

## **Chapter 17**

### **The Muskrat and Population Cycles**

The more or less periodic or cyclic of population fluctuations have drawn the attention of literate observers for centuries. Primitive peoples dependent for their livelihood upon violently fluctuating food or fur animals, or agricultural communities subject to devastating abundances of rodents or lagomorphs, doubtless have been aware — in a very personal sense — of the reality of great fluctuations since long before languages were written. The consequences of these changes to human economics may be tragic under extreme conditions, particularly in northern regions where events such as the famine in Longfellow's *Hiawatha* have had their many counterparts in actuality.

The past quarter-century has been one of especially pronounced scientific interest in the so-called "cyclic" fluctuations of wild species. A great diversity of viewpoints exists as to whether population cycles can be explained by chance variations, by climatic variations, by variations in food supply or habitat niches, or by variations in predator pressures. In the tremendous mass of existing literature on animal fluctuations, the reader may find a bewildering array of statistics, miscellaneous facts, hypotheses of all shades of credibility, and, as Cole (1951, 1954b) has emphasized, interpretations that may be subjectively colored. There have been disagreements as to whether fluctuations are or are not species characteristics. Some authors have looked for a single underlying master factor, and some, for a multiplicity of factors. Some have felt that the phenomena classed as "cyclic" are explainable in very commonplace terms and others that we are here confronted by unknowns that are among the greatest in biology, perhaps beyond human comprehension.

My own attitude is one of suspicion for the easy answers. I consider that two symposium papers (Errington, 1954a, 1957) have summarized my thoughts on cyclic phenomena about as well as anything I am currently prepared to write, and I shall quote and cite them at length in this concluding chapter.

First, from Errington (1954a):

The resulting literature [ on population cycles ] has become so voluminous in the English, German, and Scandinavian languages alone, that I doubt that any one person could now truly master it in a lifetime, even if he were competent in all of the fields of science contributing. Its scientifically reputable authors include not only biologists of many fields but also economists, meteorologists, astronomers, and mathematicians. The subject matter so treated is sufficiently complex and lacking in first-class data to make it extremely difficult to judge whether we are on the trail of the truth or not, or what the truth may mean if we have it before us.

For persons wishing to have a background of modern thought, I would recommend the symposium edited by Hewitt (1954) and, further, the books, review papers, and discussions by Elton (1942), Bump, Darrow, Edminster, and Crissey (1947), Allee, Emerson, Park, Park, and Schmidt (1949), Grange (1949), Solomon (1949), Franz (1950), Rowan (1950), Christian (1950), and Frank (1957). These illustrate the major differences in viewpoints among biologists studying population cycles, and, to resume quotation from my 1954a paper, the

reader should be prepared for divergent and conflicting opinions, without interpreting them as meaning that anyone is necessarily all right or all wrong.

My own views concerning population "cycles" have changed . . . and very probably they may change some more, very probably also in ways that I cannot now predict. As one investigator, I do not in any way claim to have the answers to the ancient mysteries of "cyclic" or like fluctuations of species, my own research specialties among these species included. But, since I have long attributed some of the outstanding confusion in the literature on population "cycles" to undue preoccupation of scholars with numerical fluctuations, *per se* . . . , my hope is that a presentation of data from a different approach may help reconcile some of the controversies that are currently so apparent. Better progress toward what are (or should be) mutual objectives in studying population "cycles" might be possible if the more distracting areas of disagreement could be reduced. I think that they can be.

This chapter, which is submitted neither as a comprehensive review nor as a solution to cyclic mysteries, is intended to be a factual presentation and discussion of evidence obtained from the muskrat investigations. By restricting its scope to the north central region of my greatest familiarity, I think that I can lay the most accurate groundwork for the following treatment. There are complexities and apparent contradictions enough in our knowledge of population cycles without here attempting approaches on a global scale at this time.

## INTRODUCTION TO SOME CHRONOLOGICAL SIGHTING POINTS

Of all of the different cycle-lengths assigned by modern investigators to animal fluctuations (Wing, 1951–57), those occurring approximately with three-to-four-year and with 10-year rhythms seem to show the greatest likeliness of validity as applying to common mammals and birds. Insofar as the shorter-term fluctuations are considered by some authors (Vinogradov, 1934; Siivonen, 1948) to be related to and a part of the 10-year, I have no intention of trying to dissociate them with more finality than is scientifically proper; but the muskrat field data have had much more of an evident relation to the 10-year cycle than to the three-to-four-year. The latter is manifested especially by vole and lemming fluctuations (Elton, 1942).

Before proceeding, I should emphasize that the actual population levels reached or maintained even by species labelled “cyclic” can be resultants of numerous factors, among them some factors that operate most irregularly in ordinary time scales: the big emergencies and epizootics, plant successions following disturbances, changes due to human land uses, the letting out and taking up slack by the density factor. The more synchronous of the recorded fluctuations of vertebrate populations have been almost a property of regions lying in northern parts of the northern hemisphere (Rowan, 1950), but not exclusively so (Elton, 1942; Bodenheimer, 1949; Wodzicki, 1950, pp. 139–41).

In the “North Woods” parts of the north central region, to quote Errington (1957),

the ruffed grouse (*Bonasa umbellus*) and snowshoe hare (*Lepus americanus*) are not only characteristic species but they are also notable for their fluctuations. They go through periods of abundance and scarcity at approximately 10-year intervals. While such periods may not be exactly synchronous in all parts of the grouse and hare range even within the region (or even locally), the over-all effect is close to a rhythmic pattern. The ruffed grouse and snowshoe hares are among the “classically cyclic” species, if any may be so designated. . . .

Neither the ruffed grouse nor the snowshoe hares are animals that I am entitled to refer to as specialties, but I can claim some familiarity with their habits and ecology, and I have had much discussion and correspondence with field biologists who have made special studies of these and related species. The picture that shapes up from all sources is that at least the ruffed grouse and snowshoe hares of central and northern Minnesota and Wisconsin have generally been reaching peak population levels in or near the years ending in ones or twos and minimal populations in or near the years ending in sixes or sevens.

