast-outs, or similar biological wastage. Differences in their abilities to recuperate from great physical damage may not then count very much from the racial standpoint. During crises, however, a battered – if not hungry and thirsty – group may be that part of the population upon which the natural restocking of muskrats in countywide areas may depend.

I have notes on the muskrat occupants of a food-poor intermittent stream representative of the better muskrat habitats of an immense area of western South Dakota. My December, 1924, catch of 149 pelts was badly damaged from strife wounds, with about half of the pelts showing major wounds in all stages of healing. For muskrats of the watershed – which at that time was about as habitable for them as it ever is – the rest of the winter imposed a highly selective test that eliminated before spring many more than survived. Even so, the emergencies of the winter of 1924–25 were benign for the muskrats of western South Dakota compared with the droughts of the thirties, which left hardly a muskrat alive within a 100-mile radius of the above mentioned watershed. Surely many of the muskrats furnishing the stock for later pioneering and repopulating had to possess durability as well as luck.

CHOICE OF HABITAT

As represented by its numerous subspecies, the muskrat *can* adjust to a surprising geographical variety. It can adjust to environmental differences ranging from subtropical rivers and coastal marshes to arctic tundras and deltas. In North America, its subspecifically collective range is understandably delimited by mountains and semideserts of the West, by the true deserts of the Southwest, and by the almost year-round bleakness of the Far North. The reasons for its thinning out and disappearance in ecologically borderline habitat of northeastern United States are passably apparent. The Southeast, however, is a region of distributional mysteries, and muskrats simply do not live over a vast terrain that does not look too uncongenial for them. This will be treated at greater length farther on in the book, but the thought may be left here that many of the southeastern streams having no muskrats are similar in appearance to those of the same watershed that *do* have muskrats within a few hundred miles northward.

Within a given subspecific range, muskrats may be found in a diversity of habitats. *O. z. zibethicus,* in the Mid-West, may live in clear streams and lakes or in sewage drains, in clean- and in foul-smelling marshes and sloughs and ponds, in deep waters or in the puddles of ditches and tile flows. Northward, its range goes far into the wilderness of the Pre-Cambrian Shield south of Hudson's Bay; eastward, into the rocky streams of the upper Appalachians and the New Jersey coastal marshes; southward, into all of the Gulf States except Florida, to the edge of the subtropics. In the Great Plains, *O. z. cinnamominus* may live in big rivers and small, in intermittent streams and artificial reservoirs, in headwater pools and extensive marshlands. *O. z. osoyoosensis* of the Rocky Mountain states may live in swift, clear streams of foothills and upper plains, in irrigation ditches and seepages, in natural marshes of lowlands, in mountain valleys, in beaver pools of both low meadows and high altitude creeks, and, sometimes, in the waters of plateaus. *O. z. albus,* of the Mid-North, may live in typical marshes, in meandering and in fast-moving streams, in the deltas of river systems, in bogs and swamps, in places along the shores of large lakes, in parts of the subarctic tundra or Barren Grounds, and in the heterogeneity of wetlands underlain either by limestone strata or by Pre-Cambrian rock.

The above four subspecies are wide-ranging ones with which I can claim a certain personal familiarity, and, in my opinion, they are all much the same animal behavioristically. Of course, they do not maintain uniform abundance throughout the different grades of habitats occupied, but they all respond, if present, to quiet waters having either edible marsh plants or other suitable food available near by. No doubt like generalizations might apply to a fifth widely distributed subspecies, *O. z. spatulatus,* of the Canadian and Alaskan Northwest, as well as to some of more restricted distribution, but, as yet, I lack sufficient knowledge of them to judge.

Although water must always, in minimal amounts and within a minimal range of stability, be regarded as integral to the muskrat's way of life as a free-living species, the value of water to the muskrat is not always proportional to the quantity thereof. There can be such a thing as too much water for the muskrat's well-being, as will be discussed later in connection with effects of flooding. Or the water can be too rough, as on wave-swept open lakes, especially those of large size or situated on high plateaus subject to strong winds. Or the fluctuations in water levels may be excessive—even in the space of hours — not only through the occasional flash floods occurring naturally but also through human manipulation of tremendous volumes of water in river basins developed for power, transportation, or flood control. Sudden rises up to several feet above normal may be expected as a result of wind tides on some marshes lying adjacent to, and connected with, large inland lakes. For coastal marshes, storms backing up salt water may have their own distinctive consequences for muskrats and their habitats.

Or the water may be too swift, as in canyons, rapids, etc., but it is often difficult to judge exactly when water becomes too swift to be navigable by muskrats. I recall the sluiceway of a small dam on the Lower Souris marshes of North Dakota. Muskrats had been observed to be unable to swim against the current immediately above, and the rate of flow there surely was not faster than that often to be seen along practically the whole length of many mountain streams and many "white-water" stretches in the Pre-Cambrian region centering about Hudson's Bay.

The best all-around food for midwestern muskrats is cultivated ear corn; and stream-dwelling populations of the corn-belt states may conspicuously reorient themselves according to the local accessibility of corn fields (Errington, 1938; 1941a). With regard to self-propagating native foods, the muskrats of northern United States usually show the greatest responsiveness to cattails (Johnson, 1925; Errington, 1941a; 1948a; Dozier, 1945; and numerous other authors). In southern coastal marshes, cattails may be considered undesirable by muskrat managers, *O. z. rivalicius* greatly preferring certain bulrushes, especially *Scirpus olneyi* (Lay, 1945; Lynch, O'Neil, and Lay, 1947; O'Neil, 1949). Bulrushes may include high-rating food plants of the more northerly marshes, as well. While inspecting muskrat habitats in Manitoba and Saskatchewan in 1948, I was reliably informed that *O. z. albus* often displayed preference toward the horsetail called "goose grass" *(Equisetum fluviatile)* rather than toward either cattails or bulrushes. It should be brought out that appraisals of utilization of a given food — for example, of a species of cattail — by muskrats of a region may involve many unknowns. Questions of variations in flavor or nutritive qualities may relate not only to soil, water, growing season, and the usual run of expected variables but also to taxonomic differences (Hotchkiss and Dozier, 1949).

