Chapter 3

Territoriality, Home Range, and Movements of the Muskrat

MOBILITY AND TENDENCIES toward fixed residence naturally have an important bearing on the daily life of a species as well as on the strength and effectiveness of its pioneering thrusts. On the whole, these phases of behavior have been better studied in birds than in mammals (Nice, 1941; Errington, 1946); but, among mammals, small rodents have become the subjects of a related literature that is already so large as to make a review of even the findings on the muskrat's nearest relatives among the microtines impractical for this chapter.

Most modern studies of free-living small rodents emphasize the limited sizes of areas comprising individual home ranges, although wider movements may be forced by emergencies or population pressures. The great overflows of the Scandinavian lemming *(Lemmus lemmus)* are surely in remarkable contrast with the habits of those members of the same species that maintain themselves in nearly sedentary residence about as other mouselike rodents do (Elton, 1942, pp. 226–30; Wildhagen, 1952).

BACKGROUND OF DATA FROM MARKED MUSKRATS

During the summers of 1935 and 1936, 463 muskrats were experimentally marked with serially numbered alumninum tags, and the salient results were tabulated (Errington and Errington, 1937); 122 of these tags yielded data of some sort. Of 214 young similarly tagged from 1937 to 1943 (including 23 also toe-clipped) and of 65 that were toe-clipped only, 18 were again handled or heard of at intervals sufficient to be informative (Errington, 1944). From 1944 to 1952, 788 more young were tagged and 9 adults or subadults toe-clipped; and, of these, 34 of the tagged and 3 of the toe-clipped were later recovered or studied further. To sum up, we have "returns" on 177 of a total of 1,539 animals thus far marked in central and northwestern Iowa. Data

were likewise obtained on the behavior of 6 individuals that were recognizable without question (though they had not been deliberately marked) as well as on many other individuals that were distinguishable in life on the basis of their isolated residences, their appearance and idiosyncracies, and the responsibility that they showed in their care of marked litters.

Specific records of movements at stages of early independence were obtained for 36 of the marked young, and only 3 of the records were for distances exceeding 50 yards from the lodges where the tagging had been done: 2 at 60 yards and 1 at about 125 yards. One partial albino was seen in company with mixed young and adults on July 13, 1935, and on several days thereafter, finally to die in emaciated condition 200 yards distant at an estimated age of two months. In the case of the albino, the unusual movement could well have been due to the animal's illness.

The muskrats marked while very young and recovered as subadults, months afterward, showed some differences in mobility that varied according to their circumstances. Some could not have moved far without inviting trouble from other muskrats. Three individuals, living in natal localities bounded on all sides either by unfavorable habitat or by home ranges or territories occupied by other family groups, were tagged and released in May and June, 1936; these were all taken in the following November and December at a mean distance of 70 yards from the tagging sites. On an overcrowded marsh, an undernourished one tagged on June 22, 1944, was taken near the same place on November 10.

The following marked young muskrats, although not subject to any special hazards of intraspecific strife, had drought conditions to contend with. One, toe-clipped and released on May 30, 1940, was trapped about November 20 in the same locality, after drought crises in both summer and fall. Another was probably killed by a great horned owl *(Bubo virginianus)* during a drought exposure; it had been tagged on May 23, 1947, on a part of a marsh that went dry, and its remains were found on top of a lodge 70 yards nearer water. Four of another litter tagged on May 23, 1947, died within a few days of each other in mid-September; of these four, three died at a lodge about 20 yards from the site of tagging – one from hemorrhagic disease and two (likely diseased also) from attack by a dog. The fourth died of disease but on the shore of another marsh three miles away, probably a couple of days after leaving its natal locality. One other marked subadult, living in the drought-exposed corner of a marsh in 1936, evidently wandered away in late summer and fall, to be trapped in November along a drainage ditch four miles away.

Thirty-eight tagged animals recovered as subadults were residents of relatively underpopulated marshy habitats or of a linear or elongated type of home range that usually permits greater freedom of movement without trespassing on the property rights of other muskrats. Ten tagged during the breeding seasons of 1935 and 1936

were recovered at a mean distance of 270 yards; three, in 1938, at a mean distance of 410 yards. Then, in 1943, one animal was recovered from its natal locality, and six others (all members of a single litter) were trapped more or less together in a small area, 100 to 150 yards from the site of tagging. Of 18 tagged, 1950–52, 13 were trapped in the fall in the vicinities of their spring and early summer tagging sites; two about 200 yards distant; one at 260 yards; and the last two, at estimated distances of 825 and 1,000 yards.

Records for individuals tagged while young and retaken when well into their second calendar year of life show both continued local residence and substantially greater movements. As an extreme case, an animal aged between 500 and 550 days was killed in early winter 1936–37 in a farmer's hog house 21 miles from its birthplace. Three tagged as young animals on a wildlife refuge, May and June, 1936, were trapped on neighboring marshes in November, 1937, from two and a quarter to three and a quarter miles from their sites of tagging. Other tagged muskrats were said to have been similarly caught, but the trappers did not report them for fear that possession might have been construed as evidence of poaching on the refuge; these muskrats, according to the "grapevine," were also caught within a four-mile radius of where tagged. (It should be mentioned that muskrats leaving this refuge would be unlikely to find attractive bodies of water much nearer than those at which the above were finally trapped.)

