Part 4

Concerning Population Dynamics of the Muskrat

Chapter 15

Self-limiting Trends and Intercompensatory Adjustments in Muskrat Populations

MAN HAS NO DOUBT OBSERVED throughout most of his thinking career that there must be limits to the numbers of animals able to maintain themselves in a given area at a given time. Malthus' (1798) essay on populations greatly influenced Darwin (1872) and can still be recommended (with reservations) to modern students. The final paragraphs of a review by Davis (1950) may here be quoted:

> Malthus of course did not completely anticipate our present concepts about populations. He did not recognize the difference between density-dependent and density-independent factors. While he was dimly aware that social structure of the population was important he apparently did not consider the possibility that a change in social structure may result in a change in population in a given environment. . . . Similarly, Malthus was not aware of the need of animals for space as such (territory) and neglected this limiting factor. Finally, Malthus did not clearly state the consequences of predator (disease) control as such. However, from his statements about the means of subsistence limiting the redundant population it is certain that Malthus realized that a reduction of the mortality due to predation would be matched by an increase in the mortality due to other causes in a stable environment.
>
> In conclusion it may be said that Malthus shrewdly analyzed many aspects of the principles of game management. He found that the gain of a population was inversely proportional to the population and that mortality factors constantly act to keep a redundant population within its means of subsistence.

Malthus' views as to populations being limited by the means of subsistence seem to have prevailed in oversimplified form in scientific thought until about the time of Raymond Pearl – though awareness of the phenomenon of self-limiting territoriality had been shown by occasional writers long before Pearl and even long before Malthus (Nice, 1941). In his book on natural regulation of animal numbers, Lack (1954) certainly emphasized food as a basic limiting factor. It is wholly apparent that many academic people as well as the lay public continue to regard populations as increasing up to the limits of their food supply unless prevented by obvious types of mortality.

It may now be emphasized, without belittling the genuine influence of food and other environmental essentials on animal life, that something not improperly called self-limitation may also operate to prevent a considerable variety of natural populations from increasing up to – or even very near – the literal limits of their food supply.

Pearl's (1925, 1937) demonstrations that many populations tended to follow a sigmoid growth curve (the Verhulst-Pearl-Reed "logistic") focused much scientific attention on a major pattern in population behavior. Allee, Emerson, Park, Park, and Schmidt (1949, pp. 301–15) presented an instructive discussion of the logistic curve and its significance, together with some more recent examples; and still later, other authors, including Andrewartha and Birch (1954, pp. 347–97) further discussed the curve.

In my own treatment of data from both original investigations and the literature, I have usually learned less from plotting on coordinate paper the population changes against time (as one does in looking for evidence of the logistic curve) than from plotting annual rates of gain (or loss) against adult or breeding densities. On the whole, the more complete records from long-term studies of higher vertebrates reveal strong tendencies for spring-to-fall (or breeding to post-breeding) populations to conform to mathematical formulas that differ with species and areas but which for a given species in a given area may remain apparently unchanged for years at a time (Errington, 1946). At one extreme, very low breeding densities often show low rates of increase, about as one might expect from the discussion of underpopulations by Allee, Emerson, Park, Park, and Schmidt (1949, pp. 399–405). Nevertheless, the lower of the breeding densities that still permit efficient mating and living relations tend to show the higher rates of increase.

Whenever it occurs, the lining up of a string of data points either along a curve of inverse gains in relation to adult densities or along the familiar logistic curve of population growth implies not only the self-limiting influence of the density factor but also compensating adjustments in rates of gain or loss and a stability of what Pearl (1925, p. 20) called the absolute base from which the law operates. Whenever the data points line up along neither curve in a definite way, the operation of something besides a density pattern may naturally be looked for.

THE IOWA MUSKRAT DATA AND DENSITY PATTERNS

In my work with the mainly stream-dwelling muskrats of Boone and Story counties in central Iowa, I have been impressed by the year-to-year extremes in population behavior.

First may be considered the spring and fall (pre-trapping) population levels of the muskrats over those parts of the Keigley's Branch and Squaw Creek drainages that were kept under regular observation from approximately the beginning of the Iowa muskrat investigations. Combined, these areas total about twenty square miles, with data on fall densities and rates of summer gain lining up as in Figure 15.1.

In the above treatment of data, the responsiveness of muskrats to patterns may show more definiteness for the twenty square miles considered as a single land unit than for most of the component areas separately, but the rates of spring-to-fall gain are still much less well-defined than for Iowa as a whole (Figure 15.2). However, if we just add the data from Goose and Little Wall lakes and vicinities to the data from the Keigley's Branch and Squaw Creek drainages, we get a much better conformity to what look like basic patterns for a 23-square-mile land unit (Figure 15.3). For both figures 15.2 and 15.3, the upper series of data points in the lower sections of the figures represent periods when the areas most nearly approached full habitability for the muskrats. Conversely, the data points lining up or grouped more in the lower left parts of both figures represent mainly the effects of drought years.

Although figures 15.2 and 15.3 have sufficient features in common to suggest capacities for adjustments of muskrat populations that may go far beyond local boundaries, it was not until the last decade of the field work along central Iowa streams that the magnitude of the upstream and downstream adjustments of late summer and early fall became apparent. I refer here to the orderly adjustments occurring in years of normal rainfall and stream-flow as well as during droughts.

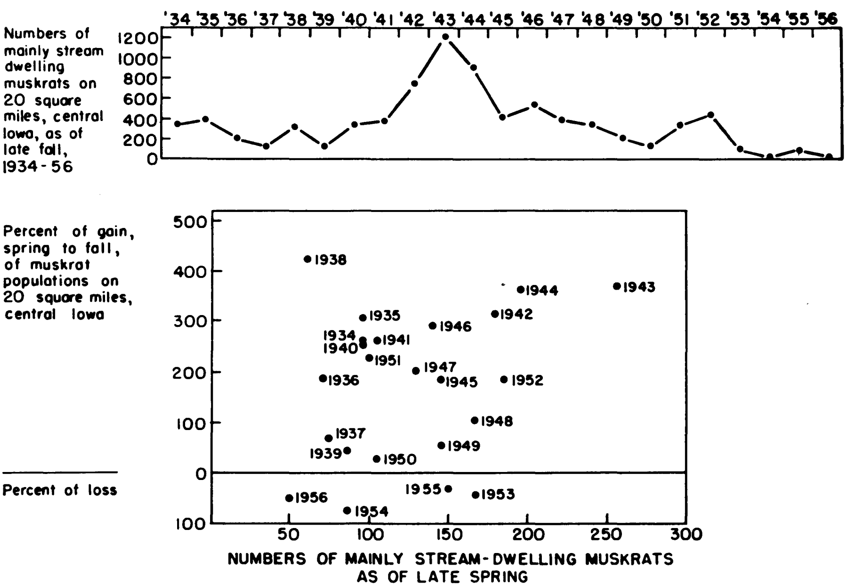

Fig. 15.1. Population changes of mainly stream-dwelling muskrats in central Iowa, 1934–56. (After Errington, 1957 — Cold Spring Harbor Symposia on Quantitative Biology.)