Among other food plants that may be selectively chosen by muskrats, or that may be patently attractive enough to cause muskrats to concentrate in a part of a marsh, lake, or stream, are burreed *(Sparganium)*, duck potato *(Sagittaria)*, sago pondweed *(Potamogeton)*, wild rice *(Zizania)*, and some of the willows *(Salix)*, and sedges *(Carex)*, smartweeds *(Polygonum)*, legumes, and composites. Other plants, like reed *(Phragmites)* and yellow water lily *(Nuphar)*, may not appear to be particularly relished yet may be important in the lives of muskrats lacking the preferred types (Errington, 1941a; Bellrose, 1950). Midwestern muskrats seem not to be very enthusiastic about flesh of lower vertebrates as a dietary staple, but hungry transients frequently settle in stream pools or in the vicinity of lake-shore springs having massed assemblages of fishes or frogs. These they exploit much as minks do or even subsist on the frozen fishes and frogs stored by the minks (Errington, 1941a). However, the muskrat stomach does not have any special morphological adaptations for a carnivorous diet (Luppa, 1956).

Takos (1947), in his careful study of muskrat feeding in Maine, used forage ratios to express correlations between occurrences of plant remains found on feeding platforms and the relative abundance of the same species of plants in the environment. His muskrats tended to utilize the most available plant species, and he found this tendency especially marked whenever the plants occurred both in high frequencies and in dense stands. Phenological events in the life histories of the plants also had a bearing on the quantities consumed by the muskrats. Arrowheads and wild rice mature more slowly than the semi-terrestrial plants and are almost always submerged in the early growing season. The sedge, *Carex lacustris,* was the only plant noted by Takos for which the forage ratio indicated a highly significant degree of selection during any of the growing season periods. He ascribed this disproportionate utilization to the fact that early spring floods drove many muskrats to somewhat elevated sedge-meadows where the sedge was one of the first plants to produce succulent green parts after the spring thaw.

Bellrose (1950) found that Illinois muskrats, while exhibiting a great deal of individual variation in food habits, had a marked preference for some plants, especially in winter. However, he felt that plants of high palatability may not support as many muskrats per unit of area as other foods that are less palatable but more nutritious.

In Iowa, the muskrat may show about all degrees of either indiscrimination or selectiveness in feeding and food-gathering. Individuals may have their favorite (or accustomed) shore retreats where they dig out tubers. They may have their overland routes to corn fields, apple orchards, or truck gardens. Others, especially in summer, may virtually mow the shore vegetation within easy reach of the water — tree seedlings, grasses, sedges, ragweed, cocklebur, or smartweed growths, eating very nearly everything of manageable size and consistency that they may come to (Errington, 1941a). In winter, even when lacking corn or rootstocks of cattails and bulrushes or other rich sources of heat and energy, muskrats at this latitude may still survive on comparatively poor cold-weather diets. If the diet is neither too harsh nor too innutritious, some solid carbohydrate or fat in combination with some flesh and green food may prevent excessive loss of weight and give the animals a chance of getting through a short winter.

The medium in which burrows must be dug influences the distribution and status of bank-dwelling muskrats when extremes of hardness or looseness are concerned. At one extreme are rocky or pebbly shores offering no den sites for miles except in occasional cracks or under the roots of big trees. At another, are friable shales or sands that hold the shape of burrows chiefly in proportion to the amount of binding by roots. Intermediate between the extremes are the agricultural soils and subsoils in which muskrats excavate burrows by the millions across central North America. Clay subsoils appear to be the muskrat's first choice for digging in the midwestern states. Elaborate burrow systems in firm soils, once established and favorably situated with respect to water and food, may be occupied and maintained more or less regularly for decades, even when subjected to considerable disturbance. And anything protecting burrow systems from caving or digging out by enemies may appreciably enhance the attractiveness of particular retreats for muskrats. Burrows may be dug under sturdy tree roots or boulders or fence corners, under junk piles or idle farm machinery, bridge structures, water tanks, foundations of buildings, hay stacks, wood piles, docks, wrecked boats, and so on.

In marshes, proper, heavy growths of emergent vegetation suitable for lodge-building — notably cattails and bulrushes — commonly attract muskrats, irrespective of what might be the nature of the shores. Submerged plants seldom provide building materials the equivalent of the superior emergents, though coontail *(Ceratophyllum)*, algal growths, and other easily wadded plants may often be used in lodge construction.

The presence of other muskrats or their habitations may have an evident conditioning effect on the behavior of muskrats in search of living quarters (Errington, 1940; 1943, pp. 879–80). Muskrats are naturally attracted to places where their species lives or has lived and, within limits, tend to gather thereabout unless driven out or psychologically repelled by the residents. This may be noted especially on the more homogeneous tracts of marshes at times when populations are building up after drastic reductions. With large expanses of suitable habitat awaiting recolonizing, the marshes, lakes, and streams having vacant or underpopulated sets of lodges or burrows draw in the muskrats decidedly better than do those that are ecologically similar though lacking the lodges or burrows. Even a very old sign may have its attractions, and newcomers rebuild flattened lodges or burrows having settling or caved-in roofs. Digging of new burrows or erection of new lodges on the part of late summer and fall populations expanding into unoccupied habitat may be the forerunner of further expansion in the years to come.

Unless previously-used burrow systems remain death-traps of infectious disease, the propensity of muskrats to investigate them has its advantages for the species. Parts of streams that are generally the last to be abandoned during droughts tend to be among the ecologically superior for muskrats and at the same time well enough honeycombed with burrows to attract muskrats again after the water returns. Along Iowa drainage ditches intersecting corn fields, stored ear corn in the ramifications of trapped out burrows may provide an added inducement for spring newcomers to settle and breed in the better places, or in those likely to be near good sources of food year after year.

At least our north central muskrats rarely appear to be directly influenced in their choice of habitat by the presence of enemies other than intolerant or hostile members of their own kind — although they may at times avoid parts of their individual home ranges (especially on or near dry land) that they learn to regard as dangerous. It has been my observation that, if a muskrat finds available the sort of habitat having an attractive or livable combination of features, it will try to establish residence there. A wooded island in a marsh may have a family of horned owls (*Bubo virginianus*) and shores packed with tracks of mink and raccoon *(Procyon lotor);* the marsh waters may literally teem with snapping turtles *(Chelydra serpentina)* or with pike *(Esox)* or similarly carnivorous fishes; the surrounding mainland may be hunted over by more horned owls, minks, and raccoons, as well as by foxes *(Vulpes),* coyotes *(Canis latrans),* or dogs; yet, other things being satisfactory, the marsh is likely to support muskrats in abundance, bank- and lodge-dwellers alike.