It should be made clear that an occasional abundance peak may carry over into the years ending in threes or fours or even later, and an occasional period of scarcity may be apparent in a year ending in a five or even considerably earlier in a decade. The grouse and hares need not fluctuate in complete agreement with each other, and the impacts of emergencies or environmental changes may be so great as to overwhelm populations, seemingly irrespective of any particular time schedule. Year-to-year differences in populations may not be great even when a high phase is shifting

to a low phase. Superimposed on the trends in annual fluctuations may be the long-term population trends of either the ruffed grouse or the snowshoe hares in a given area — as human land use and plant succession bring about their changes over the decades.

Yet, throughout these interplays of variables, something that might be called a master pattern does seem to dominate; and the one-two and the six-seven year-groupings are worth paying attention to. If there is a significant chronology in the grouse and hare fluctuations of the north-central region since the turn of the century (I am refraining from making statements about other regions), it would seem to be linked with the above year-groupings.

In Iowa and southern Wisconsin, my own long-term research specialties, the bobwhite quail (*Colinus virginianus*) and the muskrat . . . may at times show fluctuations as pronounced as those of the grouse and hares of the northern parts of the north-central region. Sometimes, the quail or muskrat fluctuations line up with those of the grouse and hares; sometimes, they do not. If fluctuations alone were all we had to compare, we would have scant grounds for expecting to find any common time schedule in the "cyclic" manifestations of the grouse and hares and of the quail or the muskrats.

The quail and the muskrats have adaptations and habitat requirements differing greatly from those of each other and little resembling those of either grouse or hares. Both quail and muskrats are far more vulnerable to certain types of emergencies than are the grouse and hares.

In this region, the staple winter food of the quail consists of grains of cultivation and other seeds that have proteins, carbohydrates, and fats in concentrated and readily available form. By midwinter, almost all of this quail food remaining in fields, pastures, and woodlots is on the ground, and, if snow covers the ground, it also covers much if not most of the food. Insofar as the quail have no aptitudes for digging or scratching down through deep snow to reach food, a winter of heavy snowfall may all but annihilate them from the more northerly parts of their geographic range.

A wintering population may collapse within a couple of weeks, whenever a foot or two of snow-covering persists as long as that. The quail, which lose weight fast after the first two or three days of a hunger crisis, begin dying of starvation after about a week — or even before the end of the first week. Contemporaneously, the ruffed grouse and snowshoe hares of the "North Woods" may winter well-fed on the plant foods that they are adapted to eat and accustomed to find above the snow. . . .

The muskrat, a semi-aquatic rodent, is naturally susceptible to drought emergencies. Factors other than drought may influence the population levels reached or maintained by the species, but it should be safe to say that there is nothing like a series of drought years to reduce the north-central muskrats and keep them reduced. In extreme cases, droughts may leave entire counties devoid of muskrats, and an experienced field observer may then need no refined measurements of environmental changes to identify the dominant factor.

For the 24 years — 1934 to 1957 — that intensive muskrat studies have been carried on in Iowa, 17 have been years of severe droughts for muskrat populations of the study areas. Only 1935, 1938, 1942, 1943, 1946, 1951, and 1954 may be rated as drought-free years for the muskrats. Whether anyone would argue that the drought years are the normal years for this series, the droughts came at intervals that look more irregular than regular; and the lack of close agreement between the fluctuations of Iowa's muskrats and the more rhythmic 10-year pattern of Minnesota's and Wisconsin's ruffed grouse and snowshoe hares should surprise no one.

During my first decade of association with Aldo Leopold, and despite the interest that I felt in the work he was doing on population cycles, I did not see how the bobwhite quail and the muskrats could have any real tie-up

with the "10-year cycle" of the grouse and hare fluctuations. If, as of the late Thirties or the beginning of the Forties, I may be charged with having biases concerning the "cyclic" status of quail and muskrats, they were the biases of skepticism.

I still make no claims that "cyclic" tie-ups between the grouse and hares and the quail and the muskrats are proven to exist. I do not know for sure whether they do or not.

By the early and middle Forties, the data from the quail and muskrats were revealing synchronies that might suggest physiological and psychological responsiveness to some common denominator. If there is a common denominator behind these synchronies, I should not expect it to be definable in ordinary climatic or environmental terms. Such a possibility would seem to be ruled out by the differences in behavior, adaptations, and habitat requirements of the species with which we are concerned.

Let us then go on to consider the evidence of synchronies we have from the quail and muskrat studies and, while doing so, keep in mind the one-two and the six-seven year-groupings that seem most meaningful from the standpoint of the grouse and hare fluctuations of north-central United States.

Both my 1954a and 1957 papers illustrated how imperfectly the fluctuations in numbers of the Iowa muskrats synchronized with the fluctuations in numbers of ruffed grouse and snowshoe hares, even within a geographical radius of a few hundred miles. While the synchronies that do exist between the muskrats and the grouse and hares in the above respects may have useful biological meaning, I question that they should be given so very much weight in our exploration of possible cyclic phenomena shown by the muskrats.

I recognize the confusion into which this may lead a reader. If, according to my reasoning, more muskrats were present during the cyclic low year of 1946 than during the cyclic high year of 1941, just what may be the basis for assigning a given year to one cyclic phase or another? What may we then expect to be in chronological agreement, to show meaningful correlations?

There are still other synchronies to consider, those relating to evident changes in the physiology of the muskrats, whether such changes resulted in population changes or not. Unless otherwise indicated, the following quotations are from Errington (1957).

#### CYCLIC PATTERNS IN REPRODUCTION

The main reproductive data tabulated in connection with the Iowa muskrat studies related to: (1) mean sizes of litters conceived by or born to fully adult females, (2) proportions of young females breeding precociously during the calendar year of their birth, (3) proportions of adult females conceiving young during the breeding season, (4) mean numbers of litters per adult breeding female during a breeding season, (5) proportions of adult females conceiving their usual Iowa maxima of four litters during a breeding season, (6) proportions of litters born later in the summer than the middle of July, and (7) proportions of late-born young among the young of the year surviving up to late fall or early winter.