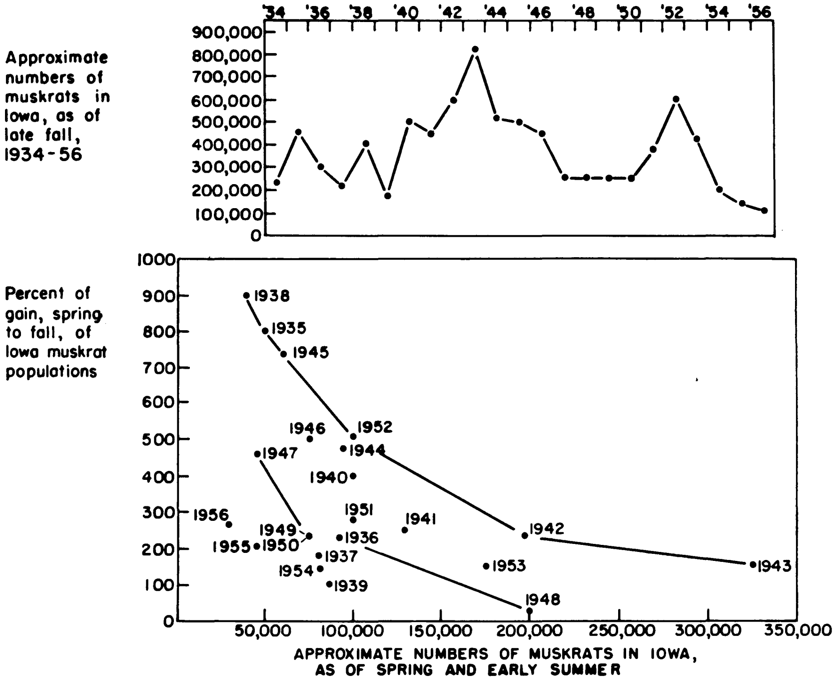

Fig. 15.2. Population changes of muskrats over the state of Iowa, 1934–56. Connecting lines in the lower part of the figure chiefly indicate population responses during normal and drought years. (After Errington, 1957 — Cold Spring Harbor Symposia on Quantitative Biology.)

At first, as in the late summers of 1947 through 1950, these adjustments seemed to have been mainly downstream and in response to drought conditions. Except for a few upstream drifters, the muskrats gave the appearance of almost flowing downstream, following the last of the water. Then, it was rather surprising to find a notable amount of much the same sort of adjustments in 1951, a year of favorable water conditions. In 1953, the movements could have been precipitated by low-water stages, but in 1954, the muskrats clearly abandoned most of their stream habitats at about their customary time, despite the fact that substantial flows of water continued over the stream beds at the height of this period of adjustment.

In 1955, of 28 trails of individual muskrats that were traced along stream channels far away from places with which the animals could have been familiar, 21 led in upstream directions. Even so, there was no evidence of congregating in upstream habitats, and late fall observations indicated that a large proportion of the adjusting muskrats finally arrived at Skunk River. In 1956, I failed to trace the destinations of most of the adjusting muskrats along the central Iowa stream areas, though massing was discovered in late fall in one upstream area. This latter area was characterized by its attractive condition for muskrats. However, it did not look any more attractive to my eyes than many of the places that the muskrats had passed through or abandoned.

Changes in local food supply and in traditions of response of the muskrats were surely influential. I would say that the extensive post-breeding movements along watercourses during the past decade have been linked more with food than with water and that the greatest variable in sight has been in the utilization of ear corn by the local muskrat populations.

In some of the earlier years of the Iowa investigations, stream-dwelling muskrats wintered at high densities, sometimes despite considerable drought exposure. The populations of those years, however, were corn-storers. It was routine behavior for muskrats to establish burrow systems next to corn fields and to pack their burrows with ear corn and to live far more sedentary lives than they did after the mid-forties.

By the early fifties, many stretches of streams were consistently occupied by highly productive breeding muskrats in early summer and

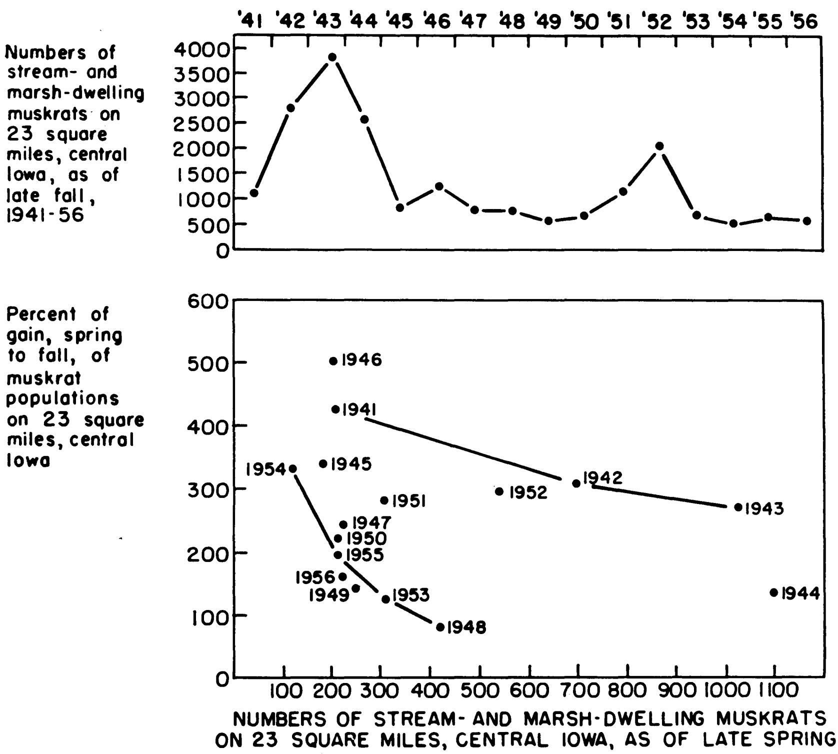

Fig. 15.3. Population changes of central Iowa muskrats, 1941–56, all regularly observed habitats combined. The 1941–43 series of data points may be compared with those for the mainly drought years in the extreme lower left. (After Errington, 1957 — Cold Spring Harbor Symposia on Quantitative Biology.)