On the other hand, old-time naturalists were prone to attribute the general scarcity or absence of muskrats in different regions to pressure of enemies, either human or subhuman. Among modern authors, Brander (1951) repeatedly emphasized the sensitivity of Finnish muskrats to disturbance or to the presence of predatory enemies.

Outright removal of entire population groups may be considered demonstrated by the results of annihilative campaigning against the muskrat as an introduced pest in the British Isles (Warwick, 1940). In parts of North America, the species may be unable to occupy otherwise livable habitat for reasons of intensive persecution (as in western irrigation districts) or utilization for food (as about Indian camps of northern wildernesses). Over-trapping for fur may, too, keep muskrat numbers locally or regionally depleted in some years, especially if the trapping is superimposed upon drought emergencies or suffered by populations already reduced through epizootics, environmental declines, or "cyclic" factors to levels from which reproductive recovery may be slow.

The favorite hypothesis of many people that the presence of alligators *(Alligator mississippiensis)* has kept muskrats from successfully colonizing muskrat-vacant parts of the southern states is to me unconvincing, especially in view of Lay and O'Neil's (1942) observations in Texas on the attractiveness of alligator holes to the muskrats. Giles and Childs (1949) also wrote, concerning the Sabine National Wildlife Refuge in Louisiana, that when this marshland area was first opened up in the early twenties for intensive exploitation of its fur resources, there were tremendous numbers of both alligators and muskrats.

This and related topics will be discussed later, but it may be said here that I have never *recognized* any evidence of subhuman predatory enemies exerting a primarily controlling influence on the muskrats of any *wide* area, anywhere in North America. What such enemies might possibly do in conjunction with emergencies or in a habitat decidedly submarginal for muskrats in the first place may not, however, be so easily dismissed. Predatory enemies would seem to be of far less importance to the population status of muskrats than would some of the nonpredaceous, as, for example, the ungulates, which through overgrazing and trampling may decidedly lower the habitability for muskrats of given marshes and streams. Anyone familiar with the properties of an ordinary midwestern sheep pasture or a lake-shore hog wallow has been introduced to ecological possibilities, from which he might go on to consider others, from denudation of vegetation by insects and plant diseases to eating of muskrat lodges by the caribou *(Rangifer arcticus)* of the tundra.

In generalizing, it may be said that the essentials of attractive muskrat habitats from sea level on up would include fresh to endurably brackish marshes and heavy stands of favored types of cattails, bulrushes, and other edible marsh emergents. In the absence of emergents, certain of the more nutritious submerged growths may furnish fair equivalents locally, though, as a rule, open expanses of water are not the best for muskrats. Food-rich waters would not have to be deep enough even to cover most of the marsh bottom to suffice in areas characterized by mild winters; and, in the northern states and Canada, shallow areas may be highly attractive — often fatally so in the end — for innumerable populations of muskrats during the warmer months. Muskrat marshes may range in size from those of thousands of acres down to small corners of lakes or bays, glacial potholes, seepages, wet gravel pits, and rush-lined pools in roadside ditches.

The better stream habitats are either rather well choked with vegetation or lying adjacent to cultivated grounds, notably the corn fields of the American Mid-West. Drainage ditches intersecting intensively farmed land may offer superb habitats for the species. Sluggish waters interconnecting lake chains or the oxbows or bayous of deltas and flood plains often are marshy. Swifter streams may show varying degrees of habitability in places where eddies occur or where scrub willows overhang mud banks or islands. Deep pools in the channels of intermittent streams and beaver ponds and floodings may afford passable retreats over wide areas otherwise deficient in muskrat habitats.

As we seek still lower in the scale of habitability, we find increasingly wide areas of high plains, deserts, mountains, or tundras, having fewer and fewer muskrats, and those muskrats are situated mainly in the better places, which in turn may be barely — and then not always — habitable for the species. Even in what may be classed as good "muskrat country," environment that grades off into the marginal and then into the uninhabitable may be occupied with varying success and duration. In years of substantial population overflows, the animals may be encountered in a remarkable diversity of places: in barnyard feedlots, under hog pens or corn cribs, in grain shocks and stacks, in city basements, at mouths of tile flows, in garbage dumps, in the banks of small brooks, along rocky lake shores, in the dry and weedy borders of marshes, in badger holes of hillsides. Their establishing themselves in such places should not be construed as reflecting either choice or necessity, exclusively. Some of it is surely due to fortuitous routes of travel taken by muskrats in combination with the strong inclinations the animals have for staying alive and the aptitudes of individuals for tolerating discomfort and danger to the extent that they can stay alive.

CONCERNING ORDINARY BEHAVIOR

The literature on 24-hour activity rhythms in cricetine and murine rodents reflects differences in opinion and seemingly opposite conclusions, much of which is resolved by Calhoun's (1945) experiments with cotton rats *(Sigmodon)* and meadow mice *(Microtus)*. Both of the latter have patterns of nocturnal activity that are subject to modification by meteorological or biotic changes in their environment. Calhoun noted similarities in the activity cycles of many nocturnal rodents, although each species shows patterns dependent upon innate morphological and physiological organization. Davis (1933), experimenting with the activity rhythms of *Microtus*, found a 2- to 4-hour rhythm in feeding activities as well as a longer 24-hour rhythm having a peak following sunset. There was a higher average activity at night. Meadow mice kept in total darkness for 24 days maintained both the short and the long rhythms. Johnson (1926) experimentally reversed the normal nocturnal rhythm in deer mice *(Peromyscus)* through manipulation of light.