Among the older muskrats remaining on fair-sized marshes on which they had been born and marked, a storm or disease victim was found on April 25, 1937, in the central vegetation and about 800 yards from its tagging site of May 27, 1936; it was judged, from what scavengers had left, to have been a sexually active male. Two mature females, tagged as young in 1938, were recovered in late December, 1939, at about 375 and 950 yards from their birthplaces; and, of the two, the one moving the farthest had passed through its first breeding season without conceiving, whereas the other had placental scars of three litters. Another mature female, tagged as a young one in May, 1950, was trapped very near its tagging site in late November, 1951. An adult male died of disease, April 29, 1952, about 640 yards from where, at the age of 13 days, it had been tagged on May 17, 1950.

A second partial albino young for which we have field records was born about June 14, 1936, and, when last handled on June 30, was somewhat undersized, though the sole member of a litter. On April 25, 1937, a rather small — for that time of year — partial albino was seen very close to the above site, in company with an adult of normal appearance. No other examples of albinism were seen on the marsh in 1936 and 1937, so the observations for those years doubtless related to the same individual. In the summer of 1938, a lodge traceable to what could hardly have been other than this same partial albino (a female) was erected about 450 yards from the old home range; and, in this lodge, the third litter of the season (seven born on August 16) included two partial albino young.

Manifest albinism is rare among our north-central muskrats, and all four cases that I have seen and handled were from one marsh (Round Lake) during the years 1935–38. At least 1935, 1936, and 1938 were years of such intensive field studies that the likelihood of other partial albino young being present but escaping notice would seem to be remote. Hence the peculiar coloration of these young should afford a means of recognition even when they could not be approached sufficiently close to permit reading of tag numbers.

Data on the movements of a stump-footed muskrat illustrate the tendency for solitary individuals to spend a few days in a given area before moving on. The animal left its distinctive tracks along a little less than a mile of a creek during the night of March 24, 1939; from then to March 29 it confined its activities to about a third of a mile of stream border, mostly within the stretch covered on the night of March 24. It was still around by April 10, but no sign of it could be found thereafter, irrespective of careful and repeated search in five sections of land upstream and two sections downstream.

An example of late winter and early spring fidelity to a home range was accidentally obtained in 1943. On February 4, I wished to destroy a covered nest that had been built on the ice of a flooded ditch, in order to learn from its subsequent repair or lack of repair whether a muskrat still lived in it. The nest was out of my reach from solid ground, so I scattered it with two light charges of number five shot from a .410 shotgun, taking off part of the top with the first charge as a warning to any possible occupant. By the time of my next visit, February 8, the nest had been rebuilt, and signs of an animal clearly in residence were seen on February 23. On March 14, an unbred female was found killed by a dog on the ditch bank at this same site, and the victim had as a marker a single number five shot imbedded under a healed wound on the skin of its back.

On April 19, 1944, a newly-mature male was captured uninjured as a transient, toe-clipped, and experimentally released at a pool nearly three miles away. At the time, the pool was muskrat-vacant, but muskrats had lived there until trapped out in the fall of 1943, and a set of burrows remained in attractive condition for muskrats. The toe-clipped transient was put directly into a partly-covered chamber of a burrow, and ear corn was dropped in after it to give it some incentive for staying. Its distinctive tracks were laid down in this vicinity until about the middle of July, after which the burrow appeared to have been abandoned.

Two other toe-clipped animals yielding data were precariously situated small subadults living in a newly excavated and foodless gravel pit pool lying adjacent to a creek. These probable litter mates moved into the gravel pit in the fall of 1947 and were first noticed foraging in a corn field on November 16. One or the other of them left the gravel pit in quest of food at such times as the weather moderated, but with poorer success as snow and ice accumulated in the corn field. By mid-February, 1948, both were extremely weak and

underweight when handled, and one was partly blind. One was found dead on February 19, with a good representation of liver lesions from hemorrhagic disease. The partly blind one outlived the other; its tracks were seen on February 23, though it probably died soon after.

The stream-side activities of a big yellow adult were traceable for several months during the drought of 1937. In late August and early September, there were other muskrats living within a half mile of the burrow system occupied by the big one, but, even then, the signs of this animal were becoming characteristic. By mid-September, the creek bed was devoid of other muskrats for a straight-line distance of about 1,200 yards downstream, and, by the end of the month, an equal distance upstream. By late October, a three-mile stretch was depopulated of all known muskrats except the big one. A few days after the trapping season opened on November 10, no known muskrats except the big one occupied a stretch of more than seven miles of the creek. This elimination of other animals through drought and fur trapping greatly simplified the problem of identifying the remaining muskrat, not only from its tracks and its appearance when seen but also from its general behavior and feeding routines. Moreover, field conditions were most favorable for repeated observations.

The big yellow one had been first fairly well recognized as an individual in late August, 1937. Though living in a set of dry burrows and raiding the adjacent corn field, it was beginning to travel back and forth between its burrows and a large pool about 200 yards upstream. From September 5 to 15, the animal used the burrows, raided the corn field from the same place as before, and commuted upstream. The animal retired to the upstream pool shortly after September 22, to raid the corn field from there, over a new route. Water returned to cover the creek bed in mid-October, but the muskrat worked out from its upstream quarters until late November, when it returned to its old burrows and renovated them. From November 30 to March 3, 1938, all foraging and other activities were centered about the old burrows. By March 19, the spring dispersal was underway, and no further sign indicating the presence of this animal was seen.