as consistently muskrat-vacant by late summer, yet they had corn fields in as close proximity to the water as they had when they were favored retreats for the muskrats the year around. The differences were not in the presence or absence of corn fields but in whether or not the muskrats discovered and utilized the corn.

Without the corn, central Iowa stream habitats had scant attractiveness or habitability for muskrats during the colder months, though as habitats, they were satisfactory for moderate densities of muskrats from late spring through midsummer. From the standpoint of the muskrats, the corn fields that they did not visit added nothing to otherwise food-poor habitats. In view of the regular raiding of corn fields and the storage of ear corn that in the thirties and early forties almost characterized the muskrats living along the stretches of central Iowa streams that later were regularly abandoned, it seems to me that decided changes in local behavioristic traditions occurred.

For all of what we still do not know about these late-summer and fall adjustments, they have given us a better understanding of the mechanisms behind the known tendencies of populations of the larger land units or combinations of units to conform to patterns. At times, such conformities were evident more or less irrespective of a wide range of local conditions and local behavior. Some muskrat populations remained essentially sedentary throughout the lives of their members, whereas other populations engaged in seasonal movements over astonishingly long distances. Exclusive of the cross-country wandering that the desperate and the geographically lost may have done, some of the movements of late summer and fall occurred along practically the whole length of small and medium-sized creeks. One may conjecture that migrants having inviting travel routes of great length — and nothing more attractive than the habitats they abandoned to cause them to establish living quarters on the way — may travel much farther than the movements actually traced along Squaw Creek and Keigley's Branch.

Of the three major marsh areas kept under regular observation in central and north central Iowa, Goose Lake was the only one having an outlet along which adjusting muskrats traveling upstream were likely to move — and fall movements along this outlet occasionally were heavy. Fall movements of stream-dwellers into Little Wall Lake had to be overland and, so far as I was usually able to judge, from a drainage ditch lying to the north. Field evidence suggested that the usual route of travel here was quite narrow, apparently to one corner of the marsh.

The third marsh, Wall Lake, being sufficiently isolated to preclude anything more than irregular discovery by cross-country drifters, has not been involved in the sort of counterbalancing with neighboring stream habitats to the extent that Goose and Little Wall lakes have been. It patently drew many muskrats from outside areas in both 1943

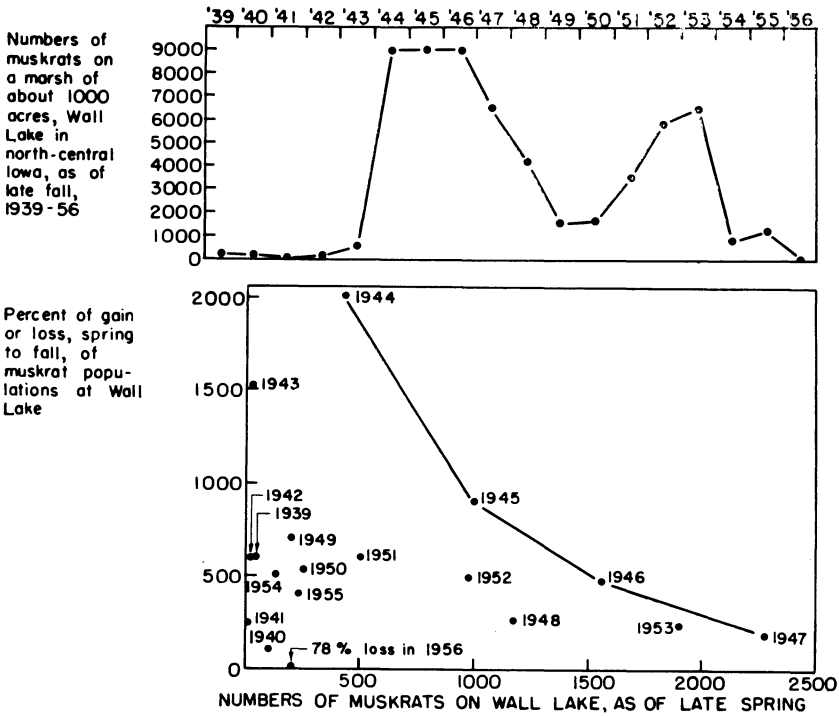

Fig. 15.4. Population changes of muskrats on a marsh in north central Iowa. The upper series of data points — connected by lines — in the lower part of the figure represent the period when the marsh most nearly approached full habitability for muskrats. (After Errington, 1957 — Cold Spring Harbor Symposia on Quantitative Biology.)

and 1944. In 1943, the year of Iowa's peak muskrat population, muskrats went just about everywhere in the course of their postbreeding adjustments. In 1944, the over-all population of central and northern Iowa not only was still high but the exceedingly wet season also left an unusually great number of water connections to serve as travel routes for adjusting muskrats. But, for the other years of our records, Wall Lake has had muskrat populations that were essentially self-contained during the spring-to-fall periods for which data have been plotted in Figure 15.4.

As in figures 15.2 and 15.3, the data points for spring-to-fall gains in Figure 15.4 lined up chiefly according to the degree that the marsh was in habitable condition. For most years, the fall population averaged about ten muskrats per acre of marsh having water covering the bottom, but this may not be correctly stated as a formula. In 1947, 1951, and 1952, the average was closer to fifteen per acre, and in 1957, the marsh was practically unpopulated, irrespective of its substantial amount of food, cover, and water.