These findings would seem basically applicable to the muskrat. In my professional trapping years in South Dakota, I covered my muskrat trapline every three to five hours, day and night, for the first few days of the open season, beginning December 1. The heaviest catches were taken in late afternoon and early evening, with daybreak also being a good time for trapping. More nocturnal than diurnal, the species may nevertheless occasionally engage in general activity throughout the daylight hours, much depending upon the weather. Quiet, foggy days of autumn may stimulate activity, and, on some days of this description, a large proportion of the muskrats resident about the bay of a lake or an open tract of marsh may be simultaneously visible. Sometimes, a sunny day will bring them out, as may an impending sunset combined with glassy waters. Irregularities in 24-hour rhythms of muskrats become pronounced during periods of crisis, evictions, or movements. The animals trying to winter on drought-exposed Iowa marshes may seldom come out of their subsurface retreats to feed except as temperatures moderate in midday.

Muskrat habitations are more or less familiar to North American outdoorsmen and have been variously referred to in both technical and popular literature. They may be classed mainly as lodges or burrows, with numerous variations of each.

Burrowing represents an elementary form of behavior in the muskrats as they lose their juvenile helplessness. At its simplest, it may consist only of crawling into or under loose vegetation. Digging or biting away of mud or vegetation may make a short burrow suitable for a temporary retreat of either young or old. Strangers passing through along a stream or following a lake shore may dig short, shallow burrows with underwater entrances and live in them from a few hours to a few days. These burrows may or may not have enlarged chambers above the water in the banks. Sometimes, the burrowing of such transients may be in dry earth, or they may enter parts of old burrow systems through holes dug in the bank. One sees much of this sort of thing about Iowa streams and marshes in April and early May at the height of the spring dispersal of population surpluses from wintering quarters.

The really complex burrow systems may be decades old, mazes of caved-in and renovated diggings, with old and new chambers at different levels, little holes and big holes, interconnected or not. They may penetrate the banks only for a couple of feet or so, in which case extensive lateral ramifications may follow the banks along the water's edge. Or, through settling of the surface of the land, the outlines of some ancient burrows may be traced almost in a straight line away from the water for 20 to 100 yards, or even farther, if they lead from the edge of a shallow slough up a low-gradient slope into the surrounding land. In extreme cases, as when the outlines of a burrow system may lead as far as 200 yards from the edge of a marsh, it would seem likely that such had resulted from gradual extensions of formerly shorter burrows as the marsh levels changed over the years rather than from the burrows remaining in use along their full lengths at any one time. Still, it is nothing uncommon in Iowa and eastern South Dakota to find currently used burrows going back 50 yards from the water, as they may radiate away from a pasture slough.

Lodge-building may be regarded as a behavioristic advance over burrowing. A lodge usually begins with a sitting place of muskrats, whether the sitting place be a floating rush raft or a mud bar or a solid foundation of almost any sort. In winter, many lodges may be put up that depend only upon the ice for support. Variations in lodge sites include boulders or piles of rocks or broken cement or dumped trash, leaning fence posts or rolls of wire out in the water, stumps and bases of trees, floating logs or boards or partly submerged wreckage of boats. A favorite place for building is the butt of an old lodge that has settled through decay and trampling by waterfowl or turtles until the whole remnant is down to or slightly below the surface of the water.

After their preliminary heaping of materials for the lodge, the muskrats usually hollow out a chamber and a passageway from beneath. The early stages of lodge-building merely provide, in effect, something to burrow into. Occasionally, the used entrances may be for a time through the side of a new structure at or above water level.

With the chamber and one or more plunge holes hollowed out, a new lodge may remain small, ultimately to be abandoned, or it may be built upon, worked over, and occupied for years.

Big lodges (which may rise up to about six feet above the water surface) may have multiple chambers, either separate from or connected with the others. In lodges having wide bases (eight or more feet in diameter) but flat, low tops — especially those decayed to a peatlike condition — rings of chambers connected by tunnels may be found encircling a solid center. The typical chamber in a typical dwelling lodge is centrally located, having a bed a few inches above the water and two or three plunge holes leading outward through the submerged base. If the lodge is situated on the marsh bottom, the tunnels may run through from a few feet to several yards of mud or peat before reaching open water. The simple chamber itself may be the only hollow part of the lodge above the water, or a passageway or two may lead to higher levels at which one to several separate or connected nests may occur. These nests, as well as the bed of the chamber over the plunge holes, may be lined with shredded vegetation. They are the places in which suckling young are likely to be kept. Transient animals frequently dig shallow holes for themselves for temporary refuge in the outer sides of lodges, the inner chambers of which are either inaccessible to them or "out-of-bounds" because of intolerant residents. Such blind nests may also be used with seeming regularity by some of the male consorts of females having young inside the lodges. On occasion, a litter of suckling young may even be found tucked away in an outside nest.

Not quite in the same category as typical lodges are some of the smaller ones built of fresh vegetation and in which litters may be kept in nests lying over the water. Sometimes, the nests may be roofed with solid, wet-heaped vegetation (usually of the easily-wadded types of submerged plants); sometimes the only upper covering of the young may be that furnished by the mother's body. Then, too, nests of coots or of diving ducks may sometimes be utilized, with or without alterations by the muskrats. Many young are born in these nests or on rush rafts or drifted debris, as well as in the chambers of the typical lodges or bank burrows.

Compared with lodge-building during the colder months, lodge-building in summer may be a rather minor activity. Old lodges may be repaired or have parts built or rebuilt to a variable extent, and sitting places and small structures may appear at almost any time during early summer and midsummer, but, from late summer on, there is a gradual increase of construction of both lodges and burrows. A great deal of this construction has been shown to be (from specimens of occupants examined) the work of subadults. Late summer lodges and burrows tend to be of the simpler designs. Then the lodges often have a chamber big enough to accommodate but a single animal, and lodges of this sort may appear by the hundreds in well-populated Iowa marshes from late July to frost. They were noted to appear about three weeks later, a thousand miles to the north, in the muskrat marshes of Manitoba and Saskatchewan. The first hard frosts stimulate burrowing and lodge-building alike, and, with the sealing of a marsh by thin ice, lodge-building may be conspicuously accelerated. After the ice comes, however, the medium-sized and large lodges have the capacious chambers and multiple plunge holes typical of marsh habitations occupied by groups of animals. These are the real winter dwelling lodges, and, unless something goes wrong, the bigger they are the more muskrats (up to a dozen or so) they are likely to harbor.