The high and low values for the above categories 3 to 7 showed little or no correlation with either the one-two or the six-seven year-groupings. This

may be seen in the data tabulated in my 1954 paper, and the subsequent data are similarly non-committal. It is still possible that changes in reproductive vigor could result in changes in mean numbers of litters conceived, in prolonged or retarded breeding seasons, and in increased or decreased survival rates of late-born young, but year-to-year variables having no visible relation to patterns in year-groupings afford likelier explanations for the observed differences.

For example, the proportions of adult females passing through an annual breeding season without conceiving depend principally upon the chance isolation of females outside of the usual travel routes or home ranges of prospective mates. We have good field data illustrating this. Many other differences in breeding performances depend upon situations that vary from year to year. Either severe early-season losses of young or a state of underpopulation of muskrat habitats may be accompanied by the birth of more litters per adult female, by prolongation of the breeding season and by increased survival of late-born young (Errington, 1951). These differences are not wholly without their evidences of some synchronizing with year-groupings, but the naturally compensating adjustments that one may expect in almost any year leave most of the reproductive data too obscured for "cyclic" correlations.

Our reproductive data on muskrats that seem most independent of compensating adjustments and the usual types of environmental influences relate to mean sizes of litters of adult females and to the precocious breeders among the young females.

Of these latter two categories of data, the mean sizes of litters seem to be influenced the least by drought, by local differences in food supply, and by population tensions among the muskrats. The litter sizes of a drought-exposed, hungry, or crowded population may average a half muskrat smaller than the litter sizes of a well-situated neighboring population, but that is about as much difference as the case histories of our Iowa study areas show in a given year. At their greatest, such differences look inconsequential compared with the differences shown between the chronological "highs" and "lows" of the "10-year cycle." Between the one-two and six-seven year-groupings of . . . [Figure 17.1], the difference in mean size of litters can be about two muskrats.

Our central and northern Iowa data on a total of 2,656 litters over a period of 22 years have a mean value of 7.49 young per litter. The minimal figures for each of three decades — 6.35 to 6.42 — came 10 years apart, in 1936, 1946, and 1956, but I do not regard that as signifying any absolute periodicity. The high-value means for the early Forties reached more of a peak, with 8.19 for 1941 and 8.41 for 1942 than did the high values coming later: 8.09 for 1949, 7.95 for 1950, 8.17 for 1951, 8.01 for 1952. The mean for 1951 was almost the same as the mean for 10 years earlier, but there seemed to have been less conformity to anything resembling periodicity in the peaks than in the years of minimal values. The mean that breaks most the smoothness of the wave-like pattern of . . . [Figure 17.1], the 7.29 for 1937, is statistically the poorest in our 22-year series.

Seventy-four, or 1.5 per cent, of samples totaling 4,785 young female muskrats examined in November and December of the calendar year of their birth had conceived young during the second half of the summer. Except for an animal giving birth to two litters during its own birth year, all of the above precocious breeders were one-litter females conceiving small (averaging 5.3 young) litters.

The data on precocious breeding . . . [Figure 17.1] lack the correlation with the one-two and six-seven year-groupings shown by the changes in mean sizes of litters conceived by adult females, but precocious breeding appears to have been rather restricted to the years centering about the chronological

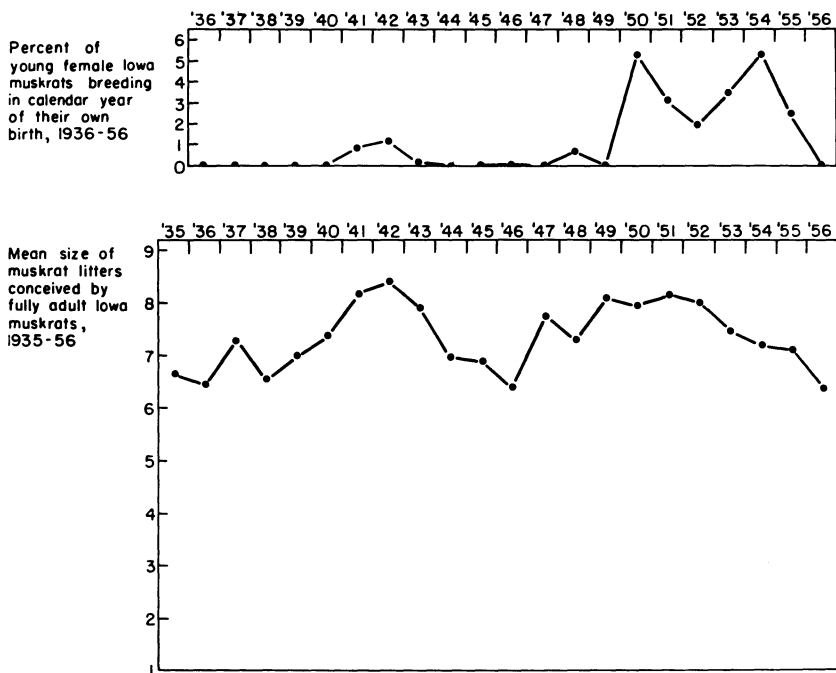


Fig. 17.1. Alignments with year-groupings shown by certain changes in reproductive performances of Iowa muskrats, 1935-56. (After Errington, 1957 — Cold Spring Harbor Symposia on Quantitative Biology.)

“cyclic highs.” It is true that the incidences of precocious breeders in the samples are much higher for the 1950 to 55 year-grouping than for that of 1941 to 43, besides reflecting a greater year-to-year prolongation of the phenomenon.