Elsewhere in Iowa, Snead (1950) carried on an extremely detailed marking and retrapping study of muskrats of all ages on the Mississippi River near Lansing. (See also Appendix H.) I know of no published break-down of his findings. I do know, however, from conversation with him, that his muskrats tended to live in very restricted home ranges, about like those of central and northwestern Iowa. This is also the impression that I have concerning the unpublished tagging data of Dr. James R. Beer for a marsh near Madison, Wisconsin.

The program of live-trapping and tagging of muskrats at Horicon Marsh by the Wisconsin Conservation Department included litter-tagging of 4,158 young muskrats (Mathiak and Linde, 1954). Of 149 young animals litter-tagged in 1949 on a 95-acre refuge area, three (members of the same litter) were trapped in November just outside of the refuge line. Five were taken as animals wandering on the ice, in-

cluding two still wandering within the refuge boundaries. No first-year recoveries from 154 litter-tagged young were reported from trapping outside the refuge in 1950. Trapping in the refuge itself in the fall of 1951 and the spring of 1952 accounted for 30 of 106 litter-tagged in the summer of 1951. Six of the total of 409 litter-tagged on the refuge were taken in their second year, off the refuge, but mostly within a half mile of the boundary; probably most of the six were animals that had left the refuge during the spring dispersal following their year of birth.

In his study of muskrats tagged on a part of Horicon Marsh that had been ditched experimentally as part of a management project, Mathiak (1953) found most distances between sites of tagging and sites of recovery to be less than 400 feet. Of 49 winter recoveries of animals tagged in the fall of 1951, 27 were taken at sites of previous live-trapping. However, he recorded three members of one litter trapped over a mile away, while no members of that litter were trapped in the experimental ditches. He found little evidence of more than local movements in 1949 and 1950, when the muskrat densities were relatively low, but, in the spring of 1952, with a greater residual population in the ditches, greater movement away from the ditches occurred. In early April, 1952, five muskrats were trapped at probable average distances of over a mile from the ditches where they had been originally tagged.

This author also found a relation between amount of movement and the distance that experimental ditches were spaced apart. Of 14 recoveries of animals tagged, 1949–51, in ditches 400 feet apart, 12 were taken within 300 feet of tagging sites and two within 700 feet. Of 43 from ditches that were 200 feet apart, 35 were taken within 200 feet of tagging sites, 7 more within 400 feet, and one within 600 feet. Of 49 from ditches 100 feet apart, 37 were taken within 200 feet, 6 within 400 feet, 5 more at distances between 410 and 800 feet, and one between 1,310 and 1,400 feet. Then, of 53 from ditches only 50 feet apart, 25 were taken within 200 feet, 10 within 600 feet, and 8 more at distances between 710 and 1,800 feet.

Dorney and Rusch (1953) found that, of 348 young marked during the breeding season of 1950, 56 were recovered during the early November trapping, including 38 from within 300 feet of where marked. In some cases, part or all of a litter appeared to have moved as a group to a new fall location. Dorney and Rusch plotted the recovery points of 31 members of 15 litters showing movements exceeding 300 feet from their original lodges, and 12 of these members had moved at least 1,000 feet. Field observations in combination with the marking data suggested that the wider movements could be explained in terms of the attractiveness of a part of the marsh that was occupied by a thinly-distributed resident population.

On the Sand Lake National Wildlife Refuge in northeastern South Dakota, Aldous (1947) obtained data from recaptures of 367 marked muskrats of different ages. Some of the travels of his animals were

accounted for by movements from bank burrows to lodges. About 70 per cent of the recoveries (mostly in the winter following the summer tagging) were under 55 yards, or within the limits of the daily feeding radius. About 20 per cent were from 60 to 165 yards, and the other recoveries were strung out to about a half mile, with one being at 1,100 yards.

Sather (1958) carried on an intensive two-year (1949–51) tagging and trapping study of the muskrats of a Nebraska sandhill marsh. In his marking and retrapping of hundreds of animals, he found summer, fall, and most winter movements confined to a radius of less than 100 yards of the marking sites. He also found, after the spring dispersal, that the adult females were more likely to maintain their original home ranges than were the males.

In the course of a Missouri study of pond and stream muskrats, Shanks and Arthur (1952) live-trapped, marked, and released 183 animals (103 in 1946, 69 in 1947, and 11 in 1948). These were retaken a total of 298 times. Only 15 of the retakes gave records of wandering beyond the limits of the original home ranges, and, among these, 11 were movements from one pond to another (a maximum distance of a half mile), one from a pond to a stream (a distance of at least two miles), and one from a pond to a pool in an intermittent stream. Muskrat populations were comparatively stable during summer and winter, with periods of movement occurring primarily in spring and fall.

Of 40 ponds visited by Shanks and Arthur in the summer of 1946, 12 contained resident adult muskrats with young; but, after the fall dispersal, only three ponds contained resident adults with their young, one pond contained an adult female and a young male, each of five ponds contained a young male and a young female, and each of two ponds contained a young female. All of the three ponds holding both adults and young into the winter months were more than two acres in area.

Williams (1950) live-trapped 84 previously marked muskrats on Gray's Lake, southeastern Idaho, in the summer and fall of 1949. Two individuals were recovered 200 yards from their sites of marking, and 63 within 50 yards. Eighteen of the marked animals were taken by fur trappers during the spring of 1950, all from the same parts of the marsh where the animals had been marked eight or nine months earlier.