Lesser structures, in considerable variety, are also more or less characteristic of frozen-over muskrat marshes. One is the small "feed house," having room for a single animal to sit or float. The feed house may grade upward in size to the smaller dwelling lodges of usual types. It may or may not have a bed and may be a mere opening in the ice under a wad of pushed-up vegetation. Although the smaller of the typical lodges are often abandoned for the bigger ones as the weather becomes colder, feed houses and push-ups may show sign of use throughout the winter – which does not necessarily mean that the same ones must be used all winter, for new ones may continually be built where muskrats are present to do the building. The relative numbers of feed houses and push-ups being built seem to reflect, among other things, the degree to which the muskrats may be crowded. Where wintering densities of the muskrats have been reduced, as by moderate trapping, survivors may rather restrict their activities to the main lodges without attempting to keep feed houses functional.

Lack of rushy building material may result in some odd structures, especially after freeze-up. On open sloughs, muskrats may push quantities of coontail or like submergents out of a hole in the ice until a frozen column protrudes, to collapse during a thaw. They may cut a hole in the ice and build around it a thin, shell-like feed house, which, too, may collapse during a thaw. They may work on an ambitious scale and pile up a great mass of soft material (mixed with sticks, water lily rootstocks, clam shells, frozen fish, and a fair sample of the transportable items within reach) as large as a big lodge of rushes or cattails; and this may house a central basin of water as big as a wash tub – or it may be built on the same plan as an ordinary marsh lodge except on an icy foundation. Sometimes a whole string of connected feed-houses and push-ups may appear along an ice-heave or a wide crack, or about openings out from a set of bank burrows.

Food storage by muskrats may be linked with building routines to some extent. Normal storage is classifiable under two main headings: (1) the partly incidental storage of vegetation used in lining nests or for construction or repairs of habitations and (2) the obviously purposeful and selective storage of nutritious parts of plants, in particular duck potato and ear corn (Errington, 1941a). The foods stored incidentally, though commonly of only fair sustentative value compared with the better foods, may at times be quite important to wintering muskrats, irrespective of whether put away with storage intent or not. However, variable amounts of good foods such as bulrush rootstocks may be incorporated along with the upper parts of the plant during lodge building. Duck potatoes and ears of corn may be packed by the bushel in the chambers and ramifying blind alleys of some bank burrows. Duck potatoes may fill most of the chamber space and extensions thereof in certain marsh lodges.

Storage in marsh lodges is difficult to generalize about. I had long been aware of Eastman's (1902, pp. 239–40) description of storage of duck potatoes in lodges and had looked for evidence in thousands of lodges personally examined in Iowa and South Dakota, yet never found this sort of storage until the fall of 1948. Then, and for several years thereafter, storage of duck potatoes in lodges was found to be of general occurrence at Wall Lake, both in the shallow, muddier outlying sloughs and in some of the deeper central parts. The quantities stored varied from about a peck to more than a bushel. My view is that this represents a behavior pattern that may or may not become established locally. When it does occur, as at Wall Lake, it may be conspicuous, but, as a rule, I would say that marsh-dwelling muskrats of this region having continued access to good sources of food under the ice — or even when they do not have — seldom practice anything recognizable as deliberate storage.

In contrast with the year-around daily foraging on the part of most muskrats dependent upon foods occurring naturally in their habitats, the muskrats having access to ear corn stored in their burrows may sometimes hardly move about for weeks at a stretch in midwinter, especially when conditions outside the burrows are not conducive to foraging.

Muskrats are primarily individualists, each living for itself irrespective of the gregarious tendencies and seemingly unified acts that may be witnessed. Though the contributions of more than one muskrat to the erection of a big lodge or their concerted attack in driving out a common enemy such as a mink or a strange muskrat may have the rewards of teamwork, such acts may be more logically ascribed to a number of individuals having similar impulses and responding to them accordingly. Huddling for warmth or companionship on rush rafts or in chambers of habitations has its evident mutual attractions, and a considerable amount of what may be termed friendly behavior often may be seen during those seasons of the year when the animals are most disposed to be tolerant toward each other. The ordinary Iowa muskrat does not seem to object to physical contact or proximity of acquaintances between late summer and late winter. A couple of months in late summer and early fall represent a period of minimal friction, when intermingling of strangers in established populations is least likely to be attended by fighting. Strangers, however, may get into trouble with residents at practically any time of year, but are most likely to do so during the breeding months.

But, as individuality is always showing up, no absolute generalizations on social relations in muskrats are permissible. Some adults remain visibly placid in their attitudes toward neighbors, young or old, even when they themselves may be suckling young. Vicious intolerance toward their fellows may be displayed by others at all seasons. Variations in irritability may, in addition, reflect the health or comfort of individuals or may be among the apparent manifestations of that as yet inexplicable phenomenon known as the "10-year cycle," to which a separate chapter will be devoted.

Generally, despite much overlapping of movements, the foci of activity of breeding females occur 20 to 40 yards or farther apart, though I have found them closer together and know that, on rare occasions, the helpless young of two different females may even be kept in the same lodge or burrow. Visiting young are sometimes tolerated in, or in the vicinity of, nests having suckling young, but my observations indicate that they often are not tolerated, nor are the previously weaned young from the same mother. The large-scale killings of weaned young by other muskrats known to have taken place on crowded marshes have been largely traceable to attacks by suckling mothers, and the victims have included the earlier-born progeny of those same mothers as well as young intruders from elsewhere. Nor do weaned young invariably need to approach the currently suckling young to invite attack. Some observed mothers seemed to kill or try to kill any free-living youngster that came within reach, anywhere.

Hostile responses of suckling mothers toward weaned young notwithstanding, the mothers may still not be especially zealous guardians of their helpless offspring. The new-born may be left scattered around on tops of lodges and rush piles – some until they die – and suckling litters may be transferred from lodge to lodge, often in an only partly responsible manner. Litters may be split up in the course of the transfers and the component parts kept in separate nests, and it does not always follow that those left in a particular place ever will be revisited. The casual treatment by a mother muskrat of her own small young under routine living conditions is in accordance with the increasing cheapness of life on a muskrat marsh as populations build up. She seems to be satisfied if she has *some* of her currently suckling litter about her long enough to wean. Once weaned, the young look after themselves as well as they can.