Late summer droughts, population crises, and possibly other factors than “cyclic” chronologies can be expected to have had irregular effects on precocious breeding among Iowa muskrats, but something a bit special may have been required to damp or to stimulate the reproductive physiology of the young. A substantial amount of late breeding or what might be called full-scale breeding by *bona fide* adults occurred during the “cyclic low” years of 1946 and 1956, when no precocious breeding was recorded from our specimen series.

Anyone wishing to do so may bring Figure 17.1 up to date by adding the 1957 values presented in Chapter 1: 2.0 per cent precocious young females (Table 2.3) and 7.58 mean size of litters conceived by adult females (Table 2.4). It may be of some significance that the litter sizes for 1937, 1947, and 1957 — the years immediately following the lowest-value years for each decade — rose as abruptly as they did, and that, at least following 1937 and 1947, the curve dropped down again before resuming the upward trend.

**CYCLIC PATTERNS IN SYNDROMES OF THE HEMORRHAGIC DISEASE**

A great many attempts have been made to link cyclic declines of animal populations with disease, and while disease has often been prominent among the population symptoms observed, it has not invariably been so. Neither have many specific diseases played any uniform roles in these population declines, even over relatively short periods of years.

Before introducing our data on disease in muskrats in relation to "cyclic" chronologies, I should like to clarify one point: With the approach of the chronological "cyclic low," we do *not* necessarily find that more muskrats, or larger proportions of muskrat populations, are contracting or dying from disease. The spread of epizootics in muskrat populations varies so much with chance and with local situations that I should not expect changes in incidence of infection to be among the better criteria for judging stages of the "10-year cycle."

On the other hand, changes in mortality rates of the animals that are infected with a serious contagious disease could fit in with year-to-year changes in the physical well-being of populations. . . .

On less than 27 square miles of our regularly observed study areas in central and northern Iowa . . . [the hemorrhagic disease] has killed a calculated total of about 8,500 muskrats of larger than suckling sizes since our intensive disease work was begun in 1943. Some data were acquired on upwards of 1,400 individuals among the victims, and, of these, 568 were found in passable to excellent condition for postmortem examination. . . .

First, from the 568 specimens, let us subtract 70 having lesions dominated by pneumonitis or lung hemorrhages. There seemed to be no year-groupings, either at high or low phases of the "10-year cycle," when pneumonic syndrome epizootics might not sweep through a muskrat population if such an epizootic got started under conditions favoring its spread. We have had locally annihilative mortality from the pneumonic syndrome on Iowa marshes during years when the muskrats had practically stopped dying from the other syndromes.

The lesions of the remaining 498 specimens diagnosed as victims of the hemorrhagic disease were mostly necrotic foci in livers and intestinal hemorrhages, together with minor hemorrhages in other parts of the body, including lungs. Victims might have few if any gross lesions in their viscera yet be members of local populations patently collapsing from the hemorrhagic disease in the space of a couple of weeks; or as much as a quarter of the volume of the victim's liver might be necrotic, with lesions in all stages of onset and healing.

These differences were discussed at some length in my 1954 paper, and I believe that they mainly reflected differences in resistance of the muskrats to the disease—or, at any rate, differences in length of time that victims were able to stay alive after becoming infected. For purposes of this presentation, I therefore feel justified in taking the short-cut of referring to superior, intermediate, and inferior resistance on the basis of lesions shown by hepatic-enteritic syndromes.

It is true that all of the animals of . . . [Figure 17.2] died, whether dying after a month's struggle with the disease or staying alive only a few days, but the apparent differences in resistance still line up with "cyclic" chronologies. . . .

The syndrome data . . . show their first big change as of about mid-year, 1944. Most of the 38 specimens posted from fall, 1943, through the summer



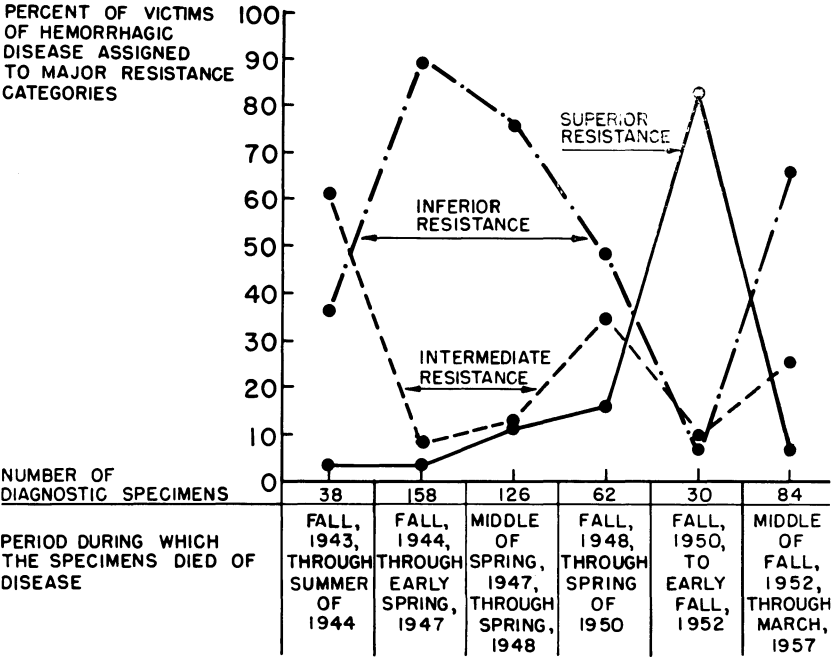


Fig. 17.2. Alignments with year-groupings shown by changes in disease syndromes in Iowa muskrats, 1943–57. (After Errington, 1957 – Cold Spring Harbor Symposia on Quantitative Biology.)

of 1944 had the liver lesions that we usually found in animals known to have stayed alive a week or longer after exposure to the infection, but a series of 85 specimens for fall and early winter, 1944 to 1945, was made up largely of victims that evidently had died before liver lesions had time to form. Thereafter, until about half-way through the spring of 1947, the lesion syndromes for 73 more specimens followed a similar pattern, seemingly indicative of lowered resistance.