In Maine, Takos (1944) reported that all of nine immature muskrats captured two or more times (a total of 28 captures) were taken within 100 feet of the original site of capture. All together, he banded 107 of mixed ages, of which 40 were recaptured a total of 184 times. His records for 11 adults captured five or more times during summer and early fall gave maximum distances from original trapping sites of up to 265 feet, mostly within a 100-foot radius. The most complete data he obtained were for an adult male, taken 28 times between April 20 and August 7, 1941. It was first captured near the periphery of its range, and the greatest straight-line distance between captures

was 260 feet. Another adult male showed the maximum distance between points of capture — 570 feet away on the morning following the previous handling. But several other adults of both sexes showed similar tendencies to range widely.

Some pronounced differences in movements of muskrats were reported for southern Ontario by Wragg (1955) on the basis of data from marking 62 adults and 28 young in nests. His data on a total of 41 recoveries involving 30 individuals were chiefly from animals marked between May and October, 1947, and taken by fur trappers in the springs of 1948 and — to a lesser extent — 1949. Fifteen of 24 recaptures made after an interval of five to 10 months (including the periods of fall and spring activity) were at distances less than 100 yards from marking sites. Nine animals were taken outside of the home marsh (175 acres), and 5 of these traveled over a mile: one of the latter was found frozen in a hole in a creek bank two and a quarter miles away. The second, marked as a "kit" in July, was taken in poor condition the following spring along a small stony creek three miles away. The third was also trapped along a creek, over a mile from the banding site. The fourth was a huge female killed by a dog in winter along a railway track over a mile from the marsh. The fifth was taken eight miles away.

Only three of Wragg's 28 young that were marked in nests were recovered in the following spring — one 175 yards, one 500 yards, and the other three miles away. A female live-trapped along a creek bank on October 24 was recaptured two days later 100 yards distant and then killed at the latter place five months later. In October, an adult male and an adult female were taken and banded on successive nights on a small lodge just being constructed; the female was captured the following spring 150 feet from this lodge, but the male was a half mile upstream.

The author noted that the nine animals leaving the marsh left an excellent environment having a population that was well below normal. In most cases, recoveries of these animals were made in less favorable places, and some of the animals were then in poorer condition than the muskrats remaining at the home marsh. Movements tended to be along water courses, but some unbanded muskrats that were frozen out of lodges in shallow water were found wandering over the ice and adjacent land or dead in the snow.

From June, 1947, and up to March, 1948, Stevens (1953) captured, marked, and released 303 muskrats (including 217 young) in the Mackenzie delta of the Canadian Northwest Territories. After at least three months, he recovered 89 marked animals in the three acres where most of the marking had been done. Fur trappers recovered 10 more, one of which had traveled four miles in the period between summer and spring, another a half mile from where first trapped and marked, and the remaining eight did not appear to have moved any appreciable distance after marking.

The Athabasca-Peace delta is another area of northwest Canada

known for its muskrats, and here Fuller (1951) marked 168 during the summer of 1947. He detected no large scale fall movements among his marked animals – nothing over 100 feet.

TRENDS OF EVIDENCE SHOWN BY FIELD DATA ON TERRITORIALITY AND HOME RANGE OF THE MUSKRAT

Territoriality (or defence of specific parts of a home range against trespassers) may be regarded as a valid phenomenon in muskrat populations, though among muskrats there are nowhere near the rigidities to be seen in the territorial behavior of some birds. The boundaries of muskrat territories are not marked by definite lines, the crossing of which by individuals living outside invariably provokes resistance on the part of defenders witnessing the trespassing. In fact, it has long been plain that adult muskrats may cut corners or approach rather closely the lodges and burrow systems comprising territorial foci of their neighbors and even that, on occasion, several adults may have undisputed access to retreats containing suckling young. I have seen as many as four adults simultaneously using one medium-sized lodge and sitting and swimming near each other without hostile displays at the height of the breeding season when young were being cared for within the lodge.

Yet, during the breeding season in particular, the females can be, and usually are, noticeably intolerant toward trespassers, and the place defended may be substantially larger than the near vicinity of a litter of young. Tracts of stream edge, lake shore, or marsh that are recognizable as territorial units may be up to hundreds or thousands of yards apart in sparsely occupied habitats; but, at higher densities, the territories show much compressibility, down to the point where they may be separated by distances of only 20 to 40 yards. Differences in territorial tolerance of muskrats may be regarded as a resultant of opportunities, individual dispositions, the impacts of physiological and environmental variations, social conditioning, and the tensions of unknown nature associated with what we call cyclic lows or periodic depression phases. During cyclic low phases, breeding densities the equivalents of between two and three pairs per acre on first-class muskrat marshes have been observed to show fully as much evidence of intraspecific strife and like manifestations of overpopulation as have densities of 8 to 10 pairs per acre living on comparable marshes during favorable cyclic phases (Errington, 1954a; 1957).

Tendencies toward equalization of distances between territorial foci are often best illustrated when more or less homogeneous tracts of inviting marshland are being repopulated by newcomers during springs following drastic overtrapping or annihilative losses from drought or disease, or at times when large expanses of new habitat may for any reason become available to muskrats for colonization. The data from area case histories indicate that muskrats may be little influenced in their establishment of breeding territories by the presence of other territories existing more than 200 or 300 yards away. As popu-

lation densities rise, territorial spacing may become increasingly a matter of compromises until the limits of tolerance of territory-jealous populations are reached.