THE IMPACTS OF EMERGENCIES

The broad subject of adaptations and distribution of organisms is one of great complexity, and where the muskrat may live or thrive depends more than anything else upon the advantages afforded it by climate and habitat. Emergencies imply the opposite of advantages, and sometimes they have terrific impacts upon the muskrat populations affected.

For muskrat populations living under edge-of-range conditions — in high plateaus, in isolated desert waterholes, in arctic or subarctic tundra, in the mysteriously unfavorable southeastern states — a minimum of resilience under the impacts of emergencies may be expected. When one of these muskrats dies, it is dead, and its death may mean one less animal in the population without any compensatory improvement of the chances of another one for living. Edges of range may often have many apparent vacancies that are to some extent habitable by muskrats yet perhaps seldom even discovered by them.

Well within its established geographical range, the muskrat may have much poor or marginal habitat — the brooks, the temporary field ponds, the out-of-the-way places where the species may now and then be found. Habitability of many of these places may vary with the year, so they have muskrats chiefly during years of general abundance. As the sorts of places into which overflow animals tend to drift, they are often sites of mortality involving large proportions of the muskrats taking up quarters. The existence of better habitats in the neighborhood of the marginal ones does not necessarily mean that muskrats may adjust to emergencies by leaving the poorer places for the better — especially if the better are occupied to capacity by intolerant residents — but it may be presumed that such adjustments stand somewhat more chance of being successful than would attempted adjustments on a mountain top or over a waterless plain.

Muskrat habitats are notably subject to changes, insofar as shallow-water zones are among the more ephemeral geological features. It is apparent that about the only thing likely to interrupt the deterioration of many glacial marshlands would be another glaciation, but of course, the different stages of filling and the unevenness with which filling occurs leave attractive waters for muskrats somewhere at almost any given time over the greater part of the muskrat's North American range. Oxbow marshes along large streams and delta marshes may come and go over short periods of years. Stream habitats, in their broader aspects, are perhaps as geologically permanent as any major habitats the muskrats have, though the flows in silted channels vary from year to year, and silting itself can progress to the point of practically making long stretches uninhabitable for muskrats. Soil erosion is an inexorable factor, even when occurring without human acceleration; and so also are climatic cycles and the constant adjustments of plant and animal communities, collectively.

Muskrats, being more dependent upon the intermediate successional stages occurring in shallow waters than upon either the earlier or the climax stages, would have limited prospects for attaining any long-term stability of population in their better habitats if only for the reason that the better habitats usually do not retain their superior food resources indefinitely. Heavy stands of cattails or bulrushes may persist for a series of years, to be killed out by high water, plant diseases, or insects, or simply to deteriorate from unknown causes. Then, particularly after low-water years, the emergent vegetation may again grow in profusion. Neither of the extremes represented by food-poor open-water lakes or ponds or by dry lowlands choked with vegetation is conducive to high populations of muskrats in northern regions.

O'Neil's (1949) descriptions of muskrat "eat-outs" and damage to marshes from concentrated feeding by wild geese in Louisiana surely bespeak drastic lowering of the habitat for muskrats of the areas affected. When an excessive muskrat population denudes an area of its better food plants, the plant growths may not recover for a long time, and the muskrats are left with little alternative except to decline. They may attempt adjustments by moving out of the denuded area, but their chances of successful adjustments are dubious unless they find suitable vacancies elsewhere. An extreme case of unsuccessful adjustment is afforded by the mass movements out in the desert away from Malheur Lake, as described in Chapter 13.

I have never known northern marshes to suffer anywhere near the damage from overuse by muskrats that seems to occur regularly in Louisiana, but the activities of carp seem to be very detrimental to *some* north central marshes. Rooting by hogs in dry or nearly dry marsh bottoms may eliminate duck potatoes, cattails, and other of the better muskrat foods. Cattle may damage a vulnerable marsh for muskrats by their trampling and feeding. The digging out of bank burrows by farm dogs falls in one of the lesser categories of emergencies but still is illustrative. In appraising the effects of these changes, consideration should be given to the question of how much *remains* of livable habitat in relation to the muskrat population after the damage has been done. With excellent areas of deep marsh remaining for low to moderate resident populations to live in, what happens to the shore zone may be rather immaterial from the standpoint of the muskrats. Disturbances or exposure of bank burrows may not impose any particular handicap on muskrats that can easily establish themselves in suitable places elsewhere in their home ranges. But, if a habitat is crowded to begin with and suffers pronounced deterioration from any cause, one need not expect adjustments to such deterioration to be fully compensating.

Human engineering may ruin or create muskrat habitat, depending upon what is done and where. The drainage of a fine marsh may be a virtually complete loss for the muskrats. If generally uninhabitable wetlands are drained, the new habitat offered by food-rich, wet ditches may represent gains for the muskrats. Flood control projects may result in a multiplicity of consequences — ranging from disastrous to highly beneficial — for muskrats. Some of the agricultural drainage that channels the water of small marshes into lakes are almost wholly detrimental to muskrats, in contrast with water manipulation for the primary purpose of muskrat management, as on the great "rat ranches" of and about the Saskatchewan River delta (Chapter 13). Irrigation diversions may lower the habitability for muskrats of original streams or marshes, create seepage marshes of varying quality, and sometimes make available to the muskrats new frontiers for expansion.

The lighter of the emergency losses suffered by muskrats may be easily absorbed in population adjustments at practically any time of year, especially during the breeding months. The drowning of a few animals in a local cloudburst, or as a result of some other special circumstance, is nothing compared with over-all effects of density on population patterns and usually may be thought to improve the life expectancy of the survivors. So also may be classed miscellaneous minor losses of accidental nature. A limited amount of drying of ditch pools, field ponds, and marshy shallows, of trampling of burrow systems by cattle, evictions through human agencies, and freezing of subsurface retreats may, of course, be of so little consequence that they could not affect populations appreciably even were the losses therefrom quite uncompensated.