For a brief period in late spring and early summer, 1947, the victims included a number having the massive liver necrosis that undoubtedly took more than a week or so to build up, but there were only nine specimens in this sample, and the influence of these . . . was swamped by the 117 other postmortems from the middle of the spring of 1947 through the spring of 1948. From the middle of the spring of 1947 through the spring of 1950, the over-all trend of 188 postmortems showed a gradual increase in proportions of victims that evidently succeeded in staying alive longer.

The hepatic-enteritic syndrome changes of the early Fifties were the most pronounced. Although the postmortems for a series of only 30 specimens may leave doubts as to the adequacy of the sample, the field data from other sources supplement very well the postmortem data from these disease victims.

During this period of the fall of 1950 to the early fall of 1952, muskrats could still die on a large scale from the pneumonic syndrome. They could still contract the disease on a large scale when it was manifested by lesions other than the pneumonic – but without dying from it except in tracts of marsh that were persistent foci of infection.

Even in the foci of infection having the deadliest of past histories, rela-

tively few of the animals living there between mid-year, 1950, and mid-year, 1952, succumbed to the disease. Specimens found at the latter places rather typically had liver lesions in conspicuous quantities and in various stages of healing, all suggesting prolonged and repeated infections. The syndromes usually to be seen in the postmortems were those to be expected for unlucky individuals that put up good fights for their lives before dying.

Other data were appraised as pointing in the same direction. Fur trappers on our Wall Lake study area found only two dead from probable disease while trapping about 800 in the late fall of 1950, but 30 of the sample of 446 trapped carcasses that I posted had liver lesions. In the fall of 1951, the trappers found only four probable or verified disease victims while trapping about 1,850, but 45 of my posted sample of 450 had liver lesions. In this connection, it should be mentioned that incidences of one or two per cent of the trapped carcasses with liver lesions would not have been surprising, but incidences of six to 10 per cent for the above samples were astounding and, in these cases, interpreted as signifying both an unusual occurrence of the disease in the marsh population and unusual proportions of infected animals remaining alive and sufficiently active to be caught in traps.

Of the 75 posted specimens having liver lesions among the Wall Lake carcasses trapped during the falls of 1950 and 1951, most were of animals less than four months of age. This itself was significant. During years when muskrats were suffering locally annihilative mortality from hepatic-enteritic syndromes of the hemorrhagic disease, the very young victims seldom had anything more than the slightest of gross lesions in their viscera; but, in 1950 to 51, it was clear that even the highly susceptible young were coping with their infections. Their livers had extensive necrosis in many cases, but such animals were rarely dying in the field.

After this two-year period of wide-spread contagion and little mortality except for the irregular flare-ups of pneumonic-syndrome epizootics, animals started dying again from hepatic-enteritic syndromes about as they had been doing in the late Forties. The syndrome changes were about as expected, and, as the mid-Fifties came on, the specimens became increasingly reminiscent of those of the mid-Forties. As of the spring of 1957, an epizootic has almost wiped out the main population the last drought left us on our study areas, and the lesion syndromes suggest low resistance on the part of the muskrats.

The standard questions regarding immunology of the muskrats or possible changes in virulence of the infectious agent that naturally come to mind are partly answered by what data we have.

The Wall Lake muskrats that almost stopped dying from the disease when they contracted it in the fall of 1950 — and showed such changes in lesion syndromes when they did get fatal dosages — were members of the same local population groups that died readily in the spring and early summer of the same year. The converse in 1952 would seem to eliminate any hypothesis that the population had merely built up resistance through contact with the disease. In 1952, the population groups of muskrats that were resisting the disease on a large scale in spring and early summer included the same ones that were dying from it, with changed lesion syndromes, in the fall.

Furthermore, these changes in syndromes and mortality in the early Fifties were not peculiar to Wall Lake nor to any one study area. At about the same time that the syndromes and mortality patterns changed at Wall Lake, they also changed on our other study areas. Field data — including those from marked animals — indicated that at least certain population groups were essentially self-contained during the seasons when the more abrupt changes took place in 1950 and in 1952. In the fall of 1952, the changes were noted

more or less simultaneously in areas situated as the points of a triangle eight, 22 and 29 miles apart and all well isolated from major routes of travel of adjusting muskrats.

In my opinion, the observed changes in syndromes were due to changes in resistance of the muskrats rather than changes in virulence of the infectious agent — though the possibilities of changed virulence should never be ignored. The concept of changed resistance makes much more sense when considered along with the other “cyclic” manifestations, along with the increasing and decreasing of mean sizes of litters and the behavioristic changes that presumably accompanied changes in the physiology of the animals.

### CYCLIC PATTERNS IN BEHAVIOR CHANGES

If changes in muskrat physiology are linked with “cyclic” year-groupings, then it would seem likely that changes in muskrat psychology might have similar chronologies.

Nothing much that is new about toleration of muskrats to crowding by their own kind has come out of the Iowa studies since preparation of my 1954 paper, but the trends of our data may here be reviewed.

For marshes dominated by . . . choice food plants, spring densities of muskrats frequently exceeding the equivalents of five or six pairs per acre were tolerated during the year-groupings of 1941 to 43 and 1951 to 52. Observed concentrations approached the equivalents of eight pairs per acre over sizable blocks of marsh in 1943 and 10 pairs per acre in 1952.

Maximum breeding densities for the same or the same types of marshes generally leveled off at the equivalents of two or three pairs per acre during the 1936 to 1937 and 1946 to 1947 year-groupings, even though much higher muskrat populations were present in 1946 to 1947 than in 1936 to 1937. (Actually, the spring of 1947 was one in which the muskrats showed less intra-specific tolerance than in 1946.) Intermediate concentrations occurred during the years intermediate in chronology between the one-two and the six-seven year-groupings.