Territorial foci may be expected to shift to a varying extent in the course of the breeding season. Such shifts may be pronounced just before young are born, when pregnant females and associated males may display indecision as to where they wish to establish residence. Much of the Round Lake study area had a general marsh population less than a pair per two acres in April and early May, 1936, yet temporary aggregations up to five pairs per acre were noted on tracts that proved to be almost muskrat-vacant later in the summer. Some territorial adjustment may also take place in response to receding waters or to disturbance by livestock of shore-zone territories. Often the females may transfer their young from lodge to lodge or "resettle" locally without detected cause other than their impulses to do so.

I have never been able to note any decided territorial intolerance on the part of the male member of a breeding pair. Males as well as females may be individually vicious and may attack other animals coming within reach, but observed males seemed much more likely to tolerate the presence of acquaintances or of inoffensive strangers and were far safer company than the adult females for weaned young.

Both sexes and all ages displayed tendencies to frequent certain parts of home ranges with which they were obviously familiar. The sizes of these home ranges for animals having opportunities for unimpeded movements varied from perhaps 60 to 80 yards in diameter for newly-weaned young and up to about a half mile for adults working underpopulated shores or toward the centers of bodies of water. When breeding populations were high and territories having intolerant females were closely spaced, the home ranges were correspondingly smaller and more circumscribed, but a certain amount of passing back and forth by local residents took place in the interterritorial avenues without conspicuous friction. A resident could often be seen approaching to recognize another resident, to turn back when satisfied. Strangers attempting to cut through well-occupied blocks of marsh were, however, likely to be beset by attackers all along the route. Sometimes a luckless transient could be watched over several hundreds of yards of its course, attacked by residents wherever it went. Home ranges of resident muskrats were almost synonymous with territories from the standpoint of these strangers, insofar as their presence was little if at all tolerated anywhere within the tracts regularly frequented by residents. It made a difference what animals belonged and what did not.

Territorial adjustments in response to environmental pressures readily take place if the muskrats are in a position to move without effective hindrance in directions in which they may find better living conditions. On underpopulated parts of lakes and marshes, movements of given family groups have been traced for total distances of nearly a half mile in the course of a month or so. Other contempo-

raneous groups having their movements blocked by either physical barriers or occupied territories of other muskrats have remained where they were, often despite severe losses and pyramiding crises for the survivors. But, territorial blockades do not necessarily prevent animals from breaking free as wanderers, to die or keep alive as they can amid the hazards of wandering.

Successful territorial adjustments that I have closely observed did not start with bold departures from burrows or lodges. There would be preliminary movements along a favored route in the direction of a prospective new site, from a relatively few yards to 35 to 100 yards or even farther distant. The main connecting trail might be quite beaten before a new lodge or set of lodges would be built and the old lodges finally abandoned. Then, if, for example, the new site threatened to dry up, the process of extension would be repeated — assuming that the muskrats in their local explorations found new accessible sites having greater attractiveness for them. If lacking further alternatives, they typically stayed where they found themselves after the last feasible move until the crisis passed or progressed to the point of mortality or eviction. This often meant that females living on drought-shrinking marshes gave birth to and raised successive litters at increasing distances from their original territories.

Adjustments in home ranges have the fundamental aspects of territorial adjustments except that they are less influenced by the jealousies of females caring for unweaned young. Free extensions, whether of territories or of home ranges, in response to drought tend to be centripetal, from shallower or disappearing waters to the deeper waters in lakes and marshes; but, where gradients vary and deeper parts are irregularly distributed, explorative trails may angle off in many directions. In drying streams, most home range adjustments are from pool to pool in the stream bed.

THE SPRING DISPERSAL OF MUSKRATS

Pronounced movements of muskrats may occur in any month in a warm or temperate climate, but, in the north-central region in which my work has been centered, they have been most evident in spring and fall.

The spring dispersal may more properly be regarded as an adjustment phenomenon than the manifestation of an inherent urge to travel. The initial activities of most Iowa muskrats after the ice goes out may show explorative tendencies, and, if the animals find prospective territorial sites close by their old wintering quarters, they are apt to settle there. Sometimes only very minor proportions of muskrat populations abandon the lodges or burrows in which they have wintered, to wander in strange places. The adjustments that then occur tend to be restricted to familiar grounds or to within a few hundred yards of familiar grounds. Populations wintering at fairly low densities in good environment during favorable cyclic phases seem most disposed to remain in the same locality. Participants in wider movements

may follow lake or marsh shores or watercourses, but, in the event of their becoming lost (as in fields or pastures, tundra or desert, or city streets), they may go practically anywhere as long as they stay alive.

The changes in social relationships between midwinter and spring, which culminate in animals either withdrawing from or being forced out of the lodges or burrows where they had previously lived together with their fellows, are basically associated with sexual awakening. However, the sexual chronology of Iowa muskrats engaging in spring dispersal may be most variable. Some of those first dispersing are precociously maturing young. Others are old animals not anywhere near breeding condition, or perhaps even senile. At the height of the dispersal, large numbers of cross-country travelers may be perceptibly behind schedule in sexual advancement.

It has by now become rather clear that the participants in the earlier stages of the spring dispersal are likely to be certain individuals. Activities on the snow or ice during late winter thaws may often be visible symptoms of unrest or insecurity, especially when some recurring external signs may be seen in the same places after each thaw and in places where the majority of muskrats appear well-situated. In central Iowa, these active animals may be killed by minks or canids, and, after predation has eliminated them as individuals, the signs of further surface activities may correspondingly diminish. When this occurs, scant evidence of wandering or of habitual transients may be seen in the locality with the coming of spring, even though the number of locally resident muskrats may not look perceptibly diminished. On the other hand, if many of such individuals showing restless tendencies in late winter do not happen to draw attention of formidable predators, and thus survive until spring, sore and harassed transients may be encountered abundantly about shore zones and the countryside. Evidently, at least a minor proportion of an ordinary wintering population of muskrats may be assigned well in advance of the dispersal to the less pleasant roles therein.