It is true that the numbers dying during severe emergencies may be so great that almost no survivors remain. This is illustrated by virtual depopulation of large expanses of muskrat range in the North American Great Plains during the droughts of the thirties and by terrific winter-killing of muskrats under five feet of ice in northern Manitoba and Saskatchewan in 1949–50. Hurricanes may be drastically lethal to muskrats in southern marshlands. The net impacts of the more severe emergencies depend chiefly upon what happens to the habitat of the muskrats. Of the examples given in this paragraph, the droughts of the thirties were followed by a period of lush marshy growths in former open-water lakes, and the muskrat populations recovered with spectacular rapidity where breeding stock remained in improved habitat; but, over much of the "West River Country" of the Dakotas, the populations of marginal stream habitats did not recover in fifteen years. Presumably, once the crisis was over, the deep-freezing of 1949–50 did not affect one way or another the real attractiveness and habitability of the Canadian marshes. On the other hand, the southern hurricanes that flooded vast tracts of choice muskrat habitats with salt water sometimes did damage that would not be repaired naturally for many years.

The often deadly local emergencies studied on Iowa streams and marshes have shown wide gradations in net population effects. From the area case histories presented in Part II of this book, it can be seen that most observed crises suffered by the muskrats were in one way or another associated with droughts, some with floods, and relatively few with other causes.

At times, there may be some slight survival of muskrats in places all but losing their habitability, and a given place may prove to be more habitable than expected, such as the dry Northeast Marsh of Cheever Lake in 1940, the dry Christianson's Pond in the winter of 1943–44, and the remaining puddles in the upper part of the Keigley's Branch observational stretch in the winters of 1949–50 and 1950–51. Still, under conditions such as these, death or departure of the ill-situated muskrats almost become certainties if the emergencies last long enough.

Departure of muskrats from drought-exposed habitats may or may not function as an agency compensating for local reductions, depending in part upon whether the emigrants succeed in re-establishing themselves elsewhere without detriment to other muskrats. The movement of juveniles from the shallower to the deeper zones of Round and Cheever lakes in 1939 seemed to represent a satisfactory adjustment, as did the southward drift across the east side of Wall Lake in 1949. The pronounced October ingress into nearly vacant Goose Lake in 1950 of animals that had been moving along the watercourses offset some of the partial depopulation of stream habitats then going on. Much the same appraisal might be made of the ingress into the wetter central area of Cheever Lake, probably from Four-Mile Lake, in 1947. The late summer and early fall drifting of 1947, 1948, and 1949, from the shallower south half of Goose Lake into the north half, had its aspects of temporarily successful adjustments, though in the end the advantages were lost in the winter-killing that followed.

On the other hand, a great deal of the overland drifting away from drying marshes and stream beds in the falls of 1936, 1937, 1939, and 1940 was attended by conspicuous mortality and complications, en route or at the remaining waters about which the wanderers tended to congregate. The failure of the dam at Four-Mile Lake in 1944 surely had a real depressive effect on the population, without corresponding gains elsewhere. Lesser-scale reductions attributable to mere lowering of water levels in late summer occurred prominently in what may be called outlying waters in the central Iowa areas, as at the Rainbolt Ponds in 1942 and along Onion Creek during most of the years when the observed tracts were occupied by muskrats — along Onion Creek even during the most favorable years. But, in some years (as in 1941), the muskrats of outlying waters were often less affected by emergencies than were those of the ordinarily more attractive and habitable streams.

In 1943, floods in late July and early August probably killed young muskrats along Squaw Creek, but without real depressive effects, considering the top-heavy fall population that was reached anyway. Midsummer flood losses on Onion Creek in 1947 were evidently compensated by later production of young, until the biological advantage of the compensation was finally lost through drought exposure. The losses of early-born young muskrats of central Iowa streams in the May-June floods of 1942 and 1944 were offset biologically by compensatory reproduction later in the summer and by better survival of the late-born young.

High water brought about emergency conditions at Goose Lake in 1943 and at Little Wall Lake in 1944 primarily through destructive flooding of the once-splendid stands of cattails. The net consequences of this loss of food resources were pronounced, in terms of year-to-year habitability as well as for the duration of the initial crises. Superimposed at Little Wall Lake were a number of lesser emergencies, as when windstorms washed the occupants of the more centrally located home ranges ashore. There the evicted animals were forced into contact with intolerant resident animals, forced to frequent strange and dangerous grounds, or forced to leave the vicinity of the marsh as wanderers. Goose Lake had a lethal situation in the winter of 1945–46 when flooding temporarily evicted muskrats from safe quarters and increased their vulnerability to minks.

For a ditch near Wall Lake, the relatively benign effects of dredging upon some old burrow systems in 1941 (Area E in Chapter 10) may be compared with the trampling of lodges by livestock in the pasture slough near Cheever Lake in July, 1939 (Chapter 6). In the first case, the animals having partly functional burrow systems and a trickle of water adjusted to the upheaval of dredging to at least some extent, whereas those in less favored sites were evicted. The livestock trampling at the pasture slough evicted the muskrat occupants decidedly ahead of the eviction schedule shown by similarly dry but undisturbed shallows in the neighborhood.

The disturbance from dog-digging endured for weeks by some muskrats of the brooklike county drain in Tract F of the Squaw Creek area in August, 1942, and the extensive digging noted in 1938 at the Story City drainage ditch obviously had less lethal effects because of the continued presence of water. At Goose Lake, digging farm dogs did the muskrats more real damage when burrow entrances were dry than when the burrow entrances had water in them. In 1947, the dogs dug out and killed muskrats in dry lodges, whereas, in wet 1951, the muskrats were clearly able to adjust to a great deal of the dog-digging of the peripheral burrows. Still more illustrative, the annihilative fox pressure upon young muskrats of drought-exposed tracts of Wall Lake in 1940 and the frequently observed responsiveness of minks to newly available muskrat prey after the disappearance of protecting waters contrast with the usual security displayed by the muskrats living under nonemergency conditions.

In combination with the effects of emergencies and of disturbance of desperate muskrats by enemies (including man), we may have the factor of disease also operating to accentuate the deadliness of the emergencies, especially where it may be borne by drought-concentrated remnants.

THE IMPACTS OF EPIZOOTICS

The muskrat is doubtless subject to a very wide variety of more or less lethal infections. Infectious diseases known (or suspected on good grounds) to kill large numbers of muskrats on occasion include: (1) pathogenic fungi, including *Trichophyton* and *Haplosporangium,* (2) protozoa, including coccidia of the genus *Eimeria,* (3) bacteria of the genus *Salmonella,* (4) plague-group bacteria, especially *Pasteurella tularensis,* the causative organism of tularemia, and (5) the hemorrhagic disease of imperfectly determined etiology with which the Iowa studies have been concerned since 1943.