During her whole maternal experience, the mother rarely does anything incompatible with her own living as an individual. She may stop to eat while gathering together scattered young, despite their weary complaining in the rushes near by. She takes much of her motherhood as matter-of-factly as she does anything that ordinarily comes to her life. It is the exceptional muskrat mother that makes any recognizable effort to defend the young against humans opening a lodge – though, were she herself cornered, she could be counted upon to attack anything in her own defense. Even her murders of luckless or indiscreet young (some of which I have had the fortune to witness at close range) show little of excitement unless it were during the approach and actual biting. After swimming away from the body of a young one that she had killed, she may as likely as not start eating.

The behavior of the male follows much the pattern of the female, to the extent that a muskrat is a muskrat. As adults, the males of the Iowa observational areas tended to be more tolerant than the females toward young during the breeding season. At other times of the year, the animals having patently bad dispositions appeared to be of one sex about as often as the other. Instances of males undertaking simple care of suckling young orphaned by deaths of females were observed in the course of intensive field studies, and it is well known that both members of a pair may work together building or remodeling a lodge — all of which conforms to accepted criteria of monogamy. Lavrov (1933a) observed that the adult males took a regular part in the rearing of the young from about the nineteenth day on to independent stages.

Sexual relations in muskrats may show sufficient promiscuity, on the part of free-living and captive animals alike, to discourage broad statements as to monogamous habits. A concept of a loose monogamy would seem most consistent with reality. Glimpses that I have had of natural mating in the species were of males being aggressive and persistent and of females being passive or coy. The females continually made some effort to avoid contact with the males, without appearing to be excited even when caught and held by the males' teeth. One female that had been mounted sixty times in seven minutes finally turned on the male and fought him off, biting him about the face.

RESPONSIVENESS TO EMERGENCY CONDITIONS

The purpose of the following will be to amplify what has just been presented about muskrat behavior, as such may be modified by the floods, droughts, cold weather, food shortages, or sociological crises to which the species may at times be subject. Some duplication of, and overlapping with, what already has been written appears unavoidable, but this is in part defensible on grounds of conveying to the reader a better idea of responses to be expected from muskrats when beset by the more urgent problems of staying alive.

Floods are part of the ecology of muskrat ranges over much of North America. The muskrats may often be affected indirectly through killing of important vegetation. Or, sudden or sustained rises in water levels may create emergencies that must be met at once. Bellrose and Brown (1941), investigating bottomland lakes of the Illinois River Valley, reported that greater differences in the abundance of muskrat houses per acre were due to changing water levels rather than to variations in type of marsh vegetation.

Bellrose and Low (1943) observed pronounced local differences in the fortunes of muskrats during flooding of Illinois River lakes in the fall of 1941. Water levels rose several feet in early October and stayed high for several weeks. On their Douglas Lake area, most of the river bulrushes were completely covered by up to two feet of water, and, where there had been at least 1,234 dwelling lodges the previous year, there was scarcely a lodge left. Most of the lodges rose with the flood waters, to become mere piles of floating vegetation. Many of these came apart under the buffeting waves, and the authors counted averages of over five muskrats sitting on rafts and floating lodges. Many sat in buttonbushes, and as many as eight were observed stacked, one on top of another, in crotches of large willows. On the Rice Lake area, the lodges were also demolished by waves, and the debris from wrecked lodges formed a mat of vegetation two to ten yards wide and a half mile long. Nevertheless, relatively few animals (averaging 1.1 per remnant of lodge or raft) remained exposed, for hundreds of acres of flooded bottomland timber lay behind the line of wrecked lodges, and this afforded the muskrats much better emergency refuge than at Douglas Lake.

Bellrose and Low's muskrats sought, where possible, to remain on the tops of their lodges during the flood crisis. Next, they apparently preferred floating rafts of vegetation and, last, branches of willows and buttonbush. Building and rehabilitation activities were carried on by the muskrats, and large numbers of lodges and rafts were built around the branches and limbs of trees, as well as on foundations of logs, boards, boats, and duck blinds. As the water receded, the muskrats continued to add to the bottoms of the lodges that had been built in trees at the height of the flood, until these took on the appearance of multiple-storied structures, often six feet or more in height as they were held cradled in the trees. After further recession of the water in early December left their emergency structures suspended, the Rice Lake muskrats moved out to the beds of river bulrushes and built their third set of lodges. In contrast, only a few of the Douglas Lake muskrats moved back into the center of the marsh from the levee where they had taken refuge.

If comparison of Bellrose and Low's observations be made with those recorded elsewhere, a basic similarity in responses of muskrats to floods becomes evident, more or less irrespective of geographical or subspecific differences — see, for example, photographs and text in Arthur's account of the Louisiana muskrat (1931, pp. 201, 215, 219, 297, 311–12). Muskrats of the vast wetlands of Manitoba and Saskatchewan personally observed in 1948 resorted chiefly to willow growths during high water periods, whether such meant building lodges and raising young in the willows when floods continued all spring and summer or merely sitting out a rise from a wind tide off a big lake. Iowa observations have brought out the same tendencies of flood-evicted muskrats to take refuge in fringing willows of streams, or on floating or protruding objects (Errington, 1937a). Nests on top of stumps or woven into brushy thickets may not be as satisfactory as typical marsh lodges or bank chambers, but young are kept and raised there. The flooded bases of hollow trees or cavities above the water under root-tangles may, when reinforced or built around by the muskrats, be fair engineering equivalents of the usual types of lodges.

If lodges remain attached to marsh bottoms, muskrats may burrow through the tops as the water rises and then later plug the holes as the water recedes. Their behavior in bank burrows has its comparable aspects. In the burrows, the animals often dig upward until, just before the water goes over the banks, they lie in the upper parts of the openings, with heads or nostrils out of water, bobbing up and down if alarmed. If the water covers the banks, the animals of course must emerge, and then they have to do something else.