An effort has been made to examine substantial numbers of muskrats traveling overland in spring outside of what could logically be regarded as their radii of familiarity. The total of 137 of such specimens that I handled in Iowa includes not only those personally collected or found dead but also 33 (mainly traffic victims) sent in by personnel of the State Conservation Commission.

Of the 137, the earliest known spring wanderer was a newly mature, newly-bred female struck by an automobile in the very last days of February. For the first week of March, 2 specimens were available: an old male and an old female, both strife-torn and in poor condition. For the second week of March, there were 4 specimens, one each of immature and newly-mature individuals of both sexes. Then, for the second half of March, with the spring dispersal really on, there were 35 specimens more or less satisfactorily grouped as 3 immature females, 20 males and 4 females maturing to newly mature, and 7 old males and one old female. As a rule, the March specimens were fairly free of strife wounds, though some individuals — proportionally more old

animals than young — were badly chewed up. Neither the old nor newly-mature muskrats were doing much breeding, but 3 of 6 newly mature females for March had corpora lutea.

For the first half of April, 31 specimens consisted of 3 immature males, 12 males and 7 females judged to have been maturing or newly mature, and 7 old males and 2 old females. Of 32 specimens for the second half of the month, one was an immature female, 13 males and 2 females were classed as maturing or newly mature, 10 males and 2 females were old ones, and 4 males were not satisfactorily aged but were probably newly mature. Many of the wandering animals became strife-torn as the month passed, notably the males congregating about the edges of densely populated marshes or those leaving such marshes. On the other hand, newcomers to underpopulated habitats, even those arriving well after the middle of April, were almost wound-free.

The females still moving from mid-April on were, like the males, with or without strife wounds, depending largely on local circumstances. One newly-pregnant young animal was severely bitten all over its body, and so was another female that was maturing but unbred.

There were 31 May specimens of wanderers: an immature male and an immature female, 12 males and a single female classed as maturing and newly mature, 7 old males and 4 old females, and 4 males and one female that were not satisfactorily aged but were probably newly mature. A single specimen of a wanderer for mid-June was an old, battered female. None of 4 mid-May newcomers (2 old males, a newly mature male, and a probably newly mature though unbred female) to an almost unpopulated marsh was strife-torn a week later; but, except for this lot and a couple of other individuals, the May collection represented the most patent of biological leftovers, with intraspecific wounds of all degrees of severity, healed, healing, and fresh. The newly-mature female had had a litter of young prior to May 27, but, by that date, she herself was footloose and bitten. In similar condition were 2 old females, one pregnant as of May 19 and another having on May 29 the placental scars of *two* earlier litters of that spring.

Warwick (1940), in his study of muskrats introduced in the British Isles, considered that only a small portion of a total population participated in the spring migration. Although the most striking instances of movement were on the part of isolated males, the muskrats sometimes traveled in pairs or in larger groups. A cited example was of a migrant party that evidently traveled to the headwaters of a stream, then over the divide to another stream, down which it passed to colonize a lake.

Recognized late spring transients on the Iowa study areas tended to occupy narrow strips separating wet marsh from cultivated or pastured land, to live in places having variable amounts of food and cover, in dry land holes, under stumps, logs, and drift, in remnants of abandoned muskrat habitations, and in flimsy nests built on shore or a short distance out in the water. Individually distinguishable transients were known to stay in temporary retreats from a few hours to several days.

The mortality that late spring transients suffered from wounds,

predators, and motor traffic may be said to have been sex-selective mainly to the extent that wandering males outnumbered wandering females at this time of year. This seemed not only to reflect the tendency of females (mated or not) to settle down and live more safely but also, in part, the usual preponderance of males in the wintering population.

Spring and summer wanderers frequent central Iowa streams with less disturbance and greater safety than do wanderers about the lakes and marshes — apparently because such socially unwelcome animals are able to spend the warmer months living more or less alone in out-of-the-way pools, brooks, and drainage flows.

The onset of the year's breeding may be counted upon to intensify frictions and intolerances, whether departure results from voluntary withdrawal or from eviction by dominant animals electing to establish breeding territories of their own in or about wintering quarters once shared with others. Beer and Meyer (1951) reported for Wisconsin muskrats a very definite connection between time of year and reproductive physiology and behavior patterns. The greatest amount of movement was during the rapid growth of the reproductive tracts and the period of high gonadotropic activity of the pituitary; the greatest amount of fighting, when the reproductive tract was at its maximum weight.

Sprugel (1951) examined known dispersal dates of central Iowa muskrats with reference to weather records for the decade 1938–47. He concluded that an average temperature of 32 degrees Fahrenheit, or above, for three consecutive days after the animals reached the proper stage of receptiveness was enough to initiate the movement — generally in the last days of February or early March — but that marked rises in temperature for particular days did not appear to be enough. Inhibitory effects of ice or snow were evident, and movements, though once begun, usually ceased for the duration of later periods of colder weather. The spring dispersal could be expected to reach its maximum two to three weeks after beginning, or in late March or early April.