The "ring-worm" fungus, *Trichophyton mentagrophytes,* is known to occur at least in muskrats of Iowa (Errington, 1942b) and Maryland (Dozier, 1943), and there is no reason to think that it may not be quite widespread over much of North America. In Iowa, observed clinical symptoms have been restricted to very young animals, which would reduce the chances of its recognition in nature. Few people have occasion to handle very young muskrats compared with those handling adults, subadults, or "kits" during the fur season.

The highest incidence of infection noted in the Iowa studies was at Round Lake. There, 35 or 9.6 per cent of 364 litters handled during the summers of 1935, 1936, and 1938 suffered from disease attributable chiefly to this fungus. Quoting from Errington (1942b):

> Ninety-eight . . . of 134 members of infected litters were recorded as contracting the ailment and, of the 98, 90 . . . apparently died. In general, incidence and severity of infection alike rose as the breeding season (mid-April to late August) progressed. The population significance of the disease, however, was conditioned by intercompensatory trends both in reproductive rates of the adults and in loss rates of the young. Not only were some losses of young — from disease as well as predation and miscellaneous agencies — offset by prolongation of breeding and production of extra litters, but, under given circumstances, losses of young through intraspecific friction had ways of increasing about in proportion to the extent that other types of losses diminished.

Jellison's (1950a) report of heavy infestations of *Haplosporangium* in muskrats near Charlo, south of Flathead Lake in northwest Montana (Appendix M), arouses currently unanswerable questions as to how serious this disease may be as a population depressant, either locally or throughout western North America, if not elsewhere.

> Typical fungus cells were found in 23 sets of lungs, or in 18 per cent of the [126] animals [obtained, December 6, 1949, from fur trappers]. Infestations varied from single cells to almost complete consolidation of the lungs by masses of fungi and their surrounding tissue nodules.

Parasitism of muskrats by coccidia has long been known, but the evidence suggests that this ordinarily is of little consequence to the muskrats. Under special circumstances, however, coccidiosis may attain greater severity, notably, as Shillinger (1938) indicated, during periods of low water.

> The coccidial oocysts passing from the digestive tract with the feces of affected individuals become very numerous in the mud of the runways and former canals frequented by the animals. Massive infestations develop, and great

> mortality has been noted after several weeks of drought on a marsh. Trappers report a decrease of three-fourths in the muskrat population within a few weeks from this cause.

The latter certainly hints of coccidiosis in epizootic form, but the population effects thereof may not be clearly dissociated from other effects of drought or possibly other diseases.

The long history of paratyphoid infections in mouselike rodents (Elton, 1942), the substantial incidences of carriers reported for certain populations of Norway rats in the United States (Meyer and Matsumura, 1927), and Chappellier's (1933) advocacy of the use of artificial cultures in controlling muskrats in France should quite prepare a reader for reports of *Salmonella* in free-living muskrats of either their original North American range or their new range in Eurasia. In fact, the first really good specimen obtained as the muskrats started to die of epizootic disease at Goose Lake in 1943 yielded a fine culture of *S. typhimurium,* to which organism was attributed the general dying that followed on that marsh until it became clear from continued study that such could not have been true. Armstrong (1942) found *S. typhimurium* in Maryland muskrats during a period of mortality, but Dozier (1947) considered the main decline due to an unidentified disease. At any rate, *Salmonella* can occur in muskrats, whether or not it may be responsible for large-scale mortality or population depression.

The plague-group bacteria include a number of organisms of proven or possible significance in the epizootiology of muskrats. In a mimeographed report on Minnesota wildlife disease investigations for May, 1935, Green and Shillinger referred to their previous isolation of *Pasteurella pseudotuberculosis* from two muskrats; and Green had once told me (about 1933?) that the collapse of a top-heavy muskrat population of a big marsh in south central Minnesota may have been due to this disease. Despite the high degree of infectiousness of pseudotuberculosis noted by Green and Shillinger in a variety of animals and their feeling that "it would appear to play an important part in the destruction of wild life," I know of no other report of its occurrence in muskrats.

Neither do I know of any actual die-offs in muskrats that were due to *Pasteurella pestis,* or plague, though sylvatic plague is established in western parts of the muskrat's range in North America (Miller, 1940), in

> ground squirrels, marmots, prairie dogs, tree squirrels, chipmunks, several of the native rats and mice, and the cottontail rabbit. . . .
>
> Sylvatic plague occurs periodically in epizootic form, with very large numbers of rodents dying of the disease. This has been noted in every area where sylvatic plague occurs. As in rats, the infection is transmitted from one animal to another through the bite of fleas, and many observers believe that a flea may retain its infection and transmit it a considerable length of time after

the host has died. . . . It appears as if sylvatic plague may exist in some rodents as a latent infection, and that those rodents act as reservoirs of the infection which occurs in an epizootic form only when the resistance of the rodent population is lowered.

Holdenried's experience with plague in California ground squirrels (Evans and Holdenried, 1943), along with preliminary accounts of the epizootiology of the hemorrhagic disease in Iowa muskrats, gave him the basis of the following comparative statements (letter, August 9, 1950):

Both diseases under proper circumstances seem to be efficient in reducing the host populations. Both diseases seem to vary tremendously in virulence. Another similarity is that there may occur times (frequently of several years duration) when it is very difficult and even impossible to demonstrate its presence; yet, when conditions are right, up it flares in its former destructiveness.

The near absence of fleas on muskrats (Fox, 1940, p. 37) must confer some protection against plague, but considering possible ways of transmission other than flea bites in an area having the disease established in its rodents, I certainly would not be surprised to learn of the finding of plague some time in muskrats of western United States. The related *Pasteurella tularensis* can sweep through populations of muskrats and beavers at times when transmission through arthropod vectors would be most improbable (Parker, Steinhaus, Kohls, and Jellison, 1951).

According to Parker, *et al.* (1951), spontaneous infection of muskrats by tularemia was first recognized by R. G. Green and J. E. Shillinger. The specimens came from northeastern Iowa (Allamakee County), and from Green and Shillinger's report, it may be seen that transmissions of tularemia to laboratory animals were obtained from two of the five muskrats necropsied. These specimens were submitted after death during what may have been a considerable die-off in southeastern Minnesota as well as in northeastern Iowa in late October and November, 1933, but in my opinion, it is far from certain that this die-off took place even mainly through tularemia. The hemorrhagic disease is also known to kill muskrats on a variable scale in the area, and both tularemia and the hemorrhagic disease are known to occur over such a great deal of central and west central North America that their impacts on muskrat populations are difficult or impossible to dissociate accurately. Tularemia has inflicted the severest detected losses on muskrats of western United States.