It should be emphasized that the maximum spring concentrations shown during the above year-groupings are not explainable merely in terms of more muskrats being present in some years than in others. In the spring of 1936, despite the low populations existing on the better Iowa marshes kept under regular observation, maximum breeding densities the equivalents of two or three pairs per acre still meant conspicuous numbers of battered transients working the marsh edges. Such transients represented a biological surplus in that animals in residence did not permit them to establish territories in the kinds of places that would be most attractive to muskrats, the relative abundance of favorable environment and the low populations of the muskrats, notwithstanding. When large numbers of muskrats remained on an area at times of acute intolerance toward crowding, breeding territories might be distributed with striking uniformity throughout good and poor environment, alike. The muskrats then seemed much more disposed to try to maintain themselves in inferior places than to try to crowd into the attractive places maintained and defended by their better-situated fellows.

In contrast, at times of the higher tolerances to crowding, the muskrats of observed marshes packed their breeding territories into the most attractive cattail and bulrush stands to such an extent that wide expanses of less attractive — but more or less habitable — environment remained sparsely occupied. The animals patently did not accept the poorer grades of environment when they could choose the better with no more trouble from antagonistic fellow muskrats than they usually had during the two chronological “cyclic highs” that I have studied.

These differences in social tolerances of muskrats of course affect the net habitability of a marsh or stream for the species. No greater numbers of the

animals can be expected to maintain themselves than will be tolerated by their own kind, irrespective of whether, for example, sufficient food may exist to feed several times the numbers that are able or willing to stay there and face trouble to utilize it. The manifestations of overpopulation (including unrest, withdrawals, and fighting) have looked the same to me for the "cyclic low" maxima of two or three pairs per acre as for the "cyclic high" maxima of eight to 10 pairs.

I think it would be accurate to say that the muskrats feel crowded when they act crowded, at levels that are numerically low as well as numerically high; and that their population tensions during the breeding season differ with the year-groupings in ways that do not seem to be correlated with the more obvious climatic and environmental differences.

Three years of our Iowa studies — 1936, 1945, and 1946, all at or near chronological "cyclic lows" — were notable for cross-country movements of muskrats in summer and fall. Cross-country movements at this time of year are much more indicative of panic or desperation than the orderly adjustments up- and downstream or from shallow to deeper parts of marshes that may be expected in any year when muskrats become dissatisfied with the places in which they are living. Footloose wandering is one of the most hazardous of activities for muskrats and it ordinarily is not resorted to on any large scale unless something is very much wrong.

While 1936 was a year of great drought crises, the drought of 1945 was only of moderate intensity from the standpoint of central Iowa muskrats. There were several other years of our period of study in which drought conditions were as bad as, or worse than, in 1945 and during which no comparable cross-country movements occurred. And 1946 was not a drought year, nor a year of any events that seemed, to my eyes, unfavorable for muskrats; but entire study areas in central Iowa were abandoned by the muskrats in late summer and early fall, to the accompaniment of large-scale cross-country movements and massing of new-comers in a few bodies of water. The year most comparable to 1946 in muskrat populations and in environmental conditions for muskrats was 1951, in the chronological "cyclic high," but practically no cross-country movements of muskrats were then detected.

The data we have on lengths of time that muskrat populations of food-rich marshes remained in their regular home ranges despite severe drought exposure in summer and fall also suggest big differences in behavior. Our best comparisons are provided by case histories, 1936 to 1952, of 44 local populations. Twenty-four populations remained an average of about five weeks after disappearance of the surface water before abandoning their home ranges to wander, and the other 20 remained an average of about three months. All except three of the 24 populations in the less tenacious group dated to years of chronological "cyclic lows" or impending "lows." Only four of the 20 populations of the more tenacious group dated to or near years of "cyclic lows," and three of these four showed the lesser degrees of tenacity for the group.

With the beginning of the Fifties, separation of populations into more tenacious or less tenacious groups became less satisfactory. The fall of 1952, which lined up with or surely came not long after a chronological "cyclic high," was a time of conspicuous abandonment of food-rich shallows on one of our marshes. During the droughts of 1953 and 1955, some populations abandoned food-rich home ranges and some did not.

Another fact that introduces doubt as to how good these observed differences in tenacity toward home ranges may be as criteria of "cyclic" influence is the lack of differences in behavior shown by populations wintering in drought-exposed though food-rich places. Data in hand relating to 36 local populations do not seem to reveal greater tendencies for abandonment under such conditions during years of chronological "cyclic lows" than dur-

ing "cyclic highs" or any other years. The majority of the animals usually held on to their accustomed home ranges in winter as long as they could stay alive.

The chronological "cyclic low" year of 1956 was not, except in one respect, a year of distinctive behavior of muskrats in central and northern Iowa. However, the one population symptom that did stand out during the summer was so pronounced as to be without counterpart during the other years of our studies.

By early summer, the drought had left only two of our long-studied areas with substantial numbers of muskrats—Wall Lake with about 200 adults maintaining about 80 territories and Little Wall Lake with about 170 adults maintaining 67 territories. Both marshes were rich in muskrat foods, but, by September, Wall Lake was drought-exposed and so was more than half of Little Wall Lake.

The remarkable thing is that Wall Lake became nearly abandoned by its muskrats *before* the surface water disappeared. As early as the middle of June, while the deeper parts could still be navigated by canoe, I found evidence of territorial abandonment; and, within the next two weeks, abandonment continued to the extent that I could find only two maintained breeding territories left on the marsh. Following this period of abandonment, a population estimated at about 45 (consisting chiefly of very large animals) maintained itself in the dry cattails and bulrushes with slight further change until late fall.

At Little Wall Lake, only 20 of the 67 territories maintained in mid-June were exposed by drought in late June, July, and August, but most of these and at least 20 additional territories were abandoned without the appearance of corresponding numbers of animals elsewhere on the marsh. This occurred at the same time as the large-scale abandonment at Wall Lake. The remainder of Little Wall Lake's 67 territories (or about 25 scattered over about 100 acres of wet marsh) were productive, and the early fall population of muskrats was about 220. In late fall, a heavy ingress totaling about 330 muskrats from outside sources resembled the fall ingress of the "cyclic low" year of 1946.