Repopulation of previously muskrat-vacant habitats afforded good opportunities for studying these movements in Iowa. It could be seen that newcomers usually first worked about a strange area and then settled in a place that appealed to them, especially one having an old lodge or burrow system or an attractive food supply. Sometimes a single animal settled in a territory and was later joined by a mate. Sometimes, residence of lone but pregnant females was established shortly before birth of a litter. Sometimes, for the period of their wandering along the peripheries of occupied territories, battered pregnant females behaved essentially as did the males that more characteristically made up the biological surplus of the spring and early-summer population. However, most participants in spring dispersals would be settled in breeding territories within a month or a month and a half after the initial movements began.

Spring dispersal of Iowa stream-dwellers may or may not be associ-

ated with floods. Flooding during the winter months may introduce serious if not lethal complications, but, unless the animals are already disposed to move from wintering quarters, they try to sit out the floods and return. Similar behavior may prevail when settled muskrats are flooded out during the breeding season. The detailed observations made by Sprugel in June, 1947, when a creek was in high flood three separate times, indicated a great deal of fidelity toward their home ranges on the part of residents forced to seek refuge some hundreds of yards away from their stream-bank burrows — even when the burrows were obliterated by silt and the configuration of the watercourse was changed.

But, for those muskrats that are, by early spring, physiologically and psychologically ready to move, a flood may be just the thing to start them, and so may a thaw that removes the ice or snow. Dispersal along ice-free central Iowa streams generally got underway almost a month earlier than about the slow-thawing farm ponds and marshes. Yet, there was evidence that population tensions mounted in the marshes in much the same manner as in the stream habitats where events were less obscured by ice and snow (Errington, 1943, p. 923).

A preliminary discussion of numbers of muskrats involved in the annual spring dispersals has been published (Errington, 1940), but the reader wishing more exact information had best consult the case histories of the observational areas given later in this book. Naturally, the volume of a dispersal depends to some degree on its sources. From some marshes having high wintering populations, spring migrants may pour along the principal watercourses or wander over surrounding lands by the thousands. Or, following a killing drought or a winter of drastic trapping, there may be practically no overland spring movements to restock suitable but muskrat-vacant habitats lying away from streams or lake and marsh chains.

In the southern coastal states (where the Louisiana subspecies *O. z. rivalicius* breeds the year around but especially during the cooler months), what may be called spring dispersal begins considerably earlier than in the north-central region. Freeman (1945) wrote that the emigration of this subspecies in Mississippi begins in January and lasts for about six weeks, coinciding with what is considered the most active breeding season. In Texas, Lay (1945) regularly found muskrat tracks in cow trails a mile from the nearest marsh, and several hundred muskrats were taken by hunters with dogs in one winter from a beach a mile away from the marshes. One muskrat was found in March, 1944, in the Big Thicket, forty miles from the nearest muskrat marsh.

POSTBREEDING AND AUTUMNAL MOVEMENT

Postbreeding abandonment of familiar habitat should be distinguished from gradual and orderly modification of home ranges, such as centripetal extensions from shore zones as water recedes in dry, hot weather. It may be expected to take place in all years and in all places where there are free-living muskrats.

Late August through September may be particularly a time for

abandonment of habitats in central Iowa. The animals involved may consist disproportionately of the immature — young of six weeks to subadults of four or five months — but also may include adults. There may be random movements of solitary muskrats, sudden appearances of several animals at once in retreats that are miles from places known to have been occupied earlier, or even truly mass migrations.

The subject of footloose mass movements by summer and fall muskrat populations is one that I feel reluctant to discuss. Like their more celebrated possible counterparts in the Scandinavian lemming (Elton, 1942; Kalela, 1949; Wildhagen, 1952), there is much about them concerning which very little is known. Those that I have witnessed personally, or had described for me by other observers, seemed to have had their inception either in deteriorating environmental conditions or in tensions associated with top-heavy populations, or in combinations of the two resulting in acute situations necessitating some kind of relief. The best examples I ever saw were in the summer of 1944, at the time of a population crisis aggravated by the dying of the principal food plants of a marsh. The behavior of mass-moving animals observed both in wet areas and on land suggests that they may have a tendency toward gregariousness when lost or uneasy — especially at seasons of minimal friction, after the breeding is over, yet before the time of tightening social relations that becomes apparent with the approach of winter. Furthermore, even when great movements of animals consist of individuals or small groups trickling through or away from an area, muskrats often display inclinations to go where muskrats have gone ahead of them, whether this is by following packed trails or simply by following scent across open spaces.

The stimulus of the chronological cyclic low warrants mention here. Within the span of the Iowa muskrat investigations, three such depression phases are believed to have occurred, centering about 1936–37, 1946–47, and 1956–57.

The biological manifestations of the first and third lows were in part obscured by drought conditions on many of the Iowa observational areas, but those of the second low were not. So far as can be judged from currently available evidence, the acute period of the latter low in central Iowa began in the summer of 1946 and continued well into the spring of 1947. Not only did we have an explosive dispersal in the spring of 1947 that spread the muskrat populations widely, but the late summer and early fall of 1946 had also been notable for cross-country movements having no ordinary explanation. Neither were the muskrats then overly abundant nor did food and water conditions look anything but favorable. The muskrats, however, were killed on highways in conspicuous numbers, and strange animals were known to have moved into some marshes by the hundreds.

Beer and Meyer (1951), in their study of the endocrinology and behavior of Wisconsin muskrats, noted a minor surge in both fighting and movement during the fall that could be correlated with physiolog-

ical conditions. Adrenal weights then reached their maximum, and there was a minor increase in pituitary weights.