According to Parker *et al.* (1951), tularemia was known to occur in muskrats in Maine, New York, Ontario, Indiana, Michigan, Wisconsin, Iowa, Minnesota, Manitoba, Alaska, Montana, Idaho, Wyoming, Washington, Oregon, Utah, and Nevada. (It also occurs, to my knowledge, in Saskatchewan, on the Cumberland Lease of the Hudson's Bay Company.) To quote from the discussion section of these authors:

The localities and streams in Northwestern United States in which either beavers or muskrats or both are known to have died within the period covered by this report [1942–50] lie within an area which includes central and western Montana, northern Wyoming, southern Idaho, northern Utah, and most of Oregon. That tularemia was at least partially responsible for fatalities in Montana, Idaho, Wyoming, Utah, and the Klamath Lake region of Oregon is indicated by the recovery of *P. tularensis* from dead beavers or muskrats, and/or the occurrence of human cases resulting from skinning or handling one or the other of these animals trapped or found dead in the streams concerned.

Surprising contaminations of natural waters with *P. tularensis* have been reported from the western states (Jellison, Epler, Kuhns, and Kohls, 1950), and Parker, *et al.* (1951) summarize:

In general, the results and data gained from the field observations and laboratory experiments indicate that water and mud contamination, and the occurrence of tularemia in muskrats and beavers are wide-spread phenomena in the Northwestern States. Water and mud contamination may be present at any season of the year and may persist for at least 16 months. It is improbable that persistence of contamination can be attributed to factors resident in land-frequenting animals. Present information suggests that the factors governing persistence are resident in the water or mud or both, and suggests the hypothesis that the organism multiplies in the water-mud medium.

The epizootiology and population effects of muskrat tularemia observed by the U.S. Public Health people in the West are well illustrated by two publications. Jellison, Kohls, and Philip (1950) estimated the 1950 spring mortality at over 500 muskrats for a marsh bordering Utah Lake west of Provo, Utah. In June of that year, one marsh had only two muskrat lodges where it had had dozens in previous years. Prior to this die-off, local trappers had seen only an occasional dead muskrat in the course of many years of experience. Then, from the comprehensive bulletin by Parker, *et al.* (1951) on tularemia in muskrat waters of northern United States the following may be quoted:

Of 668 guinea pigs used to test water samples from the Cattail Creek area during the warmer months of June, July, and August, 1948, 168 died of tularemia. . . . Of 848 guinea pigs used to test water samples taken from September 1942 through March 1943, 645 died of tularemia. [This work was done on an area of which it had earlier been written: "No muskrats were present after this date [March 16, 1942] although 60 had been trapped in the marshes during the preceding year." Also:] Hundreds of muskrats along the course of Gird Creek died during the early months of 1943. . . .

The recoveries of *P. tularensis* reported above and in earlier sections of this paper convey no adequate idea of how extensively the beaver and muskrat populations of the north half of the Bitter Root Valley were affected by epizootic tularemia during the period covered by this report, especially during the winter of 1942–43 and the following spring when the populations of these animals were virtually annihilated in numerous localities. Reports of dead beavers were numerous and some trappers reported having seen hundreds of dead muskrats. The assumption that the deaths of these animals were at least in part due to tularemia is supported by the occurrence of at least

> eight cases . . . among local trappers who had skinned dead muskrats. River sloughs, marshy areas, ponds along the courses of creeks, and other habitat areas known to have been populated by numerous muskrats in the fall of 1942 and the early winter of 1943, and marked for trapping operations in the spring, were found completely depopulated when the trapping season opened in March. It is probably safe to assume that deaths of muskrats from tularemia numbered in the thousands and those of beavers at least in the hundreds. . . .
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> It is apparent that late in 1942 and early 1943 considerable numbers of beavers and muskrats died in . . . [Big Spring Creek, central Montana] and its tributaries. One report stated that "1,500 dead muskrats were found" along a few miles of the main creek above Lewistown between March 1 and 24, 1943. Early in the same month a trapper reported that he found more dead beavers than he caught live ones. . . . The local game warden has informed us that most of the tributaries south of Lewistown were populated to capacity with beavers and muskrats prior to the epizootic under discussion and that the loss approximated 80 per cent. . . .
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> Information from various sources, including a questionnaire sent to over 2,000 trappers, indicates that beavers and muskrats have been found dead in at least 150 Montana streams in 40 of the 56 counties during the period 1939 to March 1943. While smaller streams predominate, all the main rivers are included. For some streams there have been reports of dead animals having been found only in restricted areas, while for others there are reports that animals have been found dead over long stretches of the water courses and that in some instances mortalities occur nearly every year. On the other hand, men who have trapped along certain streams for many years report never having found a dead beaver or muskrat.

Such a range of variation in mortality would insure much variation in population effects of tularemia, even if we ignored compensations in loss rates. The data available from outside Iowa give us very limited grounds for appraisals of the intercompensatory trends that may exist in the more severe disease losses of any type, but the tularemia losses in western muskrats surely seem to have their population counterparts in the hemorrhagic losses we have studied in detail in Iowa.

The disease entity designated in this book as the hemorrhagic disease of muskrats is referred to in the literature and veterinarian's reports chiefly as "Errington's disease" and may possibly occur over the entire occupied range of muskrats. The chief publications that have so far come out concerning this disease are those of Wisconsin workers (Lord, Todd, and Kabat, 1956; Lord, Todd, Kabat, and Mathiak, 1956).

Epizootics positively traced or attributed on good circumstantial evidence to the hemorrhagic disease have been reported from, in addition to Iowa and neighboring states, the marshes of Maryland and other states of the central Atlantic Coast, from Michigan, Ohio, and Ontario, from the Prairie Provinces and northwestward to the Mackenzie delta, from British Columbia to southern Oregon and eastward through Montana, Idaho, and Wyoming. I do not know if it occurs about wherever tularemia does but suspect that it does, including California, Nevada, Utah, and Colorado. No proof of its occurrence in the coastal marshes of the Gulf States seems to exist so far, but those marshes have had extensive die-offs of undetermined nature, some of which might have been due to hemorrhagic disease. Apparently, no proven cases of the disease have been recognized in the muskrat's new range in Eurasia.

Outside of Iowa, the most sweeping recent epizootics in muskrats that were assigned to the hemorrhagic disease have been at Malheur Lake in southern Oregon, in parts of Montana, Idaho, southern British Columbia and Alberta, in the Mackenzie River Delta of the Northwest Territories, in the Saskatchewan River Delta of Saskatchewan and Manitoba, in the marshes south of lakes Manitoba and Winnipeg, in North Dakota, eastern South Dakota, and the Nebraska Sand Hills, in southern and northeastern Minnesota, east central Wisconsin, eastern Michigan, southern Ontario, northern Ohio, parts of New York and Pennsylvania, and in the brackish marshes of Maryland, New Jersey, and Delaware. Some of these epizootics have been of relatively short duration; others have dominated muskrat populations to the extent of allowing little population recovery for years.

Once a deadly epizootic of the hemorrhagic disease gets started on a marsh, its course may be quite unpredictable. It may depopulate the whole area of muskrats, leaving no survivors, and it may do this either in cold or warm weather. It may depopulate only part of a marsh, then inexplicably subside for weeks or for years. It may advance over a marsh on a single front or on several fronts. It may or may not advance in several places simultaneously. Animals may die locally now and then without real epizootics getting started. Some areas or parts of areas in a region may appear essentially free of infection and others may be saturated with it, but freedom from infection should never be thought to be absolute, in view of the known inclinations that diseased muskrats may show for wandering. The hemorrhagic disease probably gets around ultimately about wherever there are muskrats, however much its manifestations may vary after it gets there or however long it may remain a lethal agency.

The many years of detailed studies of the hemorrhagic disease on central Iowa streams and at Goose Lake, Little Wall Lake, and Wall Lake have yielded data that surely must typify much to be expected of the disease over the geographic range of the muskrat. The known die-offs, occurring in such widely separated parts of North America as the Malheur marshes of Oregon, the Sand Hills of Nebraska, the marshes south of lakes Winnipeg and Manitoba, the Saskatchewan River Delta, the marshes of the Lake States and those of the East Coast are so similar to those of the closely studied Iowa areas that it may be assumed that the findings from the Iowa studies probably apply to these other places, also.

The best Iowa example of severe, locally uncompensated disease mortality is from the first real study of a hemorrhagic epizootic—the collapse at Goose Lake in fall and winter, 1943–44, with no evidence of any muskrats surviving on the marsh. Not only did the disease leave the marsh depopulated after that epizootic but it also impaired the habitability of the marsh for muskrats for the next several years because of the thorough "seeding" of infection that took place during the die-off. However, the population effects of the disease mortality on very much lower populations of succeeding years are not so easily appraised. Of what real signficance was the annihilative disease mortality of the summer of 1946, when fall ingress brought back the population to about what seemed to have been the current supporting capacity of the marsh for muskrats? Or, the partial subsidence of the epizootic of 1947, only to leave the survivors to winter-kill? But the depopulation of the north half in the fall of 1944, the substantial losses of the central part in the fall and winter of 1945–46, and the dying in scattered places in the fall and winter of 1946–47 almost certainly resulted in a net lowering of the numbers of muskrats wintering, whether or not the habitat was actually filled to capacity by breeding animals again in the spring.

At Little Wall Lake, the population effects of the sweeping spring and summer epizootic of 1945 seemed to have been quite well offset through fall ingress, and by winter the marsh may have had about as many muskrats as could have been comfortably accommodated. The epizootic at Little Wall Lake having the clearest population effect was that occurring in the summer of 1951, and this certainly did leave fewer muskrats present by late fall than should have been there otherwise, thus bringing about a reduction of the muskrat population at least by half. On the other hand, the dying of about 200 (or far more than survived) in the spring of 1947 still left a fair breeding stock for the marsh in its existing condition.

Likewise, the numerically severe losses on most of the disease-swept parts of Wall Lake in the spring of 1948 left a great adequacy of breeding stock for the marsh as a whole. Except for the parts dominated by a continuing warm-weather die-off, even the depleted tracts soon refilled to capacity. This afforded a good example of losses substituting for each other within the framework of a larger pattern. But the epizootic that did continue kept an otherwise suitable tract effectively depopulated during the breeding season, and the spreading autumnal die-off of the same year among animals otherwise favorably situated had a net depressive influence in terms of the population present by freeze-up.

The 1949–50 losses at the main Wall Lake disease foci may not have done much more than to have given the populations a better fit with respect to the drought-restricted carrying capacity of the marsh in 1949 and 1950. In 1951, when Wall Lake was in excellent condition and the survival rates of young were very high, the spring losses of adults through disease probably did result in some net lowering of the population present by fall, if only through reduction of the numbers of young born in a habitat that was far from being filled to capacity with the species.

The extensive population adjustments frequently shown by muskrats of the central Iowa stream habitats greatly complicate efforts to appraise population effects of disease mortality. A big question to consider is whether declines in some tracts were or were not counterbalanced by gains in others. Disease losses of central Iowa stream-dwelling muskrats appeared to have had as much net influence on population levels in 1945 as in any single year of investigation, with the possible exception of 1949. The disease losses suffered by muskrats of the stream habitats during late summer and fall of 1949 substituted in part for drought losses, and in some places such as the Story City ditch, it may be judged that the muskrats probably would not have gotten along much better if the habitat had been disease-free. In contrast, the disease was quite evidently depopulating long stretches of Skunk River south of Cambridge in a way scarcely suggesting substitution phenomena or any sort of compensating gain.

Numerically light disease losses may have their confusing aspects. It is hard to assign much population effect to the dying of a muskrat here and there over the observational areas, when nothing like a sweeping epizootic may be in progress. Yet, when only a small proportion of the animals infected may be dying, when light mortality may belie widespread prevalence of infection, then may we wonder about the lethal potentialities of seemingly rather innocuous infections. Considering the thoroughness with which Wall Lake appeared to be "seeded" with hemorrhagic disease by the fall of 1951 – even though very few muskrats were actually dying – might not deadly epizootics be expected there if for any reason the collective resistance of the population were drastically lowered?