Floods in cold weather may impose terrific crises. Squaw Creek in central Iowa was in a very high flood stage in late January, 1935, and the temperature dropped nearly to 30 degrees below zero Fahrenheit. The creek valley turned into a freezing lake, affording little refuge for evicted muskrats anywhere (Errington, 1943, p. 883). The affected population was almost annihilated. Under lesser extremes, as during mild weather, the animals may survive simply by sitting in the riverbank willows. Or, if forced for a time to live about a snow-covered countryside bordering flooded stream valleys, they may improvise nests, retire to land holes and eat what they can find after the manner of ordinary winter wanderers — though subject to the dangers and discomforts that beset such wanderers. If the animals succeed in enduring a crisis without leaving their familiar locality, they stand a good chance of regaining their old quarters as the water goes down. Often, the only adjustments forced by the surface waters of winter thaws or rains are the gnawing away of more chamber space higher up in the lodges or burrows, repairing of parts of retreats exposed through melting, rehabilitation of abandoned lodges, or the erection of new lodges or feed houses on the ice — all of which muskrats may do readily under ordinary north-central conditions.

It is not clear how well muskrats may find food by diving in muddy flood waters, but the fact that so much feeding on the tender bark of trees and shrubs occurs at such times indicates that foods concealed by flood waters must be largely unavailable. Foraging by flood-evicted animals on or near land is relatively easy when green summer growths abound, though a winter or early spring fare of dead weed stalks and miscellaneous coarse organic matter may only delay starvation unless supplemented by ear corn, live roots, or other of the more nutritious foods. Sometimes, muskrats may even attempt to eat dead wood. The versatility of the species in feeding (Errington, 1941a) is unquestionably of survival value during emergencies of this kind.

Bellrose and Low noted a correlation between intraspecific strife and insecurity of flood-exposed muskrats. Not only were adults observed to fight over the possession of refuge sites but kits were also frequent victims of attacking elders. And, of course, homeless and vulnerable muskrats fell prey to avian predators and other flesh eaters that were in a position to take advantage of them.

Gross dissimilarities notwithstanding, drought crises are comparable to those of floods in that they similarly upset the living routines and security of populations. Yet, for a species as dependent upon water as the muskrat, droughts have singular potentialities for deadliness and may force special adjustments (Errington, 1939a).

As entrances to their lodges and bank burrows become exposed by drought, muskrats usually engage in deepening operations. These may take the form of simple excavations or of complex systems of channels radiating away from lodge or burrow entrances. Accelerated digging may be noted in summer at about the time when residual puddles assume the consistency of liquid mud, and newly-constructed lodges may be of plastered mud and vegetation. In building a new lodge on exposed marsh bottom, muskrats may simply cut away the most convenient vegetation and pile it in a cleared space. The resulting structure may cover previously existing channels and burrows, but often the digging is done later as the structure is hollowed out and otherwise modified for use. Lodges may be similarly built in corn fields, except for the use of cornstalks and field debris instead of marsh plants as building material.

Digging in response to drought exposure is also stimulated in late fall by heavy frosts, even though comparatively large amounts of water may be left in the entrances. Digging at freeze-up is especially apt to take place on an extensive scale. Mud and peat may be piled at the ends and sides of ramifying channels. Wide, straight channels may be cut down through the mud, extended for yards, then used no more. Pockets and blind burrows may be dug from the surface and enlarged underground amid the rootstocks of water plants. Deepening of passageways may progress to a depth of a couple of feet below their original levels, or new sets of burrows may be dug under the old burrows as the water continues to go down. During periods of winter drought, old lodges may continue to be favorite retreats, but often the original chambers are abandoned in favor of new ones hollowed out below. The muskrats may enter and leave the dry lodges through holes at the lower edges or through tunnel openings close by.

Sinking of the frost line as winter advances may bring about droughtlike conditions under the ice even when plenty of water may be present at freeze-up. In many places between the northern lake states and the Barren Grounds about Hudson's Bay, ice accumulates to a depth of four or five feet, and late winter thicknesses up to three feet are nothing so very unusual for Dakota lakes and marshes. Less extreme thickening may cause muskrats to continue deepening the channels leading to chambers — or to excavate completely new burrows beneath the shallower ones of fall and early winter. The animals also take advantage of air spaces in stratified ice to improvise subsurface living quarters, plugging and reinforcing with mud and vegetation much as they would higher parts of burrows or lodges. Disappearance of unfrozen water beneath the ice may occur either as a result of natural drainage or human manipulation, as through the lowering of water in storage basins. Then, networks of dry or frozen or merely moist runways concealed from human view by ice or snow may be the sites of muskrats passing back and forth, digging and feeding and living as they can.

Muskrats may live fairly well on a marsh bottom without much unfrozen water as long as they have the protection of an ice covering overhead and an ample and accessible food supply, such as cattail or bulrush rootstocks. In sloughs dominated by water lilies, coontail, and other shallow-rooted submergents and surface plants, the food supply may become so encased in ice as to be quite unavailable to muskrats by late winter. Entire local populations may find themselves in a state of crisis within a space of days. There may be unfrozen mud underneath, but, if it contains no food to reward digging, the muskrats may be as much compelled to undertake surface foraging or wandering as those evicted outright by full exposure of the bottom through drought.

The established way of living of muskrat populations may have a pronounced bearing upon how they meet the problem of winter feeding in dry or nearly dry habitat. Such marsh-dwelling muskrats as habitually obtain their food from the marsh largely as required each day may find themselves confronted by crises exceeding their immediate adaptations if they attempt to continue their feeding routines under drought conditions. Conversely, the populations that engage in storing may winter at high densities in quarters that are restricted and nearly waterless. Much outside activity of muskrats in winter is plainly due to newcomers establishing themselves too late in the fall to make adequate preparations for cold weather. On occasion, animals are encountered living in corncribs, corn shocks, and other food-rich land retreats, but I have seldom found evidence of such animals successfully wintering in areas having rigorous winter climates.

RESPONSIVENESS TO PHYSICAL ATTACK OR DISTURBANCE

In responding to physical attack or disturbance by predators, the muskrat may show considerable geographic variation. Mention has already been made of the sensitivity to disturbance reported by Brander (1951) for muskrats in Finland. The Louisiana muskrat is said to be both more wary of traps and possible enemies inhabiting the deeper waters (Arthur, 1931, pp. 250, 286; Lynch, O'Neil, and Lay, 1947) than any muskrats that I have ever observed on northern areas.