Normal population adjustments in late summer and early fall may involve large numbers of muskrats within a half-mile, or somewhat larger, radius when underpopulated or muskrat-vacant though habitable environment exists in places that explorative animals are likely to find. Some tracts of marshes and streams may be unproductive in terms of young muskrats actually born and reared there, yet, through postbreeding adjustments, may be amply stocked with the species by fall.

In late years, the behavior of stream-dwelling muskrats in central Iowa has changed greatly. Prior to the mid-forties, the majority of these muskrats maintained themselves in year-round residence. They habitually stored ear corn in their burrows and often wintered well on this choice food despite low water conditons. Then a series of summer and fall droughts beginning about 1947 was marked by pronounced movements and by a virtual loss of the local corn-storing tradition. The old habits were not restored during 1951 and 1954, when water levels were again favorable for muskrats. By the mid-fifties, a new and distinctive pattern was becoming clear. Groups of watercourses became almost completely depopulated in late summer, through movements along stream channels. The consequently very low wintering populations were then followed by more or less repopulation of the streams with breeding animals during the spring dispersal, good to excellent reproductive success, and, once again, nearly complete depopulation in late summer.

NONSEASONAL AND EMERGENCY MOVEMENTS OF MUSKRATS

Home range adjustment and footloose wandering can occur at any season over the muskrat's range in North America, although northward little evidence of winter movement may be seen. Northern animals may well want to move then, but they cannot endure very low temperatures. Hence, whether they starve or freeze in their protected retreats, they tend to avoid exposure to intensely cold outside air. Successful adjustments of home ranges may be made under the ice and are usually manifested by new lodges appearing farther and farther from those earlier occupied. Often strings of small to medium-sized lodges reach out from shallow shore zones toward the deeper water of lakes and sloughs having much submerged vegetation.

When the sinking frost-line seals the subsurface food supply of a population of muskrats, the entire living population may come out on top of the ice. Wandering may take place without much reference to old home ranges except insofar as strangers invading lodges may be fought off by the resident animals. Movements under such conditions (also when remnant populations do their desperate best to winter in a dry marsh) may be either directed or random. If much randomness is apparent, there is also likely to be considerable wandering over outlying lands.

In discussing over-utilization of habitats by muskrats, Lynch, O'Neil, and Lay (1947) traced the sequences of events observed during the abandonment of Texas marshlands and expressed the view that something akin to mass psychology may operate. At any rate, muskrats living in parts of marshes that are relatively little damaged often join in the general exodus of animals from severely eaten-out parts.

Drought exposures have been the apparent stimulus to most of the irregular movements of muskrats studied in Iowa and neighboring states as well as in the West and North. It is here classed as nonseasonal, though its frequent coincidence with the post breeding movements and the period of minimal friction of late summer and early fall may be decidedly a source of confusion. It may even occur in the months of the spring dispersal if for any reason spring rains are deficient. And, in the fall, it may combine with the onset of winter to launch hundreds and thousands of muskrats into their troubled drifting.

One of the few permissible generalizations concerning abandonment of familiar home ranges as a result of drought is that, regardless of the time of year, some muskrats leave and some do not. Old animals are likely to stay in their homesteads the longest — in some cases for several months after the disappearance of surface water. However, at least a few young of the original residents may often remain in a dry marsh after the population reaches a remnant stage, although the *very last* animals able to keep alive are almost exclusively tough old adults. But adults of both sexes, from the newly mature to the aged, do comprise part of the population first leaving a dry marsh. Specimens collected or found dead on highways away from marshes in the earlier stages of droughts tend to have more intraspecific strife wounds if they are adults, so it may be that as a rule adults must feel more incentive to move than must the immature.

In my experience, sudden mass abandonment of drying marshes is an unusual phenomenon but it can occur. One of the best examples of which I have personal knowledge (Errington, 1943, pp. 859 and 864–65) appeared to result from drought and food shortage operating in conjunction. When the last six acres of the food-poor center of a northwest Iowa marsh went dry on the unseasonably hot day of October 22, 1940, the concentrated population remnant of possibly around 200 muskrats left the marsh and its vicinity either during or immediately after the final exposure of the central marsh bottom.

The regularity with which the shallows of some western marshes go dry from midsummer to fall imparts a certain regularity to drought-evictions of muskrat populations. Cartwright (1944) regarded drying of the potholes and shallower marshes in midsummer as a normal occurrence over much of the agricultural region of the Canadian prairie provinces, and perhaps as much may be said for the marshy areas of north-central United States. As concerns responses of the muskrats, I have often seen characteristically beaten trails leading a half mile or more from the drying to wetter sections of many large

north-central marshes. So may one think of the gradual midsummer exposure of hundreds of square miles of alkali flats along the northeast corner of Great Salt Lake, northern Utah, and of the muskrat trails, miles long, extending from the drying far-out bulrush shallows to the flowing streams and wet impoundments nearer shore.

But wherever they try to live in the drying marshes with which I am familiar, the behavior of the muskrats is conditioned by social intolerances and by opportunities for individual adjustments, and the rules they follow individually remain partly of their own making. Here, again, some move and some stay.

A high incidence of trap cripples among wandering muskrats has long been apparent in the Iowa studies during or following the trapping season (Errington, 1943, pp. 886–87). Their handicaps presumably incite their uninjured fellows to turn upon them. It also may be suspected that their irritability from suffering may make them unpopular in places where otherwise they might be tolerated. Sufferers from disease may also be especially prone to wander, perhaps to find solitude for a time in a corn shock, a tile opening, or a bank hole near a lake side.