For one abandoned territory after another, at both Wall and Little Wall Lakes, the 1956 story was similar: Residents not only failed to show any tenacity in maintaining their territories during the drought but they did not even begin to await drought-eviction before departing. The food was abundant and of superior types, inches of water still covered the marsh bottoms, and the territories were not sufficiently crowded anywhere to promote much friction. The animals simply left, to take their chances trying to get along in strange environment, living for variable periods of time in places that were usually far less attractive than their old familiar ranges, and otherwise engaging in activities that had little pleasant future for the majority of the participants. Theirs was a special kind of mass recklessness.

#### WHAT CAN THE SYNCHRONIES MEAN?

Of course, the first question to consider with respect to cyclic phenomena in muskrat populations is the extent to which we are dealing with actuality.

To quote again, now from Errington (1954a):

Palmgren (1949) and Cole . . . have discussed random series of numbers that fall in patterns similar to those of some fluctuations of animals. For one as doubtful of the validity of most population fluctuations as "cyclic" criteria as I have become . . . their writings naturally leave me with heightened

distrust of conventional methods of exploring "cyclic" possibilities in wild populations. . . .

So far as the Iowa muskrat data in my possession are concerned, I would say that straining to prove or to disprove their connections with the fluctuations of "North Woods" hares and grouse by concentrating on mere parades of numbers has scant prospect of getting anywhere unless it be farther toward analytical chaos. But, emphasis transferred from changes in numbers of muskrats to the synchronies in population symptoms that are not necessarily tied up with gross fluctuations of the muskrats seems to me most rewarding. At any rate, from the modest start we have thus made, we are entitled to say that the newer evidence as to "cyclic" changes or synchronies in muskrat physiology and psychology is worth considering.

Of population fluctuations of north-central animals, those of snowshoe hares and ruffed grouse may logically be suspected of reflecting extramundane influence if any may be — though it is apparent (Grange, 1949) that some of the more ordinary of environmental and climatic factors are important in the life equations of hares and grouse, as well. Of the known year-to-year fluctuations of animal life in this region with which the Iowa muskrat data here treated show synchronies, none would seem to be more indicative of a common denominator than the fluctuations of hares and grouse. I do not know what such a common denominator might be, whether it be labelled cosmic, astronomical, solar, extramundane, or something else.

I do not see how environmental or climatic changes, as usually defined or interpreted, can explain the synchronous decreases or increases in populations of hares and grouse of northern Minnesota and Wisconsin and the decreases or increases in litter sizes of central Iowa muskrats, nor why a series of peak years for hares and grouse should be the years during which young Iowa muskrats were found to be breeding during the calendar years of birth. Nor why peak years of hares and grouse should be the only ones during which any substantial proportions of central Iowa muskrats were known to recover from infections of the hemorrhagic disease, nor why the apparent resistance of central Iowa muskrats collapsed about the time that hares and grouse went into their declines hundreds of miles away.

And, among the population symptoms on which it has been more difficult to obtain quantitative data (but which have been prominent enough to deserve attention), we have Iowa muskrats adjusting to drought exposures, maintaining themselves in definite home ranges, tolerating crowding and trespasses on the part of neighboring muskrats, and living what could be called much more normal and peaceful and secure lives during the upgrade and peak years of hares and grouse. During the downgrade and low years of hares and grouse, Iowa muskrats behaved as if highly restless and irritable and living under a decided, if not wholly definable, handicap.

How could it be, for example, that exceptionally well-situated central Iowa muskrat populations of late summer and fall, 1946, engaged in spectacularly footloose wandering without visible incentive as the "North Woods" hares and grouse reached their "cyclic low," whereas, at more favorable "cyclic" stages, the muskrats at similar or substantially greater densities engaged in practically no footloose wandering, at times even despite drought exposures? Or that, in spring of 1947, the Wall Lake muskrats were so intolerant of crowding as to distribute themselves with notable uniformity at densities of about a pair per acre, throughout poor and excellent habitat, alike — and on Wall Lake and comparable marshes during the "cyclic high" of 1951–52, breeding populations congregated in the choicer habitats at densities up to 10 pairs per acre, at the same time that adjacent habitats having less attractiveness were almost or wholly unpopulated by muskrats?

I do not believe that these alignments are due to chance. If we had only

one set of data that so lined up, I would not feel so confident about this, but, when several whole categories synchronize as well as they do over the period of study, the probabilities of chance being the explanation become sufficiently remote to encourage looking for something else. If we were to leave hare and grouse fluctuations completely out of our calculations, we would still have far too much of a residuum of synchronies in the Iowa muskrat data to dismiss on grounds of randomness. Surely, several of these phenomena must be tied up together, whether occurring with true periodicity or not.

Once more, back to Errington (1957):

As I see them, the year-to-year changes in physiology and psychology suggested by the muskrat data are changes only in degree — neither all this nor all that at any chronological “cyclic” phase. Some individuals had large litters and several of them, some few tenaciously hung on to their established territories or home ranges, and some others were resistant to the hemorrhagic disease during the six-seven year-groupings; but the prominence with which some trends stood out for the different year-groupings affords a basis for concluding that *bona fide* changes occurred.

Probably about a decade after becoming acquainted with Green and Larson's (1938) findings on hypoglycemia in snowshoe hares, I began thinking that the population symptoms I had been seeing in the mid-Thirties and mid-Forties might be those of overstimulation followed by exhaustion. Selye's work (1949) strengthened in my mind the exhaustion thesis in possible relation to “cyclic lows,” and so did papers by Christian (1950) and Frank (1953; 1954; 1957).

Christian and Frank emphasized the role of stress in declines of high-density populations. They have undoubtedly dealt with valid phenomena — phenomena that may dominate population equations when intraspecific tensions become extreme. It is very conceivable that such stress reactions may be a principal agency of population collapse in the three- or four-year fluctuations of the vole, *Microtus*, which is phylogenetically the muskrat's closest living relative.