It may be remarkable what north central animals can tolerate in the way of disturbance, a good deal depending upon alternatives and psychic conditioning. Dogs may dig out burrows, minks may penetrate lodges on a large scale, horses and cattle may trample and hogs may root on muskrat marshes without visibly affecting the status of well-situated muskrats that are in a position to adjust. Nevertheless, disturbances of muskrats living under handicaps may have serious consequences.

Drought crises underlie some of the most decided reactions to disturbance that we see in the north central region. As an extreme case, mass use by livestock of remaining waterholes may be accompanied by so much trampling that resident muskrats leave to take their chances elsewhere, usually to embark on a brief career of lethal wandering. As another extreme case, muskrats may long persist in a dry marsh but with attachments to home ranges so tenuous that practically any disturbance — flattening of lodges by livestock, digging by predators or scavengers, opening by human investigators — causes them to leave, likewise to wander and probably to die as wanderers. After disappearance of the surface water, Iowa muskrats seldom remain on a marsh if their lodges are opened for examination, although, with favorable water levels prevailing, they might well repair their lodges overnight. It is no big job for muskrats completely to rebuild lodges if they are so disposed and have access to materials with which to do it.

Intrusions into muskrat lodges by minks may be notably subject to misinterpretation. Minks may enter through the sides and tops of occupied and unoccupied lodges alike. Openings in occupied lodges may be promptly plugged by the resident muskrats, whereas mink holes in unoccupied lodges may remain conspicuous indefinitely. It is also true that some muskrat habitations appear to be abandoned by the muskrats directly because of the activities of minks, but this need not signify any real disadvantage to the muskrats. Muskrats may abandon the less desirable lodges opened by minks much as they may abandon, of their own volition, loosely-built or shallow water structures with the coming of midwinter cold. Well-established muskrats, with a variety of alternative living places to choose from, may withdraw from some without risk. As long as their adjustments in such ways fall within the ordinary range of adaptability of the species, the muskrats do not seem to be forced to retire before the minks to the point of critical disadvantage. They can demonstrate an unquestionable ability to maintain themselves securely in the more important dwelling lodges.

Despite the general rating of the mink as the North American muskrat's supreme predatory enemy (Errington, 1943; 1946; 1954b), the two species often live in close proximity. A complex burrow system may be in use at the same time by both minks and muskrats, each species obviously being aware of the other and adjusting its living routine accordingly. Muskrats may even rear their young in lodges or burrows, of which some parts are regularly used as mink dens. In short, our north central muskrats may accept the presence of many enemies or potential enemies without undue excitement.

I have repeatedly watched muskrats approaching big snapping turtles in pools, on lodge tops, or in muddy marsh bottoms, and about all that the muskrats did for safety was to keep out of striking distance of the turtles' heads. Our Goose Lake study area had in some summers actually hundreds of snappers per acre visible at once in parts covered by shallow water, and, as far as I could see, the resident muskrats did not allow the turtles to interfere with their own way of life.

Another marsh had conspicuous numbers of northern pike in the midst of an ascending muskrat population in the early thirties, but I never saw the muskrats pay any particular attention to them. Great horned owls have nested near and hunted some of the best muskrat areas personally studied in the north central region without appearing to force muskrats into noticeable departures from their usual behavior patterns. On the other hand, muskrats may avoid solid land when such is diligently worked by canids.

If muskrats can be said really to hate any living things, the examples coming to my mind are all either of strange or unwelcome muskrats or of minks, either of which may be met more than half way, at least some of the time. Attacks, individually or concerted, by muskrats upon minks are among the interesting phenomena witnessed by people having the luck to be on the scene and the judgment to keep quiet. Dr. Maurice W. Provost turned over to me the following field notes taken from 6:50 to 7:15 P.M., September 10, 1941, from northwestern Iowa:

> Two rats watched at dam, Mud Lake. One became engaged with a mink in the rushes; the splashing was over in 10 seconds, each animal going its way. Shortly afterwards, directly at the dam, the two animals met again. This time the muskrat lunged at the mink. In a few seconds the tussle was over and the rat was swimming away. He swam two or three yards away then turned around and again pounced on the mink. This *third* struggle was very short, maybe 7 seconds. The mink disappeared and was not seen again. The muskrat nonchalantly swam away.

Bruce F. Stiles, late Director of the Iowa State Conservation Commission, described (letter, May 29, 1948) another case of muskrat aggressiveness toward a mink:

> On the morning of October 23, 1947 . . . as I leaned motionless against a tree waiting for daylight . . . I saw a mink come hopping along the low shore toward me.
>
> About twenty feet out into the water from where I stood was . . . an accumulation of brush where the day before I had noticed two muskrats sunning themselves. As the mink reached a point opposite this brush pile, he jumped out into the water into what would be a depth of probably 3 or 4 inches. Just at this time a muskrat emerged about 3 feet from the mink and dashed toward him in a menacing manner. The mink quickly hopped to one side but continued in the water whereupon two more muskrats appeared near him.
>
> The mink swam out into the water whereupon additional muskrats put in their appearance causing the mink to retreat with considerable haste to the shore. . . . He finally ran off down the shore in the direction from which he had first come and disappeared from my sight. Individual rats appearing and disappearing in quite rapid succession made it difficult for me to count, but I am of the opinion that there were seven muskrats involved. I did not actually see a rat come in physical contact with the mink although it is possible that they did so.

For all of the viciousness with which a grown muskrat will fight when at bay, or when bitten or seized by an enemy, attempts to break away to run or dive after receiving punishment are of common occurrence. The more urgent retreats following fights with other muskrats doubtless reflect social subordination, at least in part. Allee's (1942) demonstration of the role of psychological background in the fighting prowess of laboratory mice could well be thought of in terms of muskrats. Nice's (1941) generalization in her review of vertebrate territoriality that familiarity with an area enables an animal to be dominant there may be applicable not only to intraspecific but also logically to interspecific relations where antagonists are evenly matched.

With behavior patterns in many ways well stereotyped, the muskrat is not completely an automaton. It is possibly of average intelligence among rodents, often behaving haphazardly and often, if anything unusual happens, seemingly unable to keep its mind on more than one matter at a time. But it can learn to follow safe living routines, and the critical reader should not be far wrong in regarding it as a species blessed with a certain earthy practicality valuable in meeting day-to-day problems. It can and does live by the millions and contributes to the geographic features of large areas over the earth.