We cannot, however, stop with the stresses of population peaks if we are to search for any satisfying explanation for the chronologies and changes that are presented by the Iowa muskrat data. There is a lot more in sight than muskrat populations reaching peaks, to decline in consequence of built-up stresses.

If we again consult . . . [figures 15.1, 15.2, 15.3 and 15.4], we may see how little the high- and low-density years of the muskrats are in uniform agreement with the years in which we see the most evidence suggesting either relieved or intensified stress — the one-two and six-seven year-groupings, respectively. Plenty of stress can occur in muskrat populations, not only at high numerical densities — as in 1943 — but also at other times when population densities are not and have not been very high numerically, nor high in relation to visible qualities of the occupied habitat.

To reiterate: Our Iowa muskrats living in superior types of marshes may be said to have acted crowded when they felt crowded, whether their breeding densities were two or 10 pairs per acre, or whether their fall populations leveled off at 10 or 20 or 35 animals per acre over sizable tracts. Whatever may be the reasons, when our nearly a quarter-century of data lined up according to certain year-groupings, the muskrats could show much intolerance at low densities and much tolerance at high densities.

I have been asked, many times, what I thought my data signified and

many times have answered that I did not like to conjecture. My reluctance to theorize is partly due to a disinclination to flounder around outside of my fields of competence and partly, I am ready to admit, to a fear of perhaps making too good a case for something that might not turn out to be true.

I am willing to say that I think my data could be consistent with something like changes in ultraviolet radiation, as such investigators as Rowan (1950) and Shelford (1951) have proposed. As dwellers within our solar system, the muskrats may not spend much time in the direct rays of the sun or even outside of their burrows and lodges during daylight, but the possibilities of their being affected by radiation changes deserves more exploration than anyone, to my knowledge, has given them to date.

If the combination of synchronies to which I am calling attention can be explained with recourse to nothing more extraterrestrial than ordinary sunlight, they are still not explainable in terms of the meteorological changes customarily reported by Weather Bureau stations.

Nor are they explainable in terms of *quantities* of staple foods available to the muskrats.

There remains, however, the possibility that changes in *quality* of food may have underlain some of the population symptoms associated with cyclic year-groupings shown by the Iowa muskrat data. I know of no place in the literature where I have felt that this food-quality concept had been thoroughly developed with respect to any population cycle but have come to feel least surprised when finding it advanced by Finnish and Scandinavian authors — such as recently by Svårdson (1957).

Braestrup's (1940; 1942) hypothesis was that cyclic die-offs may be due to lack of availability of essential minerals in plant foods. He noted similarities in the cyclic symptoms of wild species and some of the deficiency ailments of domestic cattle. In his 1942 paper, he cited the Swedish investigator, T. Hedlund, as having found no potassium deficiency in the soil, though bacterial action resulted in great variation in the amount absorbed by the plants. "It may be possible therefore to account for the regularity of the cycles in numbers [ of wild species ] by oscillations in the biological and chemical *processes* in the soil regulated by or adjusted to climatic cycles" (Braestrup, 1940).

Braestrup's hypothesis is reflected in Kalela's (1941) careful study of lemming fluctuations in Finnish Lapland, the latter author's introduction mentioning climate-dependent variations in quality as well as quantity of food. Somewhat later, Kalela (1944), after considering evidence on fluctuations in different parts of the world and the hypotheses concerning vitamin and mineral deficiencies (including Braestrup's), formulated a hypothesis of his own to the effect that meteorological cycles may through influencing plant metabolism exert in turn an influence on animal life. His main new concept was one of critical periods during the growing season when adverse influences might profoundly depress plant metabolism and thus indirectly the animal life dependent thereon. One big theoretical advantage of Kalela's concept is that it might explain some of the regional differences to be



seen in cyclic manifestations. Kalela properly recognized the limitations of his hypothesis, but it has features that serious students of biological cycles should carefully think over.

Shelford (1951) also emphasized possible critical periods in his studies of physical factors in relation to animal populations of the Upper Mississippi Basin, concluding, among other things, that a wide variety of both vertebrates and invertebrates were especially sensitive to changes in short-wave radiation during the spring months. Moisture appeared to be paired with intensity of ultraviolet light as population factors for several species that he studied. He did find such a number of decided contrasts presented by some of the species that generalizations become very difficult, indeed, and there are variables in the data needing more accurate dissociation than currently looks possible, including behavioristic responses of animal life to weather conditions and sunlight. Then, too, some of the correlations of population phenomena (for example, of the bob-white quail) with density or emergency factors seem to me of greater over-all significance than the correlations of the data plotted in Shelford's ultraviolet hydrograms — though, in so writing, I do not wish to minimize the possible significance of the ultraviolet hydrograms.

Rowan (1950) considered the likelihood very strong that the unknown factor behind the "10-year cycle" in Canada "might be ultraviolet radiation (or some as yet undetected factor of analogous nature) exerting an influence on animal health in general." His grounds for reasoning include the following:

(f) That the cycle is especially developed in the arctic and subarctic, where winter shortage of ultra-violet supply has been demonstrated;

(g) That migratory birds, evading the northern winter altogether, appear to remain immune from the effects [that is, in terms of violent synchronous fluctuations];

(h) That at times of crash numerous diseases are on record, predisposition to disease suggesting itself as the cause;

(i) That large-scale decimation at the crash may be due to a deficiency condition or nutritional imbalance. . . .

Those facts, added together, would indicate at least a reasonable experimental approach to the ten-year cycle on a nutritional basis. Such an attempt is now under way.

What any one person can expect to do in arriving at the answer to the 10-year cycle I cannot say. The efforts of the rather numerous people who believed that they had done so in the past have all left plenty of major questions. No one person has in my estimation accounted for anywhere nearly the full range of phenomena that I at least think are related, and this perhaps may always be the case.

Still, it seems to be realistic to think that such a tremendous amount of work in connection with cyclic problems may profitably be done in the future that population students should be stimulated by potentialities rather than discouraged by the difficulties in